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Trends in Chinook salmon spawner abundance and total run size highlight linkages between life history, geography and decline

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Abstract

Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) are foundational to social-ecological systems of the Northeast Pacific Rim and exhibit a rich diversity of life histories including in their adult migration timing, age at critical life-history transitions and marine feeding distributions. In recent decades Chinook have experienced declines across much of their native range; however, changes in productivity and abundance have rarely been evaluated in relation to life-history variation. To understand trends in Chinook salmon production, and how they are related to life history, we compiled time series data from the Fraser River to the Sacramento River on total run size (pre-fishery abundance) and escapement (post-fishery spawner abundance) and fit time series models to estimate trends across this bioregion. Our analysis revealed that most Chinook populations are declining, with negative trends in escapement (57 of 79) and total run (16 of 23) size. Trends were most acutely negative for interior spring Chinook in the Fraser, Columbia and Snake Rivers and most populations in California. Summer and fall Chinook had mixed trends, with several summer and fall upriver bright populations in the interior Columbia and Fraser exhibiting increases in abundance from the 1990s to 2019. Our research reveals widespread declines of this important species, but local complexity in trends that are mediated by population-level life history, migratory behaviours and watershed-scale restoration actions. Understanding linkages between life histories and resilience should inform rebuilding efforts for Chinook salmon and highlight the need to conserve intraspecific biodiversity.

KEYWORDS
endangered species, fisheries management, life history diversity, mixed-stock fisheries, Oncorhynchus tshawytscha, time series analysis

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1 | INTRODUCTION

Migratory animals traverse diverse and often distant habitats to exploit spatial and temporal variability in climate and ecosystem productivity and to fulfil the distinct needs of each of their life stages. Many migratory species are also keystones of ecosystems, cultures and economies, and their predictable arrival sustains rich ecological and human communities (Lundberg & Moberg, 2003; Schindler et al., 2013). Migration routes traversing multiple governmental jurisdictions create unique challenges for conservation and management across of these species (López-Hoffman et al., 2017; Runge et al., 2014; Vierros et al., 2020), when natural or anthropogenic impacts on habitats and species survival rates may be felt hundreds or thousands of kilometres away (e.g. Springer et al., 2018). Climate change is also creating unique challenges among migratory species for whom timing can be a matter of life and death, and well documented climate-driven changes in the phenology of key ecological events are already impacting survival and reproductive success for some species (Dingle, 2014; Rand et al., 2006; Robinson et al., 2009; von Biela et al., 2022).

Highly mobile species often exhibit diverse life histories, phenology and reproductive strategies that have evolved in response to the range of physical and biological conditions they confront during different stages of their lives. All told, this diversity can stabilize population and ecosystem dynamics, providing more reliable ecological, cultural and economic benefits in social-ecological systems (Moore et al., 2014; Oken et al., 2021; Schindler et al., 2010). However, life histories may also influence the exposure, and thus vulnerability, of specific populations to different stressors. Effective conservation of migratory species is, therefore, contingent on understanding and protecting their diversity and on cooperation across jurisdictional boundaries to protect habitats and vulnerable populations.

Pacific salmon (*Oncorhynchus* spp.) are among the most widely distributed, abundant and diverse migratory animals on the planet and play a foundational role in ecosystems and cultures across their native range (Earth Economics, 2021). Their long-distance, anadromous migrations link the distant and productive marine habitats of the North Pacific to watersheds draining the Asian and North American continents. Salmon exhibit tremendous intraspecific life-history diversity, including diversity in age and size at key life-history transitions (e.g. seaward migration, maturity), and spatiotemporal variation in their distribution at sea, migration timing and behaviour, spawn timing and relative reproductive investment (Groot & Margolis, 1991). Driven be the selective pressures of local adaptation and the interplay between homing and straying, genetic and life history diversity is shaped by the successive demands of freshwater spawning migrations, juvenile rearing and multi-year marine feeding migrations (Quinn, 2005). This diversity promotes resilience within populations and the social-ecological systems they support, since it encompasses evolutionary adaptations and portfolio effects that stabilize population responses to climate and habitat variability, lengthen the annual duration of harvest opportunities for salmon predators (including humans), and spread risks and opportunities across multiple comigrating cohorts of salmon (Moore et al., 2014; Nesbitt & Moore, 2016; Schindler et al., 2010). However, different aspects of diversity also likely influence the vulnerability or exposure of populations to the many stressors they encounter across their range.

Among Pacific salmon, Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) are highly diverse and are perhaps the most prized species for fishers and salmon predators alike. Chinook have exceptionally high food value due to their large size and fatty flesh. They are the preferred food source for marine apex predators like Southern Resident Killer Whales (SRKW) (*Orcinus orca*, Delphinidae) whose health and demographic productivity is linked to the availability of Chinook as prey (Ford et al., 2009, 2016; Stewart et al., 2021; Williams et al., 2011). Some the most important and productive fishing areas for West Coast Indigenous communities are those with abundant Chinook runs (Swezey & Heizer, 1977; Fisher, 2004; Nesbitt & Moore, 2016). Chinook also support major US and Canadian commercial and recreational fisheries with an annual economic contribution to both countries measured in the hundreds of millions of dollars annually (The Research Group, 2009; Gislason, 2017). However, Chinook have recently exhibited declining size, productivity and abundance throughout much of their North American range (Dorner et al., 2018; Ohlberger et al., 2016; Welch et al., 2021), and Chinook fisheries have also declined dramatically in response to these changes ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020; Walters et al., 2019).

The availability of Chinook salmon for both predators and human fisheries is driven in part by their adult migration timing (also called run timing), which is highly diverse across their extensive North American range from Alaska and the Yukon to California (Healey, 1991; Parken et al., 2008; Quinn et al., 2016). In particular, the species exhibits exceptionally high run timing diversity in populations from the Salish Sea south to California's Central

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Valley (Figure 1), with Chinook freshwater entry timing ranging from late-winter entry among reproductively immature fish to early-winter entry among reproductively mature fish. In contrast with more northerly watersheds, in this part of their range multiple distinct Chinook salmon runs are observed, even within the same watershed and are commonly named based on their season of river entry (e.g. spring, summer, fall, late fall, winter). Run timing groups are also classified as 'early' and 'late' migrators based on their timing of river entry in relation to maturation and spawn timing. For example, spring Chinook are considered early migrators because they enter freshwater in a relatively immature state many months before fall spawning and undergo final maturation in rivers. Fall and late-fall Chinook salmon are considered late migrators because they enter rivers just prior to spawning and after most of their reproductive maturation process has already occurred in the ocean (Healey, 1991; Quinn et al., 2016). Summer Chinook salmon are intermediate to spring and fall runs in their run timing and state of maturity at river entry. Winter Chinook salmon migrate in the winter and spawn in late spring and summer, a unique pattern of early entry and spawn timing found only in the Sacramento River system in California (Healey, 1991).

Importantly, Chinook salmon populations also exhibit differences in their juvenile life histories, migration routes and distributions at sea, which differentially expose them to environmental variation affecting freshwater and marine survival, as well as exploitation in mixed-stock commercial fisheries. Chinook populations are generally predominated by one of two primary types of juvenile life histories: (a) 'stream-type', characterized by a year or more of stream rearing prior to outmigration; and (b) 'ocean-type', characterized by migration to sea during their first year of life (Taylor, 1990; Healey, 1991; Waples et al., 2004). These juvenile life histories result in differential exposure to freshwater stressors, such as low summer flows and warm temperatures (Jones et al., 2020; Warkentin et al., 2022). Further, differences in the timing and body size at outmigration and in their oceanic distributions can have carryover effects on marine survival. For example, interior stream-type Chinook from the Snake and Columbia basins undertake lengthy northward migrations in their first year of marine life before moving offshore and are rarely intercepted in coastal fisheries (Weitkamp, 2010). In contrast, many ocean-type fall Chinook salmon from populations in the Salish Sea are more locally distributed, with most fishery interceptions occurring in the Salish Sea and along the West Coast of Vancouver Island ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020; Freshwater et al., 2021; Riddell et al., 2013; Weitkamp, 2010). These population and life-history-specific distributional differences are generally consistent across years, which may expose populations to different physical and biological conditions during their marine lives (Shelton et al., 2019). Consequently, populations of Chinook in the Northeast Pacific exhibit both synchronous and unique responses to climate variability, food availability and fisheries exploitation (Braun et al., 2016; Sharma et al., 2012; Shelton et al., 2021; Tucker et al., 2012).

Despite the potential for life-history variation to influence the exposure of different populations to environmental stressors and fisheries, Chinook salmon population trends have not been evaluated to understand how life-history traits influence abundance trends across different regions. We, therefore, sought to quantify trends for Chinook salmon populations across the southern half of their Northeast Pacific range, which is home to rich intraspecific biodiversity in Chinook salmon (Figure 1) and to compare trends in stocks exhibiting different adult and juvenile life histories. Among the populations we assessed are many of North America's largest and most important Chinook salmon stocks ([PFMC] Pacific Fishery Management Council, 2021; [PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020), which have supported productive fisheries and ecosystems for thousands of years (Yoshiyama, 1999; Butler et al., 2010; Carothers et al., 2021; Atlas et al., 2021).

We quantified trends in escapement and total run size (escapement + harvest) for individual populations of natural-origin Chinook salmon in two separate analyses to (1) describe regional trends in spawner escapement for Chinook salmon populations, (2) quantify trends in total run sizes for a subset of populations where both escapement and harvest information was available and (3) qualitatively evaluate how these changes vary among regions and life histories, including variation in run timing, juvenile age at outmigration and oceanic migration routes. Spawner escapement data are more broadly available than total run size information and escapement is a direct measure of fish on the spawning grounds, providing a valuable metric for the services Chinook provide in freshwater systems, as prey for terrestrial and freshwater predators and as long-distance transporters of marine derived nutrients and energy. Total run size data rely on harvest rate estimates, which are often uncertain and unavailable for many stocks but nonetheless provide insight into the total production from individual Chinook populations, the influence of changing harvest regimes on population trends and the overall contribution of natural-origin Chinook salmon to North American fisheries. Our analyses addressed the two questions: (1) how have changes in the escapement and total run sizes of Chinook salmon manifested across different life histories and regions and (2) have certain Chinook life-history groups been more resilient to recent natural and anthropogenic changes than others? Taken together these findings can clarify conservation risks and population trajectories for Chinook salmon populations around the southern half of their eastern-Pacific range, informing fishery management for both productive and weak stocks, and guiding restoration activities that can bolster long-term prospects for protecting the rich intraspecific biodiversity exhibited by this iconic species.

2 | METHODS

We assembled and analysed spawner escapement data as well as information on total run size (pre-fishery abundance: escapement + harvest) to better understand key features in West Coast

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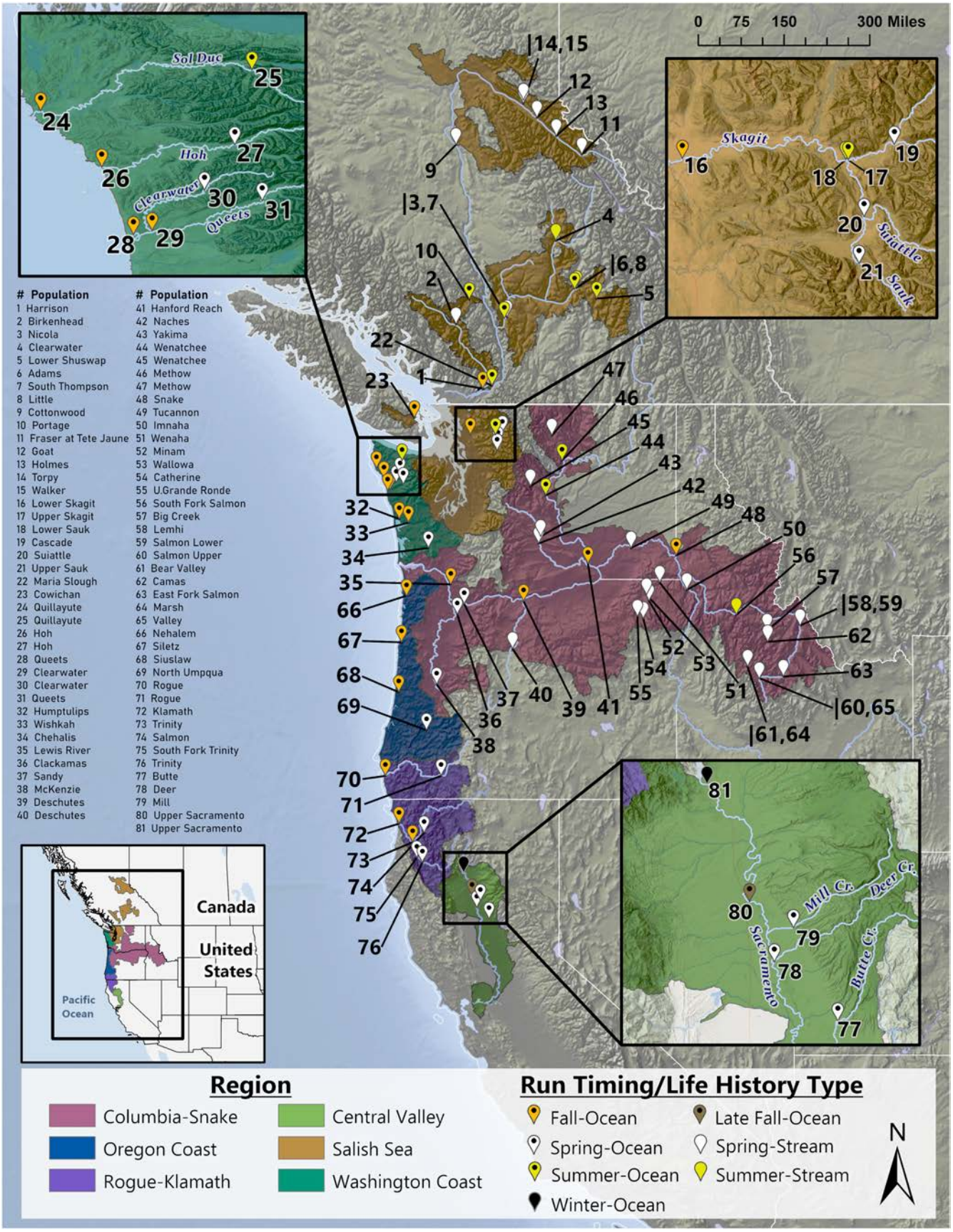


FIGURE 1 A map depicting the regional groupings, specific population locations, run timing, and dominant juvenile life history for each of the 81 Chinook populations included in our analysis. Among these populations 79 were included in analyses of escapement trends, and two populations (Hanford and Snake Fall) were only included in the total run size analysis due to their shorter time series.

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Chinook salmon population trends. We limited our analyses to populations and years where hatchery- and natural-origin fish could be reliably separated, and further compiled information on the run timing, juvenile life history and marine distributions for these populations.

Chinook population trends were analysed using a time series modelling approach, implemented in the R-package MARSS (Holmes et al., 2012). Using these time series models we evaluated temporal trends in both individual populations and populations grouped by conservation units (i.e. ESUs or CUs) and then compared populations trajectories across three key axes of life-history variation: adult run timing (e.g. spring v. fall), age at marine entry and migratory distribution in the marine phase.

2.1 | Data compilation

We compiled data on spawner escapement and harvest of Chinook populations from multiple sources. Fraser River escapement data came from Fisheries and Oceans Canada (Chuck Parken – *unpublished* data). Escapement and harvest for some populations in British Columbia, Washington and Oregon came from the Pacific Salmon Commission (PSC) escapement and harvest analysis reports ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020). Escapement data for Washington watersheds was downloaded from the Washington Department of Fish and Wildlife (WDFW) Salmonid Conservation and Reporting Engine (SCoRE) website ([WDFW]Washington Department of Fish and Wildlife, 2021) and for Columbia Basin populations from the StreamNet coordinated assessment website (StreamNet, 2021). Data on Oregon Chinook escapements came from the Pacific Fishery Management Council annual reports on salmon fisheries and escapement ([PFMC] Pacific Fishery Management Council, 2021) and from the Oregon Department of Fish and Wildlife dam passage website ([ODFW] Oregon Department of Fish and Wildlife, 2021). Additional data on Columbia Basin stocks in Oregon came from the coordinated assessments data portal (StreamNet, 2021), and escapement data for Deschutes spring and fall Chinook were provided by the US Fish and Wildlife Service (David Hand – *unpublished data*). Abundance information for California populations was drawn from the Sacramento and Klamath escapement tables accessed on the California Department of Fish Wildlife website ([CDFW] California Department of Fish and Wildlife, 2021a, 2021b, 2021c) and from Pacific Fishery Management Council (PFMC) online reports ([PFMC] Pacific Fishery Management Council, 2021).

In total, we compiled escapement time series for 231 populations of Chinook salmon and refined this dataset to a final set of escapement time series comprising 79 populations. Populations were selected based on (1) the ability to differentiate hatchery and natural-origin spawners or the ability to make strong inference that hatchery influence was low, (2) time series continuity with no or few (<4) missing years of data and (3) data quality based on the professional judgement of the authorship group. The population time series that were included in our analysis ranged in length from 27 to 89 years. Generally, estimates of escapement are reported as a single point estimate of total spawner abundance with a breakout of hatchery and natural-origin spawner totals or an estimate of percent hatchery contribution. In total our data set encompassed 4007 river-specific annual observations of spawner abundance, and these estimates were derived using a wide variety of methods. Most often escapement estimates were derived from visual surveys of spawning salmon or redds (nests), but in some locations and years mark-recapture, dam counts, weir census counts, carcass surveys and expansions from in-river test fisheries were used. In several locations escapement estimates from visual counts have been calibrated with mark-recapture or dam counts and we analysed these calibrated datasets (e.g. [PSC] Pacific Salmon Commission Sentinel Stocks Committee, 2018). Likewise, in locations where enumeration methods have shifted over time, we analysed calibrated datasets. Accordingly, we do not expect methodological differences in monitoring design to create any systematic bias in the overall trends observed in Chinook abundance (e.g. Parken et al., 2003). Where counts of jacks and large adult Chinook are kept separately, we excluded jack counts and analysed data on large adult Chinook abundance, since jacks are predominantly male and, therefore, contribute minimally to the regulation of population growth rates. In addition, jacks are often not recorded in overflights and other visual surveys, so counts of large adult Chinook were most immediately comparable between populations (Table S1). All data and code used in our analyses are freely available online and stored in a public GitHub repository (https://github.com/willatlas/ChinookEscapement-RunSize).

We developed a model to characterize trends in natural-origin Chinook salmon spawner abundance across 79 of these populations. Hatchery spawners were excluded from our analysis or presumed to make negligible demographic contributions where the abundance of hatchery fish is not regularly estimated but a preponderance of evidence suggests they are uncommon. Given the variety of methods and associated assumptions used to derive estimates of escapement in our study area (e.g. spawner or redd counts expanded to abundance, hatchery proportions estimated from carcass recoveries), annual estimates of natural-origin Chinook spawner abundance are prone to error stemming from uncertainty in the true number of fish. We, therefore, treated each estimate of spawner escapement as an imperfect observation of a true underlying state—in this case natural-origin spawner abundance—and modelled both natural variability in abundance (process error) and observation errors using a state-space approach (see *Data Analysis* below).

Estimates of harvest were also compiled for a subset of hatchery and natural populations where Chinook are tagged with coded wire tags (CWTs), and where these tag recovery data are routinely used by the PSC and PFMC to estimate exploitation rates (ERs). These estimates of annual ERs are reported by both the PSC Chinook Technical Committee (CTC) and the PFMC ([PFMC] Pacific Fishery Management Council, 2021; [PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020). Historical harvest rates for Sacramento winter Chinook prior to 2000 were reconstructed by O'Farrell and Satterthwaite (2015), and fall Chinook harvest rates

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were estimated as described in O'Farrell et al. (2013). Harvest estimates derived from a limited number of CWT recoveries are inherently uncertain and have become more uncertain over time owing to reduced harvest rates in marine fisheries (Jensen et al., 2022; PSC CTC, 2020; PSC CWT Work Group, 2008); harvest data are also reported as point estimates and do not reflect uncertainty in ERs. While these estimates reliably capture long-term changes in harvest management, annual estimates of harvest should be interpreted with caution. We, therefore, adopted a similar state-space modelling approach for estimating harvest trends over time, partitioning variability in total run size estimates into observation error stemming from uncertainty in harvest estimates and the level of process variability underlying the true pre-fishery run size. In total, harvest estimates were available for 23 populations, including two populations (Hanford and Snake Fall) where data have been collected since the early-1990s. Accordingly, we analysed total run size trends between 1990 and 2019.

In some instances, the recent adoption of mark-selective fisheries necessitated assumptions be made about the relationship between harvest rates observed in adipose fin-clipped salmon tagged with a CWT and unmarked natural-origin Chinook. Estimated harvest rates are reported by the PSC for each fishery and gear type that encounters Chinook salmon from Southeast Alaska to the South of Falcon region on the Oregon Coast; in most of these areas Chinook salmon fisheries remain non-selective. For fishing areas where mark-selective fishing has been implemented we assumed that harvest impacts were zero for unmarked wild fish; this assumption is likely a modest underestimate of fishery impacts since unmarked fish that are released in the fishery experience post-release mortality (Conrad & McHugh, 2008; Warkentin et al., 2022). In addition, at the time of our analysis some harvest estimates had not been reconstructed through 2019; in these few cases, we took the stock-specific average harvest rate in the previous 10 years and applied it to the 2019 cohort with missing harvest data. For a full summary of exploitation rate estimates and information on the sources see the (Table S2).

2.2 | Escapement trend analysis

For the first set of time series analyses Chinook salmon populations were divided into six groups corresponding to their geographic location: (1) Salish Sea, (2) Washington Coast, (3) Columbia River, (4) Oregon Coast, (5) Rogue and Klamath rivers and (6) Sacramento River (Figure 1). Columbia River stocks were further divided into three trend groups corresponding to the length of their escapement time series: (i) Snake River spring and summer runs where populations have been consistently monitored since at least 1957, (ii) Columbia River stocks with data beginning around 1967, (iii) Columbia River stocks with data beginning after 1982. Each of these analysis groups for the Columbia and Snake watersheds included some populations from analyses, which started earlier, for example in our analysis, which spanned from 1967 to 2019, 11 populations from the Snake River were analysed alongside four populations from the Columbia (Lewis, Wenatchee spring, Methow spring and Methow summer). Trends in escapement were evaluated for an additional 8 populations in the Columbia River with data starting in 1982. Information on the populations and their respective time periods included in each group examined in our trend analysis is presented in Table 1.

2.3 | Total run size analysis

In addition to evaluating trends in spawner escapement, we examined trends in total run size (escapement + total harvest) for populations where data on harvest rates were available, or where estimates of harvest from a nearby population are believed to reflect harvest impacts on the stock of interest ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020) (Table 2). Harvest data were available for a much smaller subset of populations ($n = 17$) and were applied to an additional six geographically proximate stocks. These harvest monitoring programs generally began in the mid-1980s when widespread CWT tagging of Chinook salmon and sampling of fisheries and escapements were initiated. Accordingly, our analysis of run size covers a smaller geographic and temporal (1990–2019) scope but provides greater clarity on the magnitude of variability in recruitment, harvest and population status.

These 23 populations with total run size data were divided into four separate regional analysis groups to enable time series model convergence and limit the number of parameters being estimated in each model: (1) the Salish Sea group included seven populations from British Columbia and Washington State; (2) the Columbia River analysis group, which included eight populations; (3) the five populations on the Washington and Oregon Coast; and (4) the three Klamath and Sacramento stocks (Table 2). In addition, harvest data (CWT tagging) were not available for Skagit summer Chinook until 1998, so we fit a separate time series model to the estimated harvest rates for Washington State stocks beginning in 1990, including correlations between the Skagit summer stock and other regional populations falling under the same management to produce a derived estimate of harvest rate for this specific population (details in Appendix S1; Table S3).

In many locations harvest rates have declined alongside total run sizes, meaning that spawner escapement in many cases does not capture the full magnitude of the population decline. Accordingly, failing to account for the effects of harvest on the observed escapement over time will often underestimate the level of conservation risk. Total run size is more relevant to the provisioning of some of the ecosystem services supported by Chinook salmon, including what opportunities exist for the fishers and marine predators who depend on Chinook salmon for their livelihoods, culture or sustenance.

2.4 | Time series modelling approach

To quantify changes in natural-origin Chinook salmon spawner escapement and total run size we fit 12 regionally grouped state-space

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TABLE 1 Estimated spawner escapement states ($x_{i,t}$)and trends for 79 Chinook stocks from Northern California to the Salish Sea. Trend (u_i) and percent change per year are estimated for the full time series (Start year to 2019). Mean spawner escapements from the start year to 2019 are also reported, as well as the relative magnitude of the 15-year and 5-year average escapements.

Group	Start year	Population	Pop no.	Run timing	Mean spawn	5-year % of mean	15-year % of mean	U trend	Median % change per year
Columbia	1967	Lewis River	35	fall	9753	104.8%	96.9%	0.003	0.25%
		Methow	47	spring	839	26.7%	41.5%	−0.052	−5.08%
		Methow	46	summer	1266	104.0%	107.4%	−0.018	−1.75%
		Wenatchee	45	spring	1423	32.1%	39.7%	−0.055	−5.39%
Columbia	1982	Clackamas	36	spring	1713	205.5%	137.4%	0.024	2.44%
		Deschutes	39	fall	10,092	112.4%	121.0%	0.035	3.55%
		Deschutes	40	spring	1012	39.0%	61.5%	−0.055	−5.38%
		McKenzie	38	spring	1918	99.5%	91.3%	0.035	3.57%
		Naches	42	spring	1096	65.6%	86.4%	−0.014	−1.40%
		Sandy	37	spring	1306	244.0%	165.7%	0.050	5.15%
		Wenatchee	44	summer	6999	69.3%	77.6%	−0.004	−0.35%
		Yakima	43	spring	2341	69.3%	98.3%	−0.032	−3.16%
Oregon coast	1975	North Umpqua	69	spring	5077	82.7%	95.1%	−0.009	−0.88%
		Nehalem	66	fall	8773	101.4%	90.2%	0.003	0.30%
		Siletz	67	fall	5109	117.3%	92.2%	0.016	1.66%
		Siuslaw	68	fall	19,877	74.9%	92.5%	0.001	0.14%
Rogue & Klamath	1978	Klamath	72	fall	24,006	71.5%	104.9%	−0.024	−2.33%
		Rogue	70	fall	63,293	63.3%	75.8%	−0.039	−3.82%
		Rogue	71	spring	12,313	67.4%	64.3%	−0.041	−4.03%
		Salmon	74	spring	511	47.0%	131.7%	−0.014	−1.43%
		South Fork Trinity	75	spring	199	16.6%	79.9%	−0.070	−6.75%
		Trinity	73	fall	19,940	41.2%	79.5%	−0.032	−3.12%
		Trinity	76	spring	9478	28.9%	62.4%	−0.036	−3.57%
Sacramento	1960	Butte	77	spring	2438	95.0%	165.2%	0.000	0.03%
		Deer	78	spring	1259	19.0%	48.1%	−0.054	−5.25%
		Mill	79	spring	735	29.1%	63.1%	−0.037	−3.67%
		Upper Sacramento	80	late fall	17,755	15.8%	23.1%	−0.063	−6.08%
		Upper Sacramento	81	winter	34,393	7.0%	10.5%	−0.079	−7.61%
Salish	1979	Lower Adams	6	summer	3165	197.1%	174.1%	0.056	5.78%
		Birkenhead	2	spring	440	67.3%	130.9%	−0.013	−1.24%
		Cascade	19	spring	264	78.4%	112.1%	−0.016	−1.58%
		Clearwater	4	summer	3265	37.3%	69.0%	−0.021	−2.07%
		Cottonwood	9	spring	1104	29.5%	42.6%	−0.023	−2.30%
		Cowichan	23	fall	4961	205.9%	93.8%	0.016	1.63%
		Fraser at Tete Jaune	11	spring	2892	44.4%	57.3%	−0.054	−5.22%
		Goat	12	spring	159	36.5%	74.8%	−0.063	−6.09%
		Harrison	1	fall	79,834	56.0%	75.0%	−0.024	−2.34%
		Holmes	13	spring	1467	34.3%	50.4%	−0.063	−6.06%
		Little	8	summer	5448	330.4%	234.9%	0.100	10.46%
		Lower Sauk	16	summer	722	83.9%	75.3%	−0.046	−4.53%
		Lower Shuswap	5	summer	20,527	100.2%	109.7%	0.007	0.72%
		Lower Skagit	16	fall	2176	100.5%	95.0%	−0.035	−3.45%

(Continues)

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TABLE 1 (Continued)

Group	Start year	Population	Pop no.	Run timing	Mean spawn	5-year % of mean	15-year % of mean	U trend	Median % change per year
		Maria Slough	22	summer	293	90.4%	164.8%	0.039	3.93%
		Nicola	3	spring	4087	39.8%	57.6%	−0.009	−0.94%
		Portage	10	summer	107	68.2%	83.2%	0.019	1.90%
		South Thompson	7	summer	29,826	203.7%	196.0%	0.067	6.91%
		Suiattle	20	spring	455	144.0%	98.0%	0.013	1.30%
		Torpy	14	spring	1424	39.0%	64.9%	−0.099	−9.42%
		Upper Sauk	21	spring	666	245.8%	152.6%	0.046	4.72%
		Upper Skagit	17	summer	8452	105.3%	106.8%	−0.024	−2.39%
		Walker	15	spring	231	39.8%	61.5%	−0.070	−6.71%
Snake	1957	Bear Valley	61	spring	681	44.2%	70.8%	−0.051	−4.94%
		Big Creek	57	spring	262	45.4%	71.4%	−0.060	−5.85%
		Camas	62	spring	142	38.0%	33.8%	−0.048	−4.65%
		Catherine	54	spring	430	26.7%	43.7%	−0.078	−7.49%
		East Fork Salmon	63	spring	750	29.7%	47.2%	−0.079	−7.60%
		Imnaha	50	spring	1039	32.9%	43.4%	−0.059	−5.70%
		Lemhi	58	spring	543	46.6%	37.9%	−0.037	−3.58%
		Marsh	64	spring	460	58.0%	72.2%	−0.043	−4.21%
		Minam	52	spring	501	72.9%	103.4%	−0.049	−4.82%
		Salmon Lower	59	spring	260	20.8%	39.2%	−0.094	−9.01%
		Salmon Upper	60	spring	775	28.8%	50.3%	−0.056	−5.41%
		SF Salmon	56	summer	1007	20.4%	57.5%	−0.072	−6.96%
		Tucannon	49	spring	421	15.4%	54.4%	−0.091	−8.66%
		U.Grande Ronde	55	spring	210	35.2%	37.1%	−0.037	−3.63%
		Valley	65	spring	261	34.9%	48.7%	−0.062	−5.97%
		Wallowa	53	spring	528	72.5%	114.2%	−0.050	−4.83%
		Wenaha	51	spring	588	60.7%	71.4%	−0.047	−4.55%
WA coast	1980	Chehalis	34	spring	1708	69.4%	90.5%	0.022	2.19%
		Clearwater	29	fall	1248	76.8%	85.3%	−0.004	−0.36%
		Clearwater	30	spring	84	90.5%	65.5%	−0.057	−5.56%
		Hoh	26	fall	2591	71.6%	74.8%	−0.007	−0.75%
		Hoh	27	spring	1356	75.5%	67.3%	−0.005	−0.51%
		Humptulips	32	fall	3172	85.9%	104.1%	0.016	1.66%
		Queets	28	fall	4178	72.4%	75.7%	−0.006	−0.60%
		Queets	31	spring	677	84.2%	66.3%	−0.025	−2.45%
		Quillayute	24	fall	5801	71.8%	69.5%	−0.006	−0.57%
		Quillayute	25	summer	974	100.7%	81.5%	0.008	0.78%
		Wishkah	33	fall	650	53.2%	77.1%	0.001	0.13%

time series models to the natural log of Chinook spawner abundance. These state-space time series models allowed us to partition annual variability in salmon escapement into observation and process errors. Observation errors are random and accounting for uncertainty stemming from imperfect observations, while process error is systematic and tracks the underlying variability in the process of interest, in our case changes in Chinook spawner escapement and total run size.

This time series model took the form:

$$x_{i,t} = x_{i,t-1} + u_i + w_{i,t}; w_{i,t} \sim MVN(0, \mathbf{Q}), \quad (1)$$

$$y_{i,t} = x_{i,t} + v_{i,t}; v_{i,t} \sim N(0, r_i) \quad (2)$$

where Equation 1 describes the unobserved state process x_t, in our case the true spawner escapement or total run size for a population

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TABLE 2 Estimated total run size states ($x_{i,t}$) for 23 Chinook populations with both escapement and harvest data. The source of coded wire tag harvest data used to infer harvest rates and total run size for each population are also presented, as well as the 1990–2009 and the 10-year average exploitation rates (ER) for each indicator stock. In cases where another population's ER has been applied to a population, mean ER values are left blank. Mean run sizes are for the years 1990–2019 and the relative magnitude of 5-year and 15-year run sizes are compared each population's 1990–2019 average. Median estimates for percent yearly change are reported in the rightmost column.

Group	Pop no.	Population	CWT indicator	Run timing	Mean total run size	5-year % of mean	15-yr % of mean	1990–2009 ER mean	10-yr ER mean	Median yearly % change
Salish	1	Harrison	Harrison	fa	147,655	46.4%	59.0%	43.7%	27.2%	−6.11%
	3	Nicola	Nicola	sp	4651	41.1%	80.1%	29.9%	17.3%	−5.32%
	5	Lower Shuswap	Lower Shuswap	su	46,008	55.6%	79.2%	53.8%	39.6%	−3.45%
	7	South Thompson	Lower Shuswap	su	88,143	128.9%	139.9%	–	–	3.96%
	16	Skagit su/fa	Skagit summer	su/fa	19,765	127.0%	110.7%	40.6%	45.0%	−1.86%
	19	Skagit spring	Skagit spring	sp	2356	142.9%	101.1%	43.9%	35.5%	−2.01%
	23	Cowichan	Cowichan	fa	16,678	146.1%	68.4%	66.5%	58.4%	−1.57%
WA/OR coast	24	Quillayute	Queets fall	fa	11,914	89.3%	90.3%	–	–	−0.92%
	26	Hoh	Queets fall	fa	5407	87.4%	92.8%	–	–	−1.41%
	28	Queets	Queets fall	fa	8316	86.4%	94.0%	51.6%	60.1%	−2.71%
	66	Nehalem	Salmon River	fa	19,942	100.8%	94.9%	59.8%	53.7%	1.00%
	67	Siletz	Salmon River	fa	13,975	77.7%	81.9%	–	–	−1.42%
Columbia & Snake	35	Lewis River	Lewis	fa	16,299	108.2%	111.9%	38.2%	45.0%	−0.72%
	36	Clackamas	Willamette spring	sp	2609	166.9%	114.1%	41.2%	23.0%	−0.57%
	38	McKenzie	Willamette spring	sp	3079	80.3%	73.4%	–	–	−4.07%
	39	Deschutes	Columbia URB	fa	21,786	96.0%	112.8%	52.5%	49.4%	1.92%
	41	Hanford Reach	Hanford Wild	fa	163,256	137.3%	133.5%	56.7%	61.7%	0.88%
	44	Wenatchee	Columbia su	su	15,297	84.0%	90.7%	49.3%	60.4%	−3.59%
	46	Methow	Columbia su	su	3160	118.7%	117.1%	–	–	1.75%
	48	Snake	Columbia URB	fa	10,448	191.4%	166.8%	–	–	8.74%
California	72	Klamath	Klamath fall	fa	80,019	55.1%	97.2%	39.4%	40.7%	−1.62%
	80	Upper Sacramento	O'Farrell & Satterthwaite, 2015	late-fa	21,783	18.7%	40.4%	60.1%	52.8%	−8.97%
	81	Upper Sacramento	PFMC tables	win	3652	82.5%	107.0%	25.6%	16.0%	6.82%

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(i) at time (t), expressed in log space. This state process takes an autoregressive form, relating the state $x_{i,t}$ to the estimated state in the previous time step $x_{i,t-1}$. Each $x_{i,t}$ is a realization of the state process at time t with a population-specific slope (trend) parameter u_i controlling the overall trend in the population-specific state, where each population had its own hidden state trajectory. $y_{i,t}$ is the observed quantity (the natural log of escapement or total run) for each population in each timestep. Process errors $w_{i,t}$, the true underlying variability in Chinook escapement, are drawn from a multivariate normal distribution with a mean of zero and a covariance matrix of $\boldsymbol{Q}$ (an m x m matrix where m is the number population of trends), with the diagonals representing the process error variance, and the off diagonals the covariance among process errors. We estimated unique process errors for each population, and these population-specific process errors were related to one another via unique covariance terms estimated between each population. Observation errors ($v_{i,t}$) were also estimated as a multivariate normal distribution with a mean of zero and a population-specific observation error variance r_i such that each population had its own independent observation error.

Previous research has demonstrated that salmon population trends are correlated among regionally proximate stocks (e.g. Mueter et al., 2005). For each regional grouping preliminary data analysis AIC scores (i.e. lower AIC values) revealed greater support for models with correlated process errors. We, therefore, modelled pairwise correlations among population-specific process errors in all of our regional analyses. Parameter identifiability for process and observation errors is challenging when simultaneously estimating variance–covariance matrixes for both sources of error. We, therefore, restricted our models to include only process error covariation. Observation errors were estimated independently for each population and off diagonals of $\boldsymbol{R}$ related to the covariance between observer errors were set to zero. For four populations where spawner abundance was derived from dam counts (North Umpqua, Clackamas, Yakima and Naches) we set observation error to zero.

Specific details of model parameterization and fitting, as well as parameter estimates associated with each regional escapement trend models and total run size model are reported in the (Appendix S2; Tables S4–S15).

2.5 | Interpreting trends

To quantify changes in natural-origin Chinook salmon escapement we interpreted the state $x_{i,t}$ values for each population over time and the u_i parameter as an indication of the overall trend across the time series. Generally, u_i values had high uncertainty owing to the sensitivity of the trend parameter to the initial population size (x_0) and the most recent values. We therefore interpreted the median value of the u_i parameter and converted these median values into annual growth rate (AGR) expressed as a percent change per year over the course of the time series we analysed, where $AGR = 100(e^{u_i} - 1)$.

In addition to quantifying the overall trend, we back-transformed the log(escapement) states to estimate mean escapement and total run size states ($\bar{x}_i$) for the entirety of each time series and compared them to estimated escapement or total run size state in the last 5- and 15-years (2015–2019 and 2005–2019, respectively). We then calculated the percent change from the long-term mean at these time horizons (5 and 15 years) and the number of recent years when escapement or total run size state fell below the long-term mean value. These trend values were summarized for individual stocks, regional groupings and across life-history groups to understand recent population trajectories across geographic and biologically important constellations of Chinook salmon production and biodiversity.

3 | RESULTS

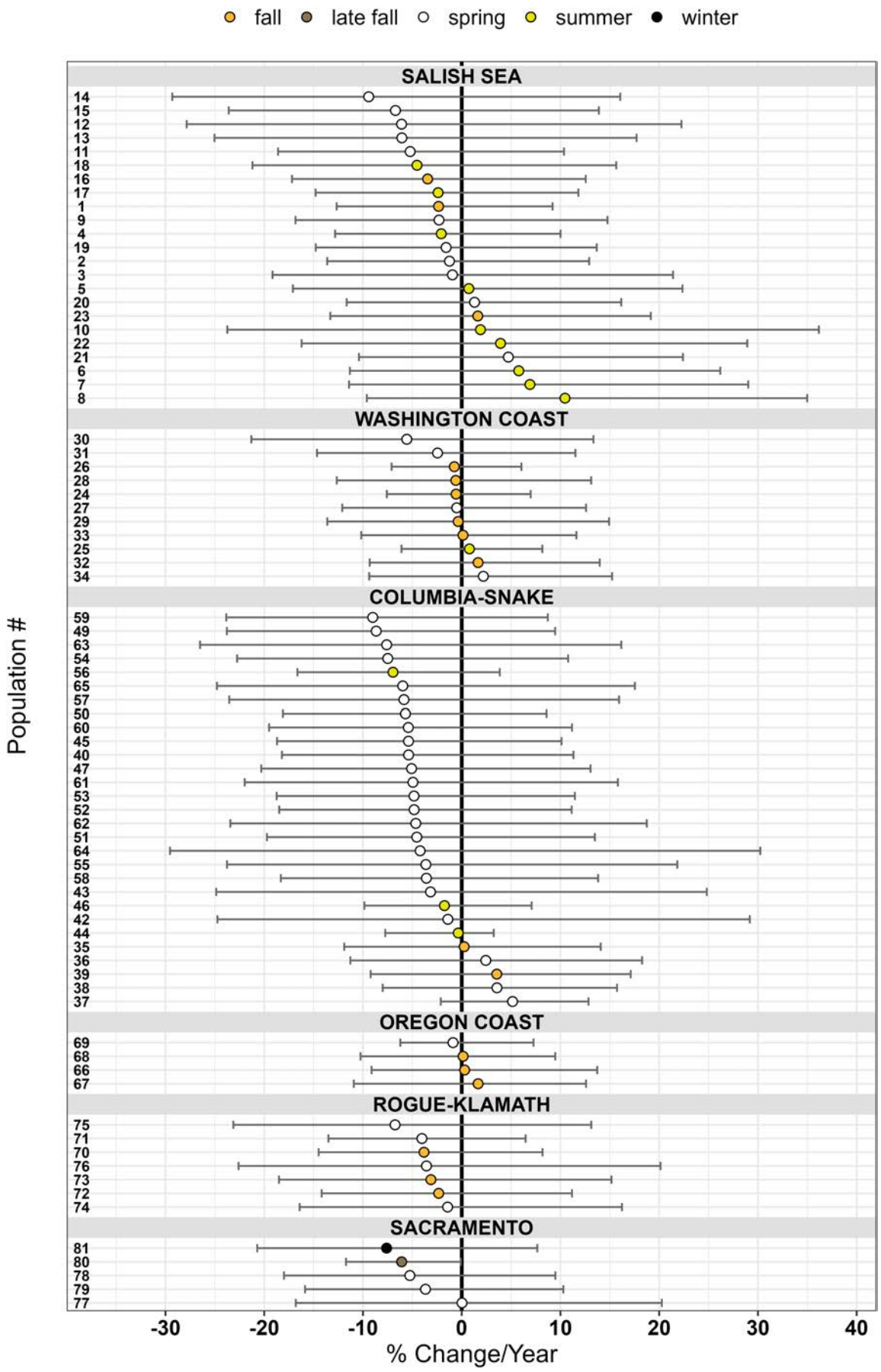
3.1 | Trends in spawner escapement

Our analysis included 47 spring-run, 20 fall-run, 13 summer-run Chinook populations, as well as one population – in the Upper Sacramento – with winter-run timing. The largest number of populations with suitable time series for analysis came from the Columbia and Snake River watersheds, with 13 populations from the Columbia and 17 from the Snake. Salish Sea populations from both Washington State and British Columbia comprised another large group of stocks with suitable time series for analysis ($n = 23$). In Canadian areas of the Salish Sea, all populations that were in the Fraser River watershed, except for the Cowichan River on southern Vancouver Island. Unfortunately, other populations in southern BC were excluded from our analysis because of a lack of information on the contribution of hatchery-origin spawners. Likewise, limited time series of data on hatchery contributions led to the exclusion of other Puget Sound Chinook stocks in Washington State. Data for the Klamath system was readily available, and we included five populations in the basin in our analysis. The availability of suitable data on hatchery contributions was notably limited for the Sacramento and San Joaquin watersheds, where a majority of populations were excluded from the analysis due to a lack of information on the contribution of hatchery fish, including among almost all major fall Chinook populations. Data availability or quality also limited the inclusion of any California coastal populations south of the Klamath River (Figure 1).

A substantial majority of Chinook populations we analysed showed evidence of declining trends in escapement (57 of 79), with many populations declining to their lowest levels on record in recent years. Median estimates for long-term escapement trends ranged

FIGURE 2 Spawner escapement trends estimated as the percent change per year for 79 Chinook stocks arranged from north to south and denoted by their population number. Points represent median trend estimates, and whiskers are 95% confidence bounds. Time series length varied by regional grouping and is reported in Table 1.

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from +10.4% per year for summer Chinook returning to the Little River in the Thompson River to −9.4% per year for Torpy River spring Chinook in the Upper Fraser; however, these median estimates were bounded by significant uncertainty owing to the high level of natural variation in salmon abundance and the influence of the starting and ending values on the estimated trends (Figure 2).

Across the 79 populations we evaluated, escapement trends varied in relation to both geographic location and life history. In general, early-migrating spring Chinook populations, especially those with obligate stream-type juvenile life histories, experienced greater declines in spawner abundance than later-migrating fall Chinook and populations with ocean-type juveniles within the same regions. A total of 85% (40/47) of the spring Chinook stocks we evaluated had negative coefficient estimates for u_i. Even among populations that experienced substantial declines in abundance 95% confidence intervals for u_i all overlapped zero (Table 1; Figure 2). These declines among spring-run populations were evident in both recent cohorts (5-year spawner abundance was −37% below long-term average levels) and in the most recent three generations (15-year average spawner abundance −24% below the long-term average) (Table 1). Five- and 15-year changes in average spawner abundance were particularly negative for interior spring Chinook in the Fraser (5-year: −56%; 15-year: −28%), Columbia (5-year: −54%; 15-year: −35%) and Snake rivers (5-year: −59%; 15-year: −42%), where spring Chinook have obligated stream-type juvenile life histories. Coastal spring Chinook stocks, which express predominantly ocean-type juvenile life histories fared comparatively better, with 50% (6/12) of coastal spring Chinook populations north of the Rogue River experiencing positive trends in escapement across their time series. More southerly spring Chinook populations in the Rogue, Klamath and Sacramento watersheds fell below their mean long-term escapement levels by an average of 57% in the most recent 5 years, with the Butte Creek spring Chinook population being a notable exception (Table 1).

Estimated correlations between population-specific process errors provide further evidence for shared trends among interior spring Chinook, both in the Fraser and the Columbia watersheds. For example, among interior spring Chinook populations in the Upper Fraser River process errors showed strong positive correlations but had negative correlations with ocean-type summer and fall Chinook populations in the Fraser and relatively neutral correlations with other Salish Sea populations (Figure S1). Likewise, interior migrating Snake River spring Chinook populations showed consistently positive process error correlations (Figure S3) but had neutral or negative correlations with fall and summer Chinook in the Lewis and Methow Rivers (Figure S4). Even geographically proximate populations of spring and fall Chinook showed evidence of negative correlations in their interannual variability. For example, in the Mid-Columbia region, fall Chinook in the Deschutes River had negative correlations with nearby spring Chinook populations in the Yakima and Naches Rivers, while Deschutes spring Chinook were positively correlated with both (Figure S5).

Fall and summer Chinook populations experienced a mix of escapement trends: 56% (10/18) of fall Chinook and 46% (6/13) of summer Chinook populations that we analysed had negative coefficient estimates for their overall trend (u_i) (Table 1; Figure 2). On average, escapement among fall Chinook populations in our analysis declined at both 5-year (−18%) and 15-year (−15%) time horizons and median trend estimates ranged from −3.8% per year for Rogue fall Chinook to +3.5% per year for Deschutes fall Chinook. On average, summer Chinook populations in our analysis experienced modest increases in spawner escapement at both 5-year (+16%) and 15-year time horizons (+18%). Trends among summer Chinook were buoyed by large increases in escapement among three stocks in the South Thompson River, where average Chinook spawner abundance in the most recent 5 years exceeded their long-term average by +243% (Table 1; Figure 3; Figure S13).

A more complete description of escapement trends among populations in each region is presented in Appendix S3, and escapement trends and data for each regional group are visualized in Figures S13–S19.

3.2 | Trends in total run size and management responses

Total run size declined over our study period for 16 of 23 stocks with sufficient data (Figures 3 and 4). These declines have been met with a mix of management responses and varied success at arresting declines. For example, on the Harrison River, a tributary of the lower Fraser, fall Chinook have declined by approximately 6% per year for the last 35 years (Table 2; Figures 3 and 5), with escapements falling below a minimum stock size threshold (MSST) in 11 of the most recent 15 years with data (Figure S13). In response, managers have restricted fisheries and reduced harvest rates from a long-term (1985–2008) mean of 51% (range: 14%–79%) to a mean of 29% from 2009 to 2019 (range: 16%–58%) (Table 2). Run sizes for natural-origin Upper Sacramento fall Chinook have also declined sharply, particularly since 2007, and total run sizes have never recovered to levels observed in the 1980s and 1990s (Figure 5). Harvest rates have remained relatively high for Upper Sacramento fall Chinook in most years, averaging 62.3% (range: 0.7%–86.5%) between 1983 and 2011, and 58.6% (range: 52.1%–67.7%) from 2012 to 2019 when new harvest control rules were implemented ([PFMC] Pacific Fishery Management Council, 2011) (Tables 2; Table S2). In contrast, harvest rates for Sacramento winter Chinook have been reduced substantially since winter Chinook were ESA listed, contributing to an estimated 6.8% annual increase in total run sizes between 1990 and 2019 (Tables 2, Table S15; Figures 3 and 5). Harvest rates on Skagit River spring Chinook were reduced in recent decades from a peak of 75% (range: 48%–84%) between 1986 and 1992, to a recent 10-year mean of 36% (range: 16%–58%). This reduction in harvest was accompanied by modest improvements in escapement and the stock has met

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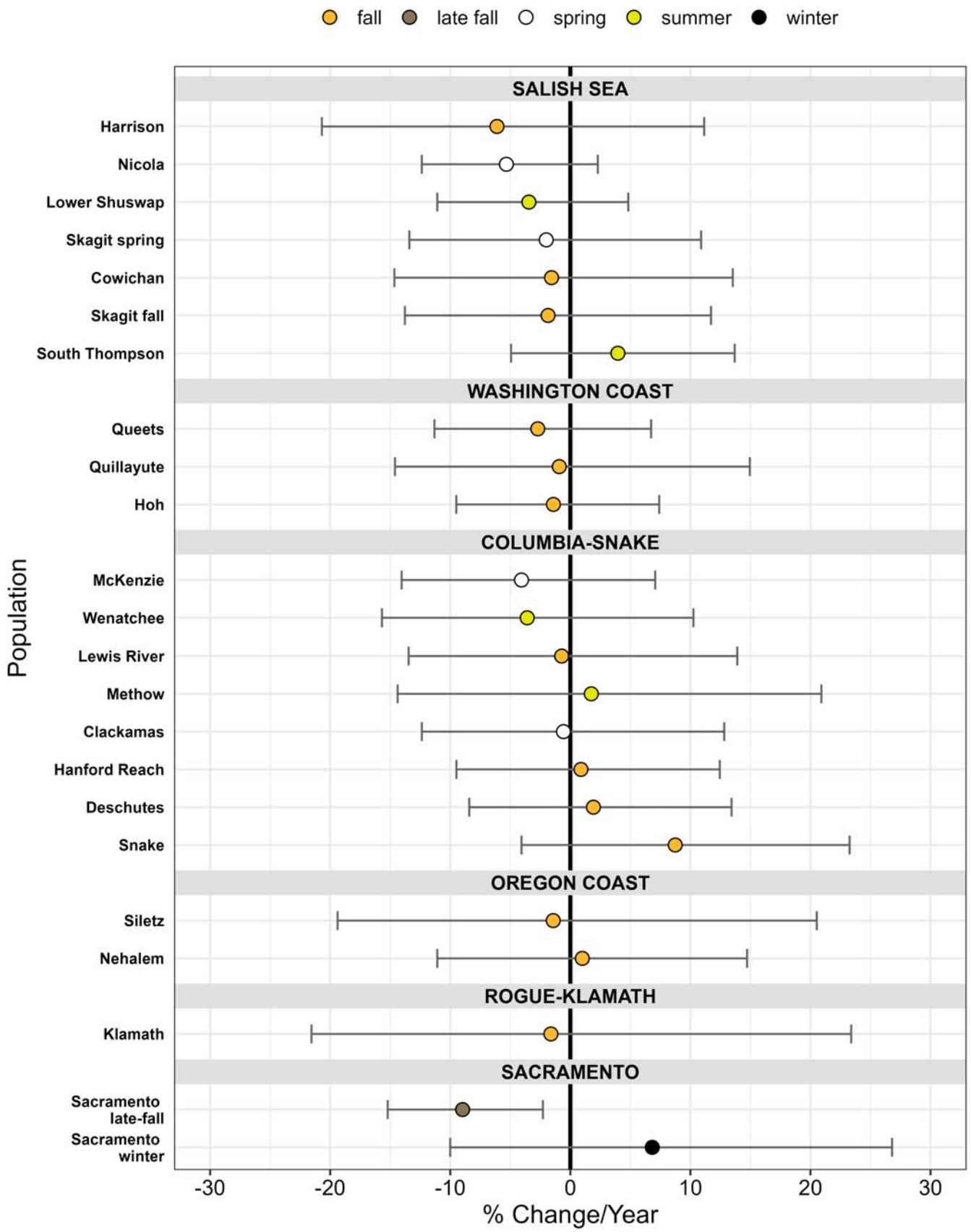


FIGURE 3 Estimated population trends, estimated as the percent change per year trend parameter (u_i) from 1990 to 2019 for total run size (escapement + harvest) in 23 Chinook stocks by population number (Table 2), ranging north from the Salish Sea south to California's Central Valley.

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or exceeded its ESA recovery target of 2000 spawners in 5 years during that period (Figures 5, Figure S13; Tables 2, Table S2). In contrast, Skagit summer/fall Chinook continue to experience harvest rates above 50% in many years, with a 10-year average of 45% (range: 24% to 66%). Since 2012, total pre-fishery abundance of Skagit summer/fall Chinook has exceeded their ESA recovery goal of 14,500 fish in each year (mean run size state: 24,229) but fishery removals have contributed to the stock failing to meet its recovery escapement goal in every year but 2016 (Figure 5, Figure S13; Table 2,Table S2).

In a smaller number of instances (5/21), total run sizes increased across the time series. South Thompson summer Chinook have been increasing in abundance since the late-1990s and between 2000 and 2019 the population surpassed its long-term average run size of 88,140 Chinook in 14 years and experienced strongly positive trend in total run size (+4.0% per year) (Figure 3; Table S12). Some stocks have experienced stable or increasing abundance even while supporting harvest rates in excess of 50%. For example, Cowichan River Chinook have also recently experienced an increasing trend after persistent low abundance lasting from the late 1990s to about 2015. Prior to their collapse, between 1989 and 1994, CWT-tagged Chinook from the Cowichan were harvested at an average annual rate of 83%. Since 1995, harvest rates have been reduced modestly but remain among the highest among Canadian Chinook stocks (1995–2019 mean: 60%). In the most recent 2 years in our analysis, Cowichan Chinook showed strong signs of increasing abundance, with the pre-fishery abundance of Cowichan Chinook surpassing their 1990–2019 mean total run size (16,678 fish) by an average of 46% (Figure 3; Table 2, Table S12, Figure 4). Likewise, Both Hanford and Snake River Fall chinook had strongly positive trends in total pre-fishery abundance, with 1990–2019 abundance peaking for both stocks between 2013 and 2015 (Figure 3; Table S2). For the four Northern Oregon coastal stocks with long-term estimates of total run size, trends in total run sizes since 1990 have been relatively flat (Nehalem: +1% per year) or have declined modestly (Siletz: −1.4% per year) (Table 2; Table S14; Figure 3). Harvest rates for Oregon Coast fall Chinook averaged 59% (range: 41%–85%) between 1985 and 2019 (Table 2; Table S2).

4 | DISCUSSION

We evaluated regional trends in spawner escapement and total run size for Chinook salmon populations from the Fraser River to the Sacramento River, a region that is home to a diverse range of locally adapted Chinook runs, to understand how changes in Chinook salmon abundance varied across geographic and life histories groups. Overall, we found that the escapement of Chinook salmon declined in 57 of 79 populations we assessed, with many populations experiencing especially poor returns in the last 5 years. Total run size data sampled a relatively shorter temporal window (1990–2019) and revealed similarly negative trends in abundance for many populations, but also shed light on some of the notable bright spots for Chinook. These trends also highlight the degree to which population-specific harvest histories have contributed to survival and abundance trends over time, and how fisheries targeting these stocks have or have not responded to changes in their productivity. Despite numerous individual cases of declining abundance and survival, we found that the 23 Chinook stocks with total run size data continue to be harvested at rates >50% in many years, contributing an estimated 3.8 million natural-origin adult Chinook salmon to fisheries catches between 2010 and 2019 (PSC CTC, 2020; PFMC, 2020).

Chinook salmon escapement trends appear to be responding to the combined drivers of management and shifting environmental conditions. Many of our study populations had low escapements from the 1970s to the 1990s, when harvest rates in mixed-stock marine fisheries were very high (e.g. 60–80%. Morishima & Henry, 2001; PSC CTC, 2020). Although the risks posed by mixed-stock fishery impacts were known during that time (e.g. PFMC, 1978; Fraidenburg & Lincoln, 1985), widespread changes in fisheries management were not initiated until the last decades of the 20th century, when several Chinook population units were listed as threatened or endangered under the US ESA (e.g. Columbia, Puget Sound, Sacramento ESUs), and an updated Pacific Salmon Treaty was ratified in 1999 (Myers et al., 2018). Reductions in harvest rates and a period of relatively favourable environmental conditions led to variable but generally increased Chinook run sizes and escapements from Northern California to the Salish Sea from about 2000. In the last decade, most but not all populations experienced increasing variability and a general pattern of declining spawner abundance and total run sizes. These findings align with other recent research documenting declining trends in freshwater and marine survival, as well as increasing synchrony in survival across large swaths of their Northeastern Pacific range (Kilduff et al., 2015; Dorner et al. 2019; Crozier et al., 2021; Welch et al., 2021).

Recent deteriorations of freshwater and ocean conditions supporting Chinook salmon production have negatively affected many populations and escapements have declined despite efforts to reduce harvest rates. These recent declining trends have coincided with warming climate conditions in the marine and freshwater habitats of Chinook salmon with no historical analogue (Lindley et al., 2021; Schoen et al., 2017); including a marine heat wave, which has impacted marine ecosystems in the North Pacific since 2014 (DiLorenzo and Mantua 2016), increasing abundances of marine mammals that prey upon juvenile and adult salmon (Chasco et al., 2017; Nelson et al., 2019), and a period when the abundance of pink salmon (*O. gorbuscha*) in the North Pacific has peaked at over 500 million fish, creating the potential for cascading effects of competition between pink salmon and other pelagic predators (Ruggerone & Nielsen, 2004; Ruggerone & Irvine, 2018). Unprecedented variability in flow and river temperatures have also impacted Chinook and other salmon species (Crozier et al., 2019; Hinch et al., 2021; Tonina et al., 2022; von Biela et al., 2022). While climate-driven disturbances and novel ecosystem conditions have likely contributed to negative trends across the regions we evaluated, California

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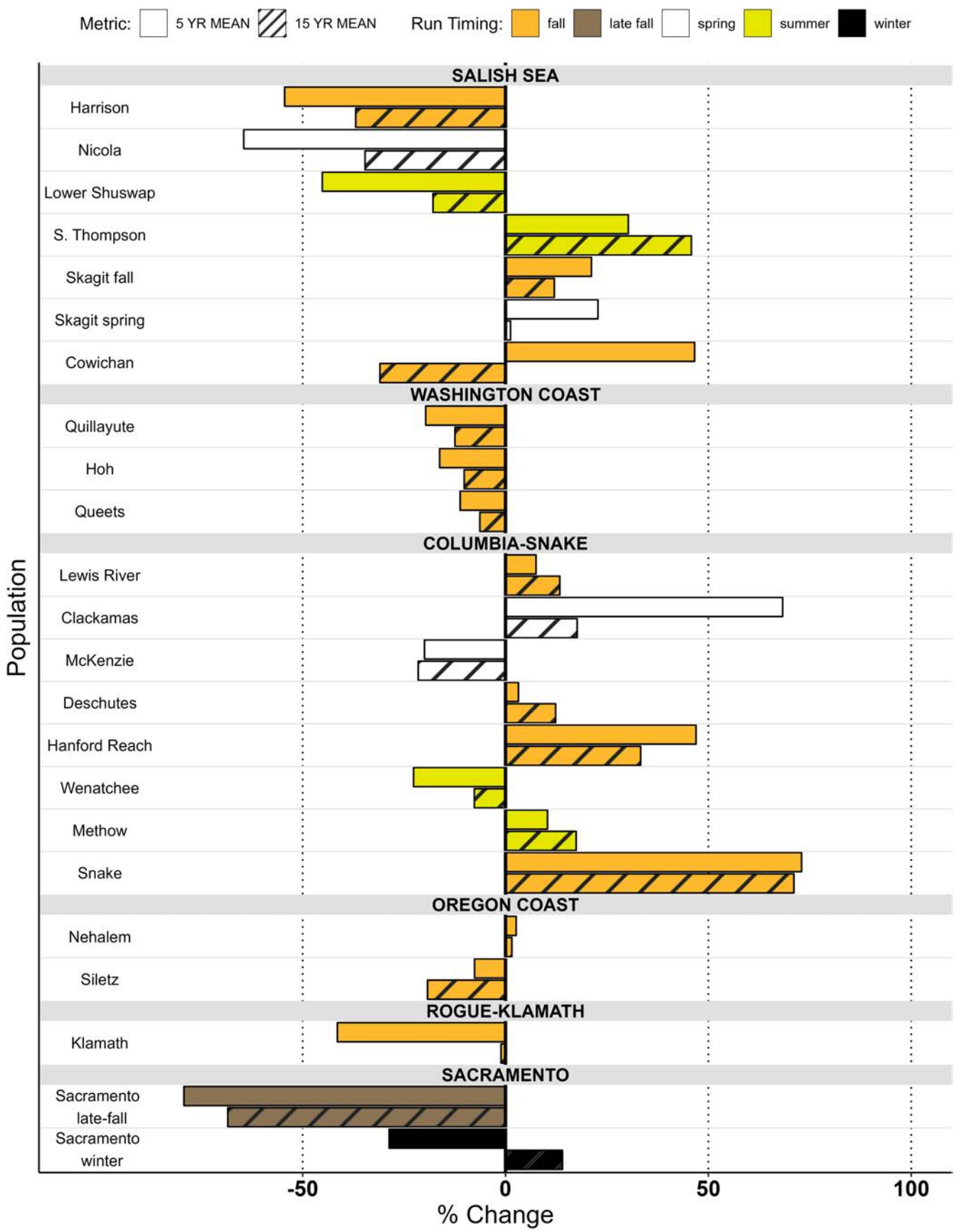


FIGURE 4 Changes in total run size relative to the 1990–2019 average estimated for 23 populations with total run size data across the most recent 5-years and 15-years in our dataset.

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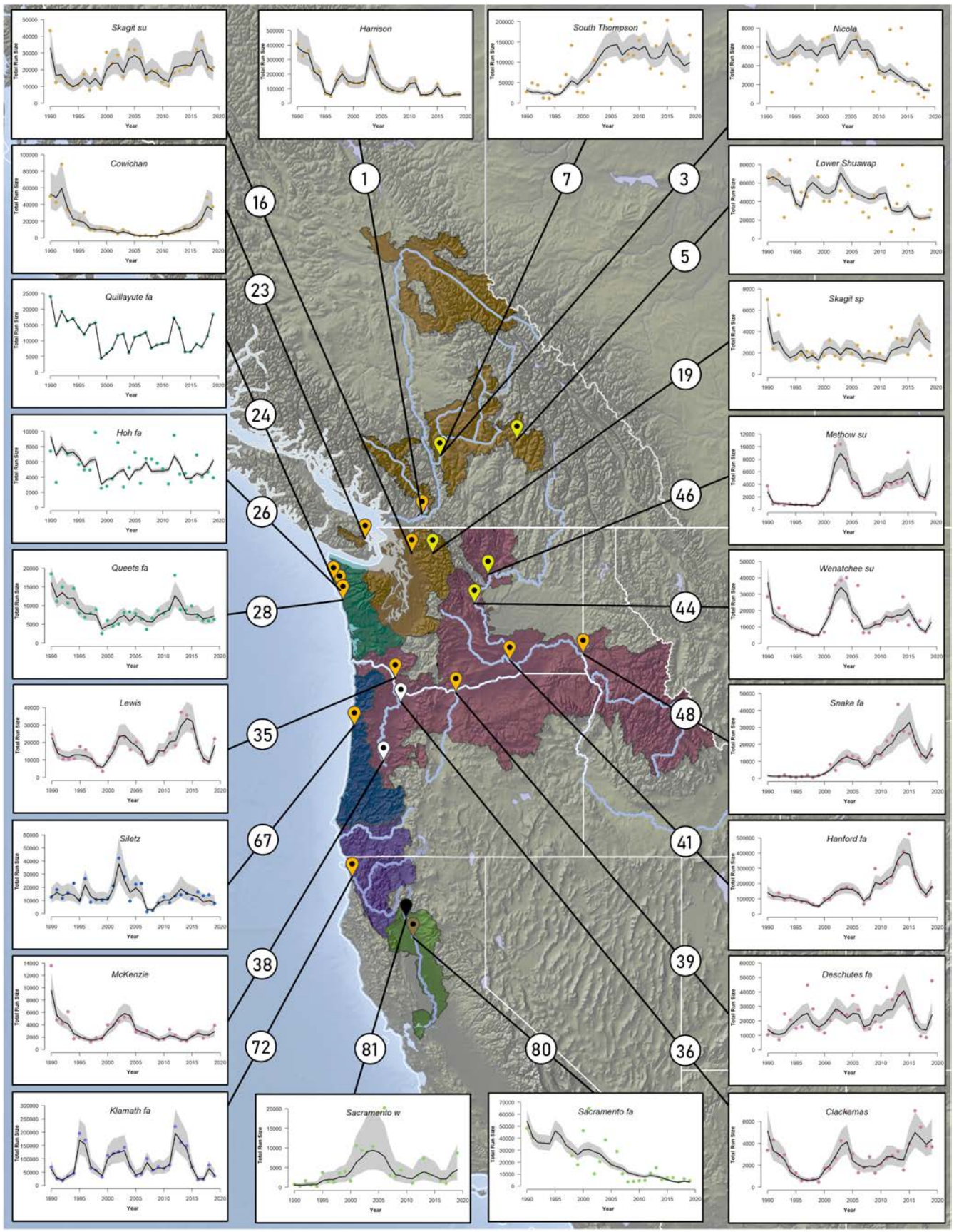


FIGURE 5 Median estimated total run size ($x_{i,t}$) trends (black lines) and 95% confidence intervals (grey shading), plotted alongside 5-year and 15-year changes in abundance and estimated overall trends from 1990 to 2019. Populations are mapped and colour coded by region for ease of identification.

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and Southern Oregon have been further impacted by a prolonged drought affecting freshwater systems (Kogan & Guo, 2015). The negative effects of these disturbances and ecosystem shifts have been precipitated and intensified by more than two centuries of anthropogenic climate change, marine and watershed habitat alterations, and hatchery practices that have eroded the resilience and productivity of Chinook salmon (McClure et al., 2008; Satterthwaite & Carlson, 2015; Dorner et al., 2018; Beechie et al., 2021; Munsch et al., 2022). Chinook salmon are also getting smaller over time, with potentially serious implications for their demographic productivity and ability to support fisheries in the future (Ohlberger et al., 2018; Oken et al., 2021; Xu et al., 2020). These changes in size are likely driven by a multitude of factors including shifting climate and marine food webs, competition with pink salmon, and harvest; and much like survival trends these changes in size are shaped by life history, watershed of origin and marine distribution (Buckner et al., 2022). Many Chinook populations we evaluated have also experienced higher-than-average en route and pre-spawn mortality in recent years (Bowerman et al., 2021; Doutaz et al., 2021; Teffer et al., 2018; Thompson et al., 2012). Indeed, the effects of climate warming are being felt by the Chinook salmon and their associated social-ecological systems from the Yukon to California (Crozier et al., 2021; Katz et al., 2013; von Biela et al., 2022).

Life history, and in particular run timing, appears to be associated with differences in escapement and total run size trends. Our analyses revealed declines among most spring Chinook stocks (40/47), particularly those populations with stream-type juvenile life histories (e.g. interior spring Chinook in the Columbia, Snake and Fraser Rivers) but also among most of California's spring-run Chinook salmon, which have a predominantly ocean-type juvenile life history. These stocks had near-record low spawner abundances in most of the last five years of our study period and, if their current population trajectories continue, they face a high risk of extinction ([COSEWIC] Committee on the Status of Endangered Wildlife in Canada 2018, 2020; [NMFS] National Marine Fishery Service, 2016). This trend is reflected in the ESA and COSEWIC listing status of spring Chinook we assessed with 72% (34/47) of populations listed as threatened or endangered, and five more populations listed as special concern or protected under US state-level legislation.

The particularly severe declines experienced by spring Chinook likely stem from risk factors that are exacerbated by their early-migrating life history. Spring runs in the Columbia, Snake, Fraser, Klamath and Sacramento Rivers undertake some of the longest migrations among the populations we studied and depend on heavily industrialized and urbanized watersheds during rearing and migration. These lengthy migrations in anthropogenically altered watersheds pose considerable challenges for spring runs as both smolts and adults (e.g. Cordoleani et al., 2018; Schaller et al., 2013). Some coastal spring Chinook stocks from Washington and Oregon had qualitatively similar but less extreme declining trends, suggesting that the risk of decline may be related in part to their early-migrating life histories. Interior spring Chinook populations may experience added stress due to the predominance of yearling smolt migration stream-type life histories, which extend their dependence on freshwater rearing areas (Crozier et al., 2019; Gustafson et al., 2007; McClure et al., 2008). In addition to ongoing climate changes, these areas have suffered from the impacts of logging, grazing, forest fires and irrigation withdrawals contributing to reduced baseflow and elevated stream temperatures (e.g. Doutaz et al., 2021; Warkentin et al., 2022). Recent research has revealed distinct survival trends for stream-type and ocean-type stocks even within the same regions (Freshwater et al., 2022), and interior spring Chinook with obligate yearling life histories are also thought to undertake more offshore oceanic migrations, driving differential exposure to North Pacific-scale climate changes (Lindley et al., 2021; Weitkamp, 2010).

In some instances, spring Chinook have benefitted directly from ecosystem restoration or dam removal. Three populations of spring Chinook – in Oregon's Clackamas and Sandy rivers, and California's Butte Creek – stand out for their stable or increasing trends in abundance. These populations have all been the focus of major dam removals, fish passage improvements or ecosystem restoration efforts. Improved juvenile and adult passage at the three dams in the Clackamas watershed have contributed to a rebuilding of spring Chinook abundance in the basin, with the average 2015–2019 escapement exceeding the long-term average by 103%. On the Sandy, natural-origin spawner abundance has increased since the removal of Marmot Dam in 2011, and in the last 5 years escapement has been 144% higher than the 1982–2019 average. Butte Creek is an outlier among the spring Chinook populations we evaluated in California, with relatively strong recent escapements, which increased dramatically following watershed-scale restoration actions that included completion of the Butte Creek Fish Passage Improvement Project, and improved summertime flow and temperature regimes with imported water from a nearby basin ([ACWA] Association of California Water Agencies, 2017). Collectively, these bright spots reveal that large-scale restoration actions can have positive population-level impacts on Chinook salmon (Booth et al., 2016).

Summer and fall Chinook populations had more mixed trends, with only about half of their populations (16/31) experiencing declining escapement as indicated by a negative median trend estimate (u_i) and several populations experiencing increasing trends in abundance. The relative stability of some summer and fall Chinook populations and their ongoing ability to support social-ecological services may be due in part to differences in their life histories and habitats, which moderate their exposure to stressors and climate change impacts in freshwater and at sea. For example, these later-migrating Chinook typically undertake shorter adult spawning migrations, arrive in freshwater closer to reproductive maturity and usually depart freshwater during their first year of life (Healey, 1991; Quinn, 2005; Taylor, 1990).

In fact, most ocean-type summer and fall Chinook returning to the interior areas of the Columbia and Fraser watersheds had stable or positive trends in both escapement and total run size and continue to support major harvest in fisheries. These interior spawning ocean-type populations, colloquially referred to as *upriver brights* in the Columbia, have exhibited increasing abundance

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over the last 30 years. These populations share several life-history attributes, freshwater habitat similarities and patterns of distribution at sea. In the ocean summer and fall Chinook from the interior Fraser, Columbia, Washington and Oregon Coasts typically migrate north along the continental shelf to the coastal areas of Northern British Columbia and Southeast Alaska where they feed and grow for several years before undertaking their return migrations (Weitkamp, 2010). Juveniles among these northerly migrating populations depart freshwater during their first year of life, feeding and growing in riverine habitats as they migrate downstream, and typically arriving in their estuaries in May and June, but individuals within these stocks can exhibit a high degree of variability in the timing of marine entry (Bottom et al., 2021; Chalifour et al., 2021; Scott et al., 2019). This extended seaward migration allows fish to achieve a relatively larger size at marine entry and may give these juveniles a survival advantage compared to other ocean-type populations when confronted with unpredictable marine conditions in their early marine life (Beamish et al., 2010; Duffy & Beauchamp, 2011).

Declining abundance and collapsing productivity has given fishery managers slimmer margins of error, creating trade-offs between conservation risks and harvest goals when depressed and healthy populations overlap in mixed-stock fisheries ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020; Moore et al., 2021; Parken et al., 2008). Management responses to declining Chinook salmon populations in the last several decades have included reduced harvest rates, investments in dam passage and removal, hatchery reforms to reduce the demographic and genetic influence of hatchery-origin spawners and habitat restoration. In some places these efforts have paid dividends and have either stabilized abundance or led to recovery among Chinook salmon. For example, Cowichan River fall Chinook fell below their PST-established escapement goal of 6500 spawners in every year from 1997 to 2015. During this period, fishery managers in Canada made modest reductions in the average harvest rate (1990–2009 average ER = 67%; 2009–2017 average = 58%) and changed hatchery practices by reducing the number of hatchery fish released. These management changes coupled with local investments in freshwater and estuarine habitat restoration, and improved water management were followed by a dramatic rebuilding among Cowichan River Chinook. Natural-origin spawner abundance has exceeded 6500 every year since 2016.

In other places, conservation and management actions have lagged declining trends or have been inadequate to address the scale of the challenge, contributing to the erosion of social-ecological values supported by Chinook salmon. In Washington State, some Chinook populations continue to be harvested at high rates in mixed-stock fisheries despite their declining abundance. For example, between 2009 and 2017 the average exploitation rate estimated for CWT-tagged summer Chinook returning to the Skagit River exceeded 50% (range: 24.7%–73%), and Queets River fall Chinook were subjected to average harvest rates greater than 60% (range: 46.6%–80%) ([PSC CTC] Pacific Salmon Commission joint Chinook Technical Committee, 2020). Skagit River summer and fall Chinook met their ESA recovery goal of 14,500 spawners in 1 year between 2009 and 2019 but on average nearly half of the run was harvested (mean: 46.7%), mostly in marine mixed-stock fisheries. Spawning ground escapement and total run sizes for Queets River fall Chinook also edged downwards towards the PSC established minimum escapement goal of 2500 from 2009 to 2019 and Queets River spring Chinook fell below their PSC escapement goal in all but 4 years between 2005 and 2019. For these stock(s), where CWT-tagging programs enable estimates of harvest, about 70% of fishery impacts occurred in mixed-stock fisheries outside of Washington State waters, limiting the efficacy of local recovery actions by state and tribal management agencies and reducing access to salmon fishing opportunities for communities in these watersheds (Atlas et al., 2021; Malick et al., 2017).

We have identified trends for a subset of Chinook salmon populations in North America, but our analysis was necessarily limited in both its geographic and temporal scope. We opted to focus on the southern half of the North American range of Chinook, primarily because this region is home to the greatest variation in Chinook run timing and life-history diversity, and because data were readily available for many of these populations. Short and variable-length time series of data also create considerable uncertainty and challenge comparisons of Chinook escapement trends across regions where time series length differ. Accordingly, inter-regional comparisons of population trends should be interpreted with caution. In addition, fluctuations or stability in escapement among Chinook populations is influenced strongly by fisheries management, making escapement an imperfect indicator of the biological status of Chinook populations. However, consistent declines in Chinook escapement even after reductions in harvest rates that have corresponded with declining abundance, highlight the severity of the declines now being observed among many Chinook populations. Total pre-fishery abundance for Chinook salmon populations is a more useful indicator of biological trends. While total run size data sets were only 30 years in length (1990–2019), the fact that these populations were evaluated across the same range of dates improves our ability to draw direct comparisons in their trends.

Despite climate change headwinds, restoration actions can still contribute to increased abundance and productivity for Chinook salmon. Restoring natural hydrological and ecological processes and riverine connectivity through dam removal and floodplain reconnection are paramount for Chinook in their migratory corridors, juvenile rearing areas and headwater spawning areas (e.g. Beechie et al., 2021). Dam removal on the Snake River is among the clearest pathways to recovery for Chinook in the Columbia Basin, and recent analyses indicate that unless survival rates are improved for out-migrating Chinook smolts and returning adults extinction is likely for many of these stocks before the end of the 21st century (Crozier et al., 2021). Removing dams from migratory corridors may also boost marine survival of out-migrating smolts, since carryover effects from migration through the hydro

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system including reduced condition or energy storage at ocean entry have been linked to lower smolt-to-adult returns (e.g. Gosselin et al., 2021). Dams that are complete migratory barriers to Chinook, or that inundate former spawning habitats, reduce the quantity of habitat for spawning adults and rearing juveniles for both stream- and ocean-type life histories, diminishing the productive capacity of watersheds for Chinook (Liermann et al., 2010; Parken et al., 2006) and disrupting downstream physical and ecological processes (Ward & Stanford, 1987). Dam removals have led to some of the most notable successes in wild salmon recovery (Hatten et al., 2015; Pess et al., 2008). Likewise, dam removal in the Klamath Basin holds immense promise for Chinook recovery but with spring Chinook in the basin experiencing record low returns the number of strays or colonizing salmon likely to reach newly accessible areas of the Upper Klamath may be limited without urgent action (Thompson et al., 2019).

Our analysis of Chinook abundance trends reveals clear winners and losers, even in the face of a rapidly changing climate, highlighting the importance of intraspecific diversity for stabilizing social-ecological systems (Des Roches et al., 2021). For example, ocean-type summer Chinook in the Interior Fraser, and fall upriver bright Chinook in the Columbia have increased or been stable in their abundance since the 1980s. The responses of individual populations to changes in climate can be sudden and unexpected. For example, in Alaska's Nushagak River, home to Bristol Bay's largest Chinook salmon population, the relative contribution of different spawning areas to annual returns has been shown to fluctuate in response to changing environmental regimes (Brennan et al., 2019). These changes are unforeseen and unpredictable, making the maintenance of intraspecific diversity a critical element of resilience for populations and fisheries (Moore & Schindler, 2022). A rich diversity of Chinook populations and life histories has evolved to fill a variety of niches in freshwater and ocean ecosystems, and these populations continue to evolve in response to natural and anthropogenic drivers. Protecting and rebuilding all these elements of Chinook biodiversity and maintaining the adaptive potential of populations will be essential for their future in the face of a changing climate.

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DATA AVAILABILITY STATEMENT

The data used in all analysis are presented in the supplemental materials in table form with attributions to their original source therein. Data and code are also posted on a public GitHub repository, which can accessed at https://github.com/willatlas/ChinookEscapement-RunSize

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SUPPORTING INFORMATION

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Indigenous Systems of Management for Culturally and Ecologically Resilient Pacific Salmon (*Oncorhynchus* spp.) Fisheries

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*Pacific salmon (*Oncorhynchus *spp.) are at the center of social–ecological systems that have supported Indigenous peoples around the North Pacific Rim since time immemorial. Through generations of interdependence with salmon, Indigenous Peoples developed sophisticated systems of management involving cultural and spiritual beliefs, and stewardship practices. Colonization radically altered these social–ecological systems, disrupting Indigenous management, consolidating authority within colonial governments, and moving most harvest into mixed-stock fisheries. We review Indigenous management of salmon, including selective fishing technologies, harvest practices, and governance grounded in multigenerational place-based knowledge. These systems and practices showcase pathways for sustained productivity and resilience in contemporary salmon fisheries. Contrasting Indigenous systems with contemporary management, we document vulnerabilities of colonial governance and harvest management that have contributed to declining salmon fisheries in many locations. We suggest that revitalizing traditional systems of salmon management can improve prospects for sustainable fisheries and healthy fishing communities and identify opportunities for their resurgence.*

Keywords: traditional knowledge, salmon, sustainable fisheries, mixed-stock fisheries, Indigenous governance

In an era of escalating anthropogenic threats to global biodiversity, there is a need to understand the diversity of human–nature relationships and identify stewardship practices and knowledge that can foster resilient social–ecological systems (Bennett et al. 2016). There is growing recognition that the ecological knowledge and stewardship practices of Indigenous peoples can offer pathways for effective and socially just conservation and resource management (Turner and Berkes 2006, Polfus et al. 2016, Ban et al. 2018, Artelle et al. 2019). For example, Indigenous peoples manage more than 40% of Earth's ecologically intact landscapes (Garnett et al. 2018), and Indigenous-managed lands have similarly high vertebrate biodiversity to parks and protected areas (Schuster et al. 2019). The knowledge and legal jurisdiction of Indigenous communities has also benefited conservation and recovery of species ranging from grizzly bears (*Ursus arctos horribilis*) to Dungeness crabs (*Metacarcinus magister*; e.g., Service et al. 2014, Frid et al. 2016, Kitasoo/Xai'xais First Nation 2018).

Pacific salmon (*Oncorhynchus* spp.) form the foundation of social–ecological systems encompassing communities from California to Kamchatka and Northern Japan (Yoshiyama 1999, Muckle 2007, Tabarev 2011). Indigenous peoples of the Northern Pacific Rim have harvested salmon for subsistence and livelihoods for more than 10,000 years (Cannon and Yang 2006, Muckle 2007). Archaeological and ethnographic evidence points to long-term intensive use of salmon (Campbell and Butler 2010, Cannon et al. 2011, Ritchie and Angelbeck 2020) with deliberate and well-honed systems of salmon management (Carpenter et al. 2000, Turner and Berkes 2006, Menzies and Butler 2007). Resource management systems are the sum of the social and cultural processes that encode norms for the use of natural resources, and the technologies and understandings that

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underpin management actions (Lertzman 2009). Indigenous management systems promoted the sustained productivity of precolonial salmon fisheries, which likely rivaled early colonial commercial fisheries in their scale (e.g., Craig and Hacker 1940, Glavin 1996, Meengs and Lackey 2005). These systems were rooted in traditional laws, cultural and spiritual beliefs, and management practices that promoted sustained abundance and access to wild salmon by limiting the risks of overharvest and population collapse (Swezey and Heizer 1977, Harris 2001, Haggan et al. 2006, Ritchie and Angelbeck 2020).

In Canada and the United States, Indigenous management of Pacific salmon was painfully and intentionally disrupted beginning in the mid-nineteenth century and replaced by colonial government authority. This transformation fundamentally altered the scales, methods, and locations of salmon harvesting, stripping rights and jurisdiction from Indigenous people and beginning a struggle for access and governance authority that continues to this day (Higgs 1982, Newell 1993, Harris 2001). However, many modern salmon fisheries are struggling to provide sustainable social, economic, and ecological benefits; for example, in Canada, the number of commercial licenses has decreased, catches have crashed, and many salmon populations face conservation risks (Price et al. 2017, Walters et al. 2019).

Despite the destructive impacts of colonization, Indigenous culture and knowledge are resurgent in Canada and the United States. Salmon remain integral to the food security, cultural practices, health, and economy of Indigenous peoples (Chan et al. 2011, Marushka et al. 2019, Steel 2020). Although different legal and societal circumstances have contributed to this resurgence across North America, Indigenous communities are increasingly responsible for the management of fisheries, and stewardship of lands and natural resources within their homelands. Amid this ongoing transformation there is increasing recognition that Indigenous knowledge and management systems can contribute to restoring the productivity and resilience of aquatic ecosystems and fisheries (Turner and Berkes 2006, Lepofsky and Caldwell 2013, Salomon et al. 2019). Fisheries science and management should therefore seek solutions beyond the bounds of fisheries science, learning from and empowering Indigenous knowledge to benefit salmon-dependent communities and ecosystems (Reid et al. 2020).

In the present article, we provide examples of Indigenous salmon management systems, discussing the scale, methods and values that guide Indigenous management of salmon and contrasting them with contemporary fisheries management. We also give examples of how these technologies are being brought back to life, highlighting opportunities for their application to contemporary management and cogovernance challenges (supplemental table S1). Having supported vibrant salmon-dependent communities for millennia before European settlement, we believe that revitalizing Indigenous salmon management systems can support long-term opportunities for equitable and sustainable harvest of wild salmon across western North America.

Contemporary salmon management: History and challenges to sustainability

The changes in governance, technology, and fishery management that began with European colonization of western North America in the nineteenth century gave rise to a commercial fishing industry that has shaped the economics and fate of salmon fisheries in profound ways. In the present article, we review some shifts in salmon management systems and the social and ecological issues they have posed. Given the diversity of modern and traditional salmon fisheries, it is beyond the scope of this article to provide a comprehensive analysis of their respective strengths and weaknesses. Indeed, there are commercial salmon fisheries that are archetypes of sustainable natural resources extraction and management, such as the Bristol Bay, Alaska, sockeye salmon fishery (Hilborn et al. 2003). Instead, we identify a set of frequent challenges to the sustainability of contemporary salmon fisheries and point to areas in which Indigenous management systems, knowledge, and harvest technologies can provide pathways to sustainability.

The commercialization of fisheries transformed the values and understandings guiding fisheries management, because colonial governments and fishing companies sought to develop and extract resources for global markets (Newell 1993, Yoshiyama 1999, Harris 2001). The rise of combustion engines, monofilament nets, and other fishing technologies powered increasingly effective salmon fishing, whereas canning and refrigeration allowed huge quantities of salmon to be packed and shipped to global markets (Newell 1993, Meggs 1991, Taylor 1999, Morishima and Henry 2000). In the rush to extract wealth from the watersheds of the Pacific Northwest, salmon habitats were damaged, sometimes irreparably, by logging, mining, diking, dam construction and other destructive land use (Baird 1875, Stone 1892, Miller 2010). Habitat destruction coupled with extreme harvest pressure precipitated declines in salmon populations from the Skeena in British Columbia (BC) to the Sacramento River in California (Ricker and Smith 1975, Higgs 1982, Ricker 1987, Yoshiyama 1999).

Among the most profound transformations in management brought on by colonization was the shift to mixed-stock ocean fisheries, which gradually replaced Indigenous in-river salmon fisheries as the primary method and scale of harvest (Cobb 1921, Higgs 1982, Morishima and Henry 2000). Mixed-stock fisheries intercept fish during their oceanic feeding migrations, harvesting salmon from numerous populations. Many salmon in the Eastern Pacific traverse US, Canadian, and international waters during their migratory life cycle, and fish are routinely harvested outside their country and Indigenous territory of origin (PSC 2020a).

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Therefore, the migratory life cycle of salmon poses additional challenges to sustainability by creating mismatches between management decisions, fishery opportunities, and the biologically relevant processes that support salmon populations (e.g., river disturbance, rainfall and temperature, and ocean climate and productivity; Bottom et al. 2009, Malick et al. 2017). These mismatches have created adverse downstream consequences for people, ecosystems, and salmon through intensive mixed-stock harvest, resource development, land use, and overproduction of hatchery salmon by industrial nations around the Pacific Rim (e.g., Moore et al. 2015, Sexton et al. 2020, Vierros et al. 2020). Supporting greater engagement and participation in monitoring and management among Indigenous peoples and local communities is one avenue toward alleviating the negative impacts of these scale mismatches (Herse et al. 2020).

Managers have long recognized that mixed-stock harvest can undermine the sustainability of salmon fisheries, if smaller or less productive populations are harvested in fisheries targeting abundant stocks (Ricker 1973, PFMC 1978, Hilborn 1985). In these instances, overharvest can threaten the long-term viability of wild salmon populations and fisheries (e.g., Connors et al. 2019). Management measures to limit the impacts of these mixed-stock fisheries may also be harmful to fishing communities if they reduce fishing opportunity for locally abundant populations (Martin 2008, Langdon 2015, Walters et al. 2019). By the 1960s, concerns over declining salmon runs drove efforts to curb overcapitalization through license privatization, consolidation, and buybacks efforts in both Canada and the United States (Newell 1993, Brown 2005, Carothers 2010). Efforts to shrink the commercial fishing fleet ultimately reduced the number of commercial licenses and fishing boats in remote and Indigenous communities, undermining access to salmon-fishing livelihoods and food security (Carothers 2010, Langdon 2015, Angel 2017, Steel 2020). The social–ecological and economic viability of commercial salmon fisheries has been further undermined by infrequent or unpredictable openings (e.g., Martin 2008, Walters et al. 2019), fluctuations in prices driven by global markets, and management objectives that are often narrowly focused on maintaining maximum sustainable yields (Adkinson and Finney 2003, Bjorndal et al. 2003, Hilborn 2006, Healey 2009).

Responding to the need for cooperative management of ocean salmon fisheries between the United States and Canada, the Pacific Salmon Treaty (PST) was first ratified in 1985 and was updated in 2019 to enable bilateral management of salmon fisheries (PSC 2020b). Although the treaty seeks to foster equitable and transparent management of salmon between the two countries, the legal primacy of this agreement has shaped management objectives, allocation, and monitoring in both countries, often with limited input from salmon-dependent communities (Knight 2000, Vierros et al. 2020). Therefore, contemporary salmon management governs resource use across vast spatial scales, and decision-making flows downstream from centralized government authorities operating under bilateral treaty arrangements. Centralized systems of command and control resource management decouple local resource users from management decisions, limiting the ability of local knowledge and values to penetrate decision making processes (Holling and Meffe 1996), thereby reducing access and agency within local communities that depend on fisheries or other natural resources for their livelihoods (figure 1; Leal 1998, Healey 2009, Pinkerton et al. 2014).

The management of fisheries in both countries is challenged by a lack of baseline data on salmon abundance, run timing, and harvest rates in mixed-stock fisheries (Halupka et al. 2003, Malick et al. 2017, Price et al. 2017). Monitoring salmon populations across the vast western North American range of salmon is costly and logistically challenging, and in many regions most populations are currently unmonitored (e.g., Connors et al. 2018). Harvest rates, migration timing, and marine distributions for many stocks are inferred from nearby intensively monitored populations—often hatchery-reared salmon—that are marked with coded-wire tags and adipose fin clips and recovered during fishery monitoring and spawner enumeration (e.g., Morris et al. 2007, English et al. 2018, Shelton et al. 2019). However, given the limited number of indicator stocks in many areas of BC and Alaska, and evidence that migration timing, routes, and fishery interceptions may vary considerably between proximal stocks, estimates of harvest inferred from indicator populations may yield unreliable estimates of harvest for many populations (Beacham et al. 2020).

Habitat loss, climate-driven declines in ocean survival, and efforts to minimize impacts on populations with variable conservation status have eroded salmon fishing economies (Martin 2008, Angel 2017, BCWSAB 2018). Given these challenges and risks of mixed-stock fisheries, managers have recently prioritized precaution and reduced salmon fishery openings and harvest quotas (Walters et al. 2019, Fisheries and Oceans Canada 2019a). In fact, in 2019, the total quantity and landed value of salmon caught in the Canadian commercial fishery was the lowest on record and commercial fisheries were closed along much of the BC coast (Fisheries and Oceans Canada 2019b).

Traditional Management Systems

Indigenous management systems offer alternatives to contemporary resource management because of differences in cultural values and knowledge that have motivated their development. Whereas colonial societies have largely emphasized extraction of resources for short-term profit, resource management by Indigenous peoples has tended to emphasize multigenerational sustenance and reciprocity (Trosper 2002, Ban et al. 2019, Curran et al. 2020). Indigenous management systems, guided by traditional knowledge and law, also share several key attributes with contemporary resource management; for example, both are guided by knowledge gained through the continuous

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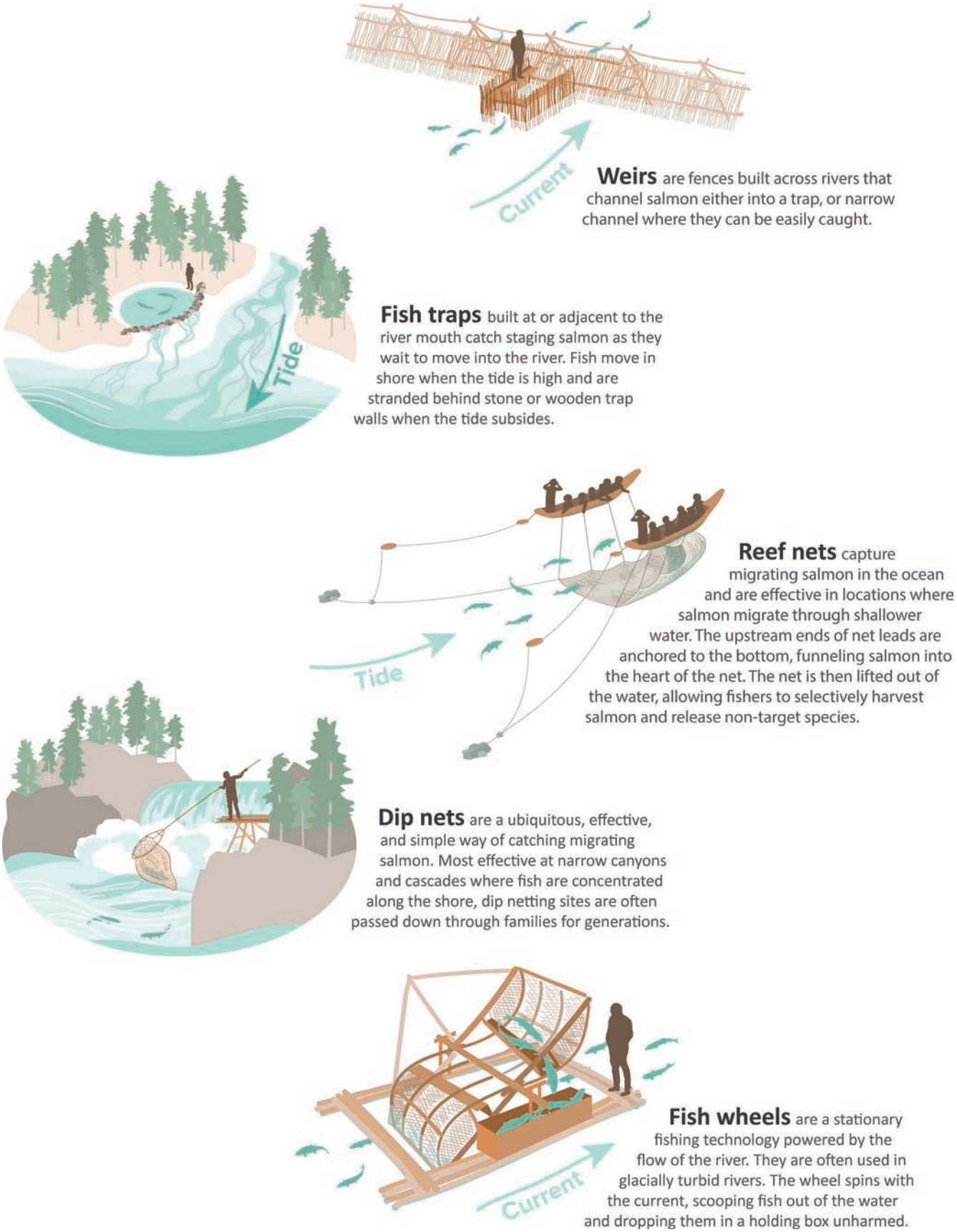


Figure 1. A variety of traditional Indigenous fishing technologies and details of their use.

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observation of natural systems (Carpenter et al. 2000, Turner and Berkes 2006, Lertzman 2009). However, key differences exist in the scale, time horizons, and organizational hierarchies of Indigenous and contemporary resource management systems (figure 1).

Indigenous peoples of the Pacific Northwest have long established and complex institutions of governance that emphasize the conscious protection of the nonhuman world. Each nation or tribe possesses unique laws and stewardship practices. Despite their unique knowledge and traditions, Indigenous understandings of ecosystems, and the management systems that flow from traditional knowledge tend to incorporate a much deeper recognition of the connection between humans and ecosystems, placing humans within a broader family of life (Walens 1981, Berkes et al. 2000, Salmón 2000, Claxton and Price 2020). Indigenous laws are derived from millennia of experiences in very specific geographies that have shaped their morals, values, and traditional knowledge (Turner et al. 2000, Berkes 2012, Turner 2014). These laws have laid the foundation for Indigenous governance and decision-making.

Resilient resource management systems begin with governance structures that sufficiently address the health of ecosystems within legal and political institutions (Nadasdy 2003, Turner and Berkes 2006). On the Northwest Coast, high human population density created acute awareness among precolonial Indigenous peoples of the pressures their food and material resources faced, as well as the detriment of waste (Anderson 1996). In the case of salmon, this awareness guided stewardship and ceremonial practices that reflected the place of salmon as a vital economic and subsistence resource. Just as global economics shape the values and actions of colonial political institutions, salmon fisheries have shaped Indigenous institutions. Contrasting maximum sustainable yields–based fisheries management, Indigenous fisheries took what was needed for subsistence and trade, curtailed harvest when these needs had been met, and regulated access to reduce the risk of overharvest (Harris 2001).

In each Indigenous community, oral histories about human and nonhuman relationships lay the foundation for how to conduct one's self in the natural world (Anderson 1996, Cajete 1999, 2018, Turner and Berkes 2006, White 2011). These stories provide "original instructions" for how to care and relate to the land (Nelson and Shilling 2018). Spiritual lessons and cultural beliefs act as the glue, holding together these systems and fostering direct emotional involvement with natural resources (Anderson 1996).

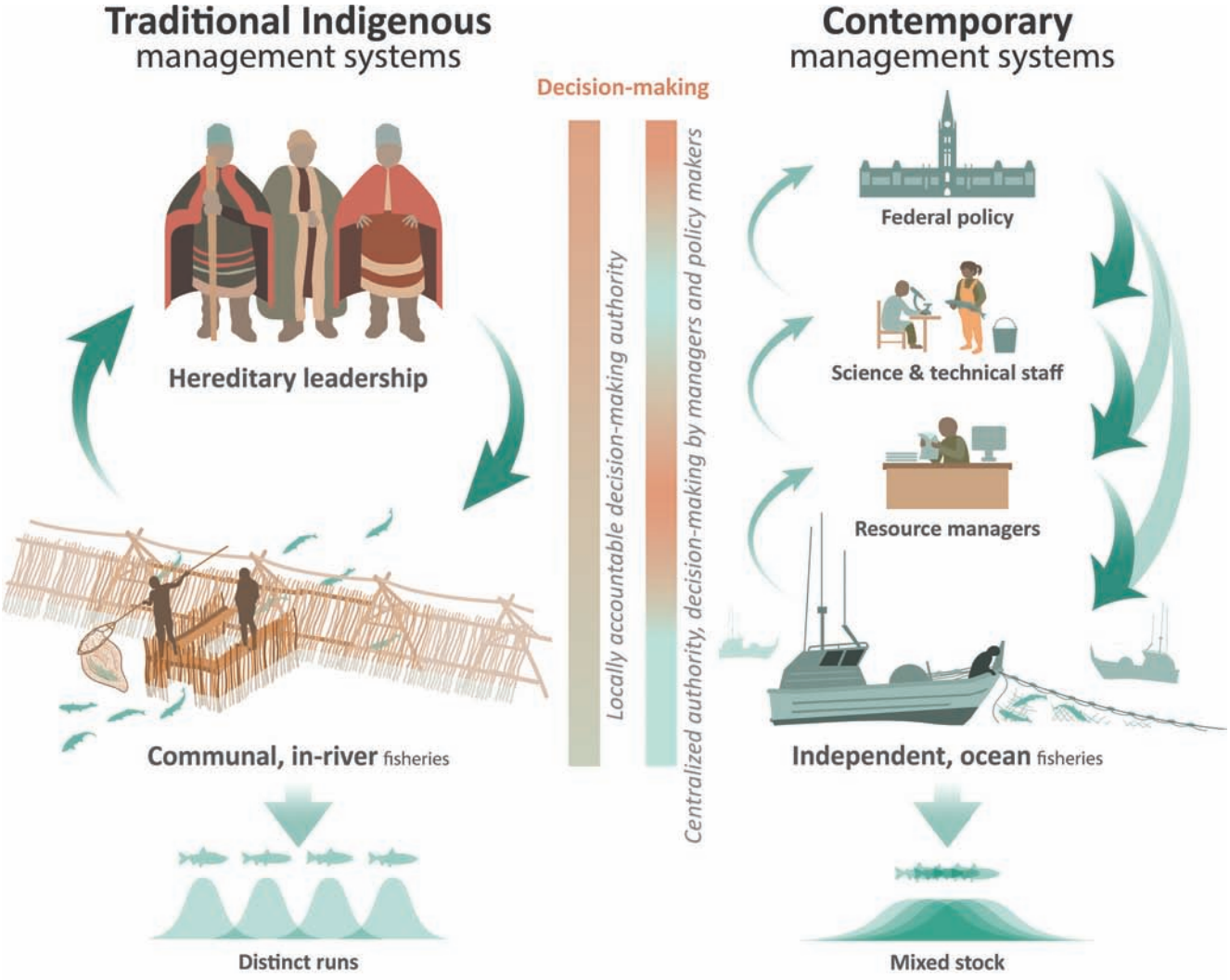
Indigenous management systems are placed based and typically govern resource management decisions locally, controlling resource access, land use, and stewardship decisions across ancestral territories (Leal 1998, Turner et al. 2000, Berkes 2012). These placed-based systems of Indigenous salmon management contrasts sharply with most contemporary sport and commercial fisheries (Gayeski et al. 2018b), where fleets or harvesters are highly mobile and can track changes in resource abundance, limiting their sensitivity to localized population declines (e.g., Schindler et al. 2010, Pitman et al. 2019). Proprietary access rights and hereditary management authority were traditionally upheld through family connections and systems of public reciprocity, which promoted equitable and sustained use of salmon. In addition to codifying the rights of chiefs or families to manage access and exclude outsiders, a clear set of responsibilities flowed from these rights, including the imperative to sustain the productivity of the resource and share the benefits within the community through reciprocal exchange (Trosper 2002, Brown and Brown 2009). From California to Alaska, these reciprocity-based world views center the responsibilities of rights holders to salmon and their community, and were perpetuated through ritual practices, taboos and laws that protected future abundance, and promoted the long-term stability of precolonial salmon fisheries (Swezey and Heizer 1977, Trosper 2002, Haggan et al. 2006, Menzies and Butler 2007, Johnsen 2009, Mathews and Turner 2017, Ban et. al. 2019).

At the forefront of any Indigenous management decisions are achievable and actionable principles. On the Central Coast of BC, the Haíłzaqv (Heiltsuk) Nation has was shown this in modern management plans, with simple but powerful legal principles guiding their work: "the right to use a river system comes with the responsibility to maintain a river system," or " the primary focus should be on what is left behind, not what is taken" (Housty et al. 2014). For example, among Indigenous salmon fishing communities from California to Alaska, the First Salmon Ceremony is a near-ubiquitous practice honoring and encouraging the life-giving return of salmon. This ceremony is followed by a short-term moratorium on fishing, allowing the first runs of fish to reach their spawning grounds before fisheries commence (Swezey and Heizer 1977, Amoss 1987, Jones 2000). Likewise, proprietary access rights limited fishing effort, and mandated weir openings allowed fish to escape upstream uncaptured (Swezey and Heizer 1977, Harris 2001, Ritchie and Anglebeck 2020). These cultural beliefs and practices not only regulated harvest impacts within biologically sustainable bounds but reflect a belief that salmon willingly gave themselves to support the survival of the people (Menzies and Butler 2007, Losey 2010).

Traditional technologies and approaches for sustainable salmon harvest

The methods employed by Indigenous salmon fishers varied widely, but very often included fishing technologies that support selective harvest and release of nontarget species (Stewart 1977). In addition, a large majority of fisheries were—and, in some cases, continue to be—conducted in terminal areas, targeting a single population of salmon with an in-river weir, trap, dipnet, or spear (Stewart 1977, Sweezy and Heizer 1977, White 2006, Menzies and Butler 2007). In the present article, we describe some of the common Indigenous salmon harvesting and management technologies (figure 2).

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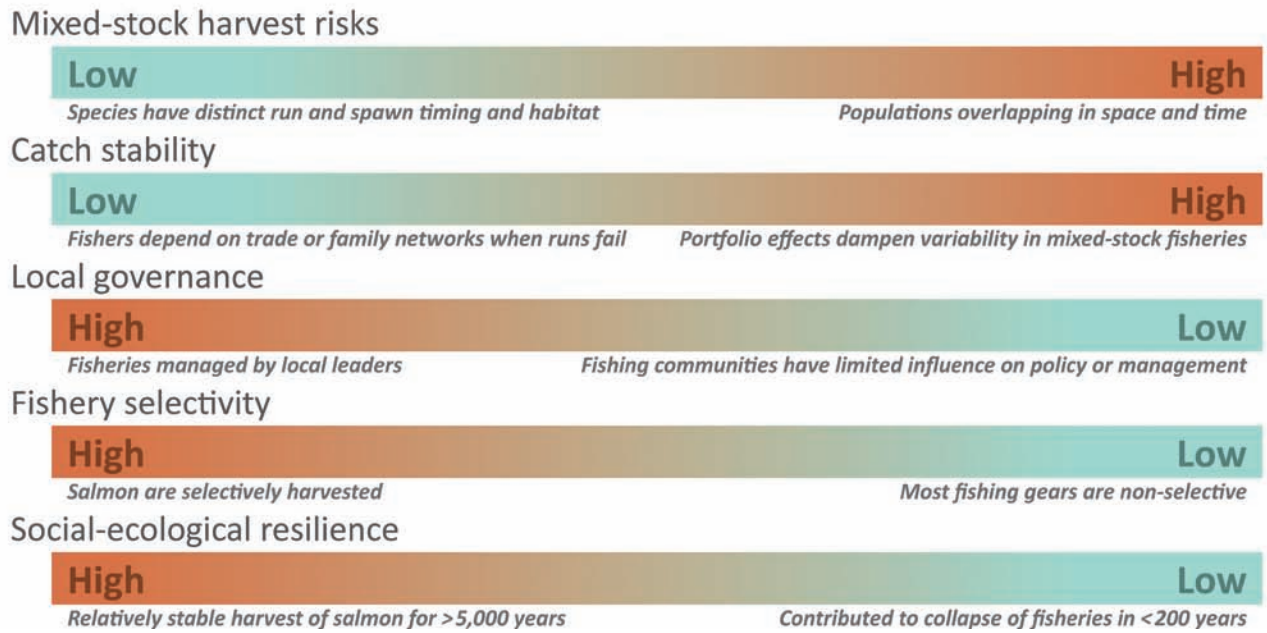


Figure 2. A comparison of Indigenous and contemporary fishery management systems depicting how decision-making authority is distributed within each system, with insights into their social–ecological performance across five key metrics.

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Weirs. Fish weirs—river-spanning fences that channeled salmon into traps or fishways—were perhaps the most widespread salmon fishing technology employed by Indigenous people across the Eastern Pacific Rim from California to Alaska (Stewart 1977, Moss et al. 1990, Harris 2001, Moss 2013). Archaeological remains confirm their use at least 5,000 years ago (Moss and Erlandson 1998) and indicate widespread use over the last several thousand years (Swezey and Heizer 1977, Prince 2005, Nagata et al. 2012, Moss 2013).

Because weirs typically span the entire width of the river, they can fully obstruct upriver migrations of returning adult salmon. If used by fishers unaware or unconcerned about their impacts, a weir can quite easily wipe out a salmon population (Harris 2001, Ritchie and Anglebeck 2020). However, authority over a specific weir location was typically held by hereditary leaders who regulated access in accordance with Indigenous laws guiding reciprocal relationships, thereby promoting sustainability and ensuring access for the many upstream communities that depended on them (Swezey and Heizer 1977, Trosper 2002, Mathews and Turner 2017). The presence of thriving Indigenous societies and abundant salmon returns at the time of European contact is evidence of the deliberate management of salmon fisheries by Indigenous people, and the efficacy of weirs in place-based management systems (Copes 2000, Jones 2000, Johnsen 2009). Historical and ethnographic records of Indigenous management systems and beliefs highlight deliberate conservation measures that allowed returning salmon to pass weirs and reach upriver spawning areas, and strictly enforced rules that governed their use (Swezey and Heizer 1977, Berger 1982, Harris 2001, Ritchie and Anglebeck 2020). In many cases, multiple weir locations coexisted within a single river (Thomassen 1994, Harris 2001, Prince 2005), demanding cooperative management between numerous interconnected villages to ensure a mutually sustainable food supply. For example, salmon fishing on the lower mainstem Klamath River in Northern California was controlled by Yurok leaders who had been initiated into the role of overseeing weir construction and fishing. One weir, built each summer at Kepel during the height of the Chinook migration, was left open at night to allow unimpeded passage and was removed from the river after a period of 10 days, allowing the salmon to migrate freely into the territories of the upriver tribes on the Klamath and Trinity Rivers (Swezey and Heizer 1977). Weirs were therefore a primary instrument of precolonial adaptive management and fisheries governance.

In the Babine watershed a tributary of the Skeena River in BC, the Lake Babine Nation (LBN) practices ongoing salmon management and conservation. The watershed is the largest sockeye system in Canada (by area; Price and Connors 2014) and produces approximately 90% of Skeena River sockeye (Cox-Rogers and Spilsted 2012). Since time immemorial, LBN has managed and harvested Babine salmon using wood stake *k'oonze* (weirs) constructed at the outlet of Babine Lake (river kilometer [rkm] 96). The use of traditional weirs by LBN persisted into the early twentieth century, providing subsistence food resources and economic surplus to trade with nations in all directions (Fiske and Patrick 2000, Harris 2001). Matrilineal descent within clans determined resource allocation within LBN society and ensured that resource areas, including *k'oonze*, were managed sustainably (Earle and Ericson 1977, Bishop 1987, Rabnett 2000). Between 1904 and 1905, despite strong resistance, the weirs were forcibly removed by the federal government, disrupting thousands of years of Indigenous management of Babine salmon (Department of Marine and Fisheries 1905, Hackler 1958). In the years that followed, much conflict and disruption to LBN life has been documented, including extensive starvation among communities (Fiske and Patrick 2000).

Although Indigenous terminal fisheries were outlawed in the late nineteenth century, these technologies are currently undergoing a revival, with several examples of their reemergence informing our understandings of how they can be used in a modern context for monitoring and sustainable harvest. In 1946, the Department of Marine and Fisheries (now Fisheries and Oceans Canada) installed a weir at the outlet of Babine Lake to monitor the abundance of returning adult salmon (supplemental figure S1). Ironically, this weir closely resembled the traditional LBN weirs that spanned the entire width of the river, with multiple openings for fish passage. Since 2008, operations at the Lake Babine weir have been run by LBN, providing crucial data to support salmon management. Between 1965 and 1971, artificial spawning channels were added to two subbasins in the watershed by DFO, supporting additional spawning capacity in the Babine watershed (Ginetz 1977). Together, the weir and channels support terminal food, social, and ceremonial fisheries and commercial fisheries in years of abundant returns, creating sustainable local economic development opportunities for the nation and its communities. When Skeena River sockeye abundance is sufficient to trigger a commercial opening LBN members and other upriver nations conduct selective in-river commercial harvest. Likewise, when sockeye returns to Babine Lake exceed escapement goals, LBN conducts Excess of Salmon Spawning Requirements (ESSR) fisheries at the weir or at the mouths of the Fulton and Pinkut spawning channels (Fisheries and Oceans Canada 2019a). The reinstallation of the weir, including the data it generates to support management, and the employment, cultural wellbeing, and food security, and economic opportunity it provides to LBN, stands testament to the timeless ecological and cultural value of this traditional management system.

In 2013, the Haíłzaqv Nation revitalized traditional-style weir building in the lower Koeye River (rkm 3) to monitor returning sockeye abundance (figure S1; Atlas et al. 2017). Designs for the Koeye River weir were based on images in Stewart (1977). Archaeological and ethnographic evidence points to the use of weirs at larger creeks and rivers in Haíłzaqv territory including the Kunsoot, Neekas, and Kwakusdis Rivers (Carpenter et al. 2000, White 2006, HIRMD 2014). In the Haíłzaqv language the word *gvúláyu* refers to a fish trap made of saplings at the mouth of the

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Table 1. A glossary of terms.

Term	Definition
First Nations	Indigenous people in Canada who are not Inuit or Métis. There are 630 million First Nations and more than 1.5 million Indigenous Canadians.
First generation story	A story originating from the first generation of Indigenous peoples, such as creation stories.
Food, social, and ceremonial fisheries	First Nations fisheries that are constitutionally protected in Canada as an inherent right.
Indigenous peoples	People descended from the original precolonial inhabitants of a particular place on earth. Indigenous people maintain connection to the lands, cultural practices, and traditions of their ancestors, and remain distinct from the dominant societies in which they live.
Indigenous management	Management systems grounded in the worldviews and daily practices of Indigenous people.
Management system	The social and cultural processes that encode norms for the use of natural resources, including the technologies and understandings that underpin decision making Lertzman (2009).
Mixed-stock fishery	A fishery that captures salmon from many populations.
Reconciliation	A government-to-government process undertaken by Canadian and Indigenous nations to reconcile historical harms done by colonization and foster more equitable relationships into the future.
Selective fishery	A fishery that captures target species but allows for the live release—with minimal harm—of nontarget species.
Social–ecological system	A system composed of interconnected biological, social and economic, and governance components.
Terminal fishery	Fisheries that catch salmon returning to a single river, typically with minimal bycatch of fish from other rivers. These fisheries may be conducted in river or at the head of an inlet where the river enters the ocean.
Wild salmon	Salmon born and reared in their natural habitat. By contrast salmon of hatchery origin or raised in fish farms are not wild.

river, which is distinct from *ckvá*, a trap made of stones on the beach (Carpenter et al. 2000). First generation stories confirm the existence and importance of weirs in Haíłzaqv Territory. In the story of Cúmqlaqs, her son who was a supernatural carpenter, constructed the first salmon weir or trap in the lower reaches of the Tŋki River in Húỷát. This salmon weir or trap was created to nourish the first ancestors of the village T̓iásu in Húỷat (Boas 1932).

Despite evidence for their historical importance, there was no living memory of weir building among the Haíłzaqv when the Koeye weir project began in 2013, and in addition to population monitoring, the project has contributed to a revitalization of weir building among the Haíłzaqv people. About 500 sockeye are captured each year at the Koeye River weir and marked with PIT tags and visually identifiable tags for subsequent mark–recapture estimates of spawner abundance and survival to spawning (Atlas et al. 2020). In recent years the Haíłzaqv have also increasingly used the weir as a terminal fishing site for small-scale subsistence harvest, providing a few hundred sockeye annually for the community and youth at the Koeye River summer camp.

By fishing at the weir, Haíłzaqv managers can gauge the strength of the sockeye run in season and adjust harvest accordingly. Therefore, weirs offer a method to integrate monitoring and harvest. Given declines in productivity among BC sockeye populations (Peterman and Dorner 2012), high fuel costs, and mixed-stock harvest risks, this nascent community-run terminal fishery supports a cost-effective and risk-averse approach to harvesting sockeye for subsistence use (Steel 2020).

Fish traps. Like weirs, fish traps were widely used in traditional terminal fisheries (table 1, figure 1). Although many types of fish traps existed, stone fish traps built adjacent to river and creek mouths are a ubiquitous feature of the Northwest Coast intertidal landscape. From Washington State to Alaska, thousands of fish traps remain in estuaries of salmon-bearing streams, a living testament to the utility, durability and widespread application of stone fish traps (Langdon 2006, Menzies and Butler 2007, White 2011, Caldwell et al. 2012). These fish traps were built in numerous different configurations and shapes—depending on their location and target species—and were used for generations during the late summer and fall, because families and village groups visited seasonal camps to target specific salmon runs (White 2006, 2011). Typically, fish traps were built in river mouths and estuaries, although examples of in river traps have been documented (White 2006, Menzies and Butler 2007). In some instances, archaeological evidence suggests that both fish traps and weirs were used (Elroy White, Central Coast Archaeology, Bella Bella, BC/Canada, personal communication, 2 March 2020).

As salmon staging in the river mouth moved inshore with the tide they swam into the traps, and were captured as the tide ebbed, allowing fishers to harvest salmon and release those that were unwanted. Oral accounts from Haíłzaqv and other coastal Indigenous knowledge holders indicate selective harvesting of chum and pinks in more advanced states of maturation; their lower oil content made them suitable for smoking and long-term storage. Sockeye and coho were often eaten fresh (White 2006). Women led the smoking process, and supervised harvesting and fish selection (Jones 2000, White 2006). Trap walls were opened following harvest or during periods of inactivity to allow salmon to escape (Menzies and Butler 2007, White 2011).

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The assertion of colonial jurisdiction and law increasingly excluded Indigenous fishers from the use of fish traps and weirs by the late 1870s. As opportunities for subsistence livelihoods declined and the imposition of the cash economy drove Indigenous people into the cannery workforce, discriminatory laws enabled adoption of fish traps by European settlers in the late 1800s (Boxberger 1989, Newell 1993). Incorporating technological innovations from the Great Lakes region and Scandinavia, the first European salmon traps were constructed on the lower Columbia River beginning in 1879 (Collins 1888). These traps consisted of wood pilings and attached cotton or wire mesh, which were effective in passively corralling large numbers of returning adult salmon for harvest or release (Cobb 1921). Salmon remained free swimming within a fish trap and were rarely entangled, giving the gear a product–quality edge (Buschmann 1903). Having demonstrated considerable success in Columbia River salmon fisheries, commercial trapping rapidly expanded to in-river and coastal fisheries on the Washington coast, Puget Sound, BC, and Alaska between the 1880s and early 1900s (Collins 1888, Cobb 1921).

Despite the fish trap's potential for selective commercial harvest and sustainability in rivers and estuaries of western North America, colonial fisheries were mostly unregulated in the early twentieth century, and fish traps became a destructive force to wild salmon populations (Cobb 1921, Boxberger 1989). With unlimited entry among white settlers to commercial fisheries, fish traps (favored by large salmon canning corporations because of the gear's remarkable efficiency) contributed to rampant overharvest and insufficient escapement to salmon spawning grounds (Johnson et al. 1948, Boxberger 1989, Lichatowich 1999). Overharvest prevented Indigenous people in the United States and Canada from accessing the resource for subsistence (Boxberger 1989, Taylor 1999, Harris 2001). Fish traps were eventually banned from Oregon to Alaska between 1934 and 1959, primarily for political reasons and the gear's perceived contribution to salmon decline (Johnson et al. 1948, Higgs 1982, Arnold 2011).

In 2016, the nonprofit organization Wild Fish Conservancy initiated a collaborative experiment with lower Columbia River commercial fishers in Washington State to revive the fish trap and evaluate the feasibility of trap for selective harvest (figure S1). Many salmon populations in the Columbia Basin are listed under the US Endangered Species Act (ESA). However, there are also abundant hatchery-produced salmon, and selective fishing gears are needed to reduce impacts on ESA listed wild salmon and enable harvest of hatchery fish (WFWC 2013, Gayeski et al. 2018a, Tuohy et al. 2019). Results from the Columbia River have shown the potential of fish traps to support a transition to selective fisheries; nontarget species have high rates of postrelease survival (94%–100%) when the gear is operated with a conservation-minded approach and regulated appropriately (Tuohy et al. 2019, Tuohy et al. 2020).

There is interest in revitalizing fish trap technology for subsistence and commercial use in Canada. For example, the Lax Kw'alaams First Nation has proposed using a modern fish trap in the tidal waters of the lower Skeena River (WFC 2019). The Skeena River is the second largest salmon producing river in BC, but salmon populations have declined by 56%–99% in the last 100 years (Price et al. 2019), and mixed-stock harvest poses challenges to the sustainability of fisheries targeting larger stocks (Walters et al. 2008). These declines combined with uncertainty in preseason and in-season escapement forecasts, precautionary management and commercial fishery closures have severely affected food security and economic opportunity for Lax Kw'alaams and other Skeena First Nations. Historically, Lax Kw'alaams people used selective fishing methods widely, including intertidal fish traps, and managed salmon resources according to culturally defined stewardship principals and traditional laws (Smethurst 2014, Letham et al. 2015, Ministry of Justice 2016). Modern fish trap technology will allow for selective harvest, capturing fish alive with minimal harm and reducing bycatch mortality of nontarget stocks (supplemental table S2).

The Lax Kw'alaams fish trap pilot project will provide research and monitoring opportunities, support the Lax Kw'alaams food, social, and ceremonial fishery and potentially support development of a sustainable high-value fishery (Gayeski et al. 2018a, Tuohy et al. 2019). By enabling sampling of salmon populations from across the watershed, it will create a platform for the development of collaborative research with upriver nations, governments, and other partners. There is a critical need to improve long-term and in-season knowledge of abundance and run composition among Skeena River salmon (Walters et al. 2008). The proposed fish trap technology will provide monitoring opportunities for earlier and later season sampling across various tide stages and river levels with minimal bycatch mortality, thereby addressing key challenges associated with the current gillnet test fishery used for in-season escapement estimates in the Skeena River (Tyee Test Fishery; Walters et al. 2008).

Reef nets. Reef nets are a sophisticated fishing technology invented by Straits Salish peoples. They have been used in fisheries along the tidal marine approaches to major salmon rivers such as the Fraser and Cowichan in BC, and the Skagit and Nooksack in Washington State, where modest depths and high concentrations of migrating salmon enable reliable fishing (Easton 1990, Claxton 2015). The long leads of the net are anchored at their ends, tapering back in a funnel shape toward a central net that is fished between two boats. Migrating fish are observed from an upright position, or from a raised platform in many modern reef net vessels. When fish have entered the heart of the net the sides are raised into the adjoining boats allowing the fish to be harvested selectively or released. Despite being protected under treaty agreements, reef nets were outlawed in Canada in the early 1900s (Claxton 2015), and reef net sites used by Indigenous peoples were appropriated in Washington

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State to make way for commercial fish traps (Lummi Tribal Archives 1894).

Reef netting canoes were traditionally captained by individuals who held inherited rights to long-established reef netting locations. Sacred ceremonial rights accompanied initiation into the role, and reef nets were themselves sacred objects imbued with feminine life-giving qualities (Claxton 2015). The construction and use of reef nets was governed by the law and tradition of Straits Salish Indigenous peoples, and this technology was a major source of subsistence, wealth, and cultural stability for Straits Salish people in the precolonial era.

Today, reef nets are undergoing a renaissance among Indigenous and non-Indigenous fishers alike, because conservation concerns have increasingly necessitated selective harvest of abundant sockeye and pink salmon while limiting the impacts on ESA and the COSEWIC (Committee on the Status of Endangered Wildlife in Canada) listed populations of Chinook, coho, and steelhead in the Salish Sea. In 2013 the WSÁNEĆ Nation revived their reef net fishery in areas around the Saanich Peninsula on Vancouver Island in Southern BC (Claxton 2015). Likewise, in Washington Lhaq'temish (Lummi) fishers have partnered with distributors to market selectively harvested wild salmon as a value-added brand, and commercial reef net fishers have continued to operate reef nets in selective fisheries in the San Juan Islands, providing high quality, high value salmon for consumers. These fisheries exemplify the powerful transformations that can be achieved through the wider adoption of selective and terminal Indigenous fisheries, however the long-term viability of these fishing operations is threatened by ongoing declines in Fraser sockeye and the recent catastrophic impacts of the Big Bar slide on Upper Fraser salmon populations.

Seine nets. Numerous historical accounts document the widespread use of beach seines by Indigenous salmon fishers across the Northeast Pacific Rim. These nets, typically made from nettle fibers, spruce roots, or woven cedar bark, served as an indispensable tool for selective harvest (Stewart 1977). Stone seine weights have been found on the bottom of the Koeye River, and the remains of these nets are often found in archaeological excavations in wet sites in which the absence of oxygen slows decomposition of organic materials (e.g., Croes 1995). On the North and Central Coast of BC, seines were also used extensively during the smokehouse days in the first half of the twentieth century, when families would spend the fall season harvesting and processing fish at smokehouse camps (White 2006, Menzies and Butler 2007). In Southeast Alaska, small purse seines are still commonly used for subsistence fishing (Langdon 2015).

In watersheds in which nonselective mixed-stock fisheries pose conservation concerns, there are efforts to use beach seines and purse seines as tools for selective harvest. For example, the Confederated Tribes of the Colville Reservation began operating a purse seine for subsistence and commercial harvest, releasing ESA-listed steelhead and Chinook salmon, while harvesting marked hatchery fish (UCUT 2020). Similarly, First Nations on the Lower Fraser River in BC are evaluating and implementing selective harvest using beach seines to reduce bycatch impacts on endangered Upper Fraser coho stocks (Raby et al. 2014).

Dip nets. Dip netting is an ancient method of salmon harvesting, long practiced at specific locations where rapids, waterfalls and other constrictions facilitate use of the method. Very often, access rights to these locations are passed down through families who have used harvesting sites for generations. Perhaps the most famous example of the technology comes from Celilo Falls (rkm 302)—or *Wyam*, as it is called by the tribes of the Columbia Plateau—on the Middle Columbia River (figure S1). The falls were a major cultural site and gathering point for Native people who would fish for salmon in the rushing waters of the falls (Fisher 2004). With 15,000 years of human use, *Wyam* was among the oldest continuously occupied communities on the North American continent, which ended abruptly in 1957 when the construction of the Dalles Dam inundated the site. Among the tribes displaced from Celilo, dip net fisheries continue at many other locations in the Columbia River, including immediately below the Dalles Dam. Similarly, in BC dip net fisheries are important for the tribes of the Fraser Canyon (rkm 182 to 352). Prime dip net sites are often inherited and passed down through generations, and the tradition remains vibrant to this day despite years of harassment and arrest at the hands of fisheries officers during the twentieth century, and declining salmon returns in the Fraser (Harris 2001, Mack and Youngman 2020).

At Moricetown Falls on the Bulkley River (rkm 48), a major tributary of the Skeena River in BC, the Wet'suwet'en people have long harvested salmon using dip nets (Johnson Gottesfeld 1994). Since 1999, Wet'suwet'en Fisheries and Fisheries and Oceans Canada have worked collaboratively with fishers to monitor escapements of sockeye, coho, and steelhead in the Bulkley River. By seining and marking fish downstream of the falls and recapturing migrating fish in the traditional-dip net fishery at Moricetown, the nation and government partners are producing reliable mark–recapture estimates of abundance for these three culturally and economically important stocks (Gottesfeld et al. 2009). This project, which merges scientific mark–recapture with ongoing harvest and Indigenous management by the Wet'suwet'en is a powerful example of the opportunities that flow from linking traditional modes of harvest and management with scientific data collection.

Fish wheels. Fishwheels are an ancient fishing technology that Indigenous peoples have employed since precontact times (Cobb 1921, Menzies 2006). Originally constructed

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from cedar wood and nettle fiber mesh, fishwheels mounted on floating platforms that included multiple revolving baskets (typically two or three large, flat dip net-like vanes) designed to catch fish and carry them into submerged holding areas unharmed (Menzies 2006). Much like watermills, the mesh vanes of fishwheels were turned by the current and so were best suited to shallow and swift-moving waters (Snively and Corsiglia 2001). As the baskets rose upward out of the water, they scooped up fish (principally salmon) ascending the river, and as the fish slid down the vanes toward the horizontal axle of the cylindrical fishwheel, they encountered wooden baffles that guided them into the submerged baskets (Corsiglia and Snively 1997). There they would remain until released unharmed or retained for food. In the words of Nisga'a Sim'oogit (Chief) Eli Gosnell, "the flowing river kept salmon alive until they were either harvested or released; we always took only the fish we needed and no more" (quoted in Menzies 2006). Over the course of the twentieth century, however, fishwheels have been employed throughout the Pacific Northwest for commercial, subsistence, as well as research and monitoring purposes (Meehan 1961), and their extreme efficacy eventually led to their prohibition for commercial purposes across many jurisdictions (such as in the Columbia River in Washington and Oregon; Aguilar 2005).

One of the most renowned contemporary uses of this in-river fixed gear involves the Nisga'a Nation, the people of the Nass River in northern BC, who have combined this traditional technology—now made of aluminum and nylon mesh (Alexander and Link 2001)—with modern analytical methods for fish stock assessment and monitoring, producing higher quality data and generating more accurate predictions about the fishery than had been previously available (figure S1; Link and English 2000, Snively and Corsiglia 2001, King 2004). Since 1992, the Nisga'a Lisims Government's Fisheries and Wildlife Department has conducted extensive fisheries research on the Lower and Upper Nass River using multiple fishwheels as a platform for fish counting, measuring, tagging, releasing, and recapturing (Link and English 1998). The Nisga'a fishwheel program has enabled the monitoring of salmon escapement and harvest, the study of factors limiting salmon production, as well as the participation of Nisga'a citizens in the stewardship of the Nass River (Link and English 2000, Nisga'a Lisims Government 2019). This highly successful program provides yet another example of obtaining otherwise inaccessible insights through the coupled usage of ancient and contemporary technologies and practices.

Cultural resurgence

For generations, Indigenous people across western North America have actively sought to counteract the effects of colonial dispossession of their lands, and to assert their sovereignty (Harris 2001, Fisher 2004, Claxton and Price 2020). Today, Indigenous people are working to rebuild institutions that were decimated by colonization, and communities continue to revitalize cultural and institutional resilience through self-governance, land-based learning, and intergenerational knowledge sharing (e.g., Beveridge et al. 2020). Across Canada and the United States, Indigenous people are actively shaping the future of their communities and homelands, successfully protecting and recovering ecosystems for the benefit of human and nonhuman life (Housty et al. 2014, Schuster et al. 2019, Curran et al. 2020).

The ability to harvest traditional foods, tell stories and pass on stewardship knowledge is fundamental to Indigenous identity and wellbeing (Alfred 2009). This sharing of culture through harvest and stewardship strengthens and affirms connections to identity and place. Through the practice of cultural reciprocity, Indigenous peoples perpetuate the vibrancy of communities, families, and placed-based ways of life (Trosper 2002, Artelle et al. 2018, Claxton and Price 2020). Salmon are emblematic of those connections to place, supporting food security, cultural identities and wellness that goes beyond meeting nutritional needs.

Among Indigenous peoples of the Pacific Northwest, harvesting salmon is inseparable from stewardship. With thousands of fish traps, weirs, and midden across the Northwest Coast, the history and connection between people and salmon remains powerfully visible on the landscape (White 2006, Caldwell et al. 2012). The use of these traditional harvesting technologies has been dormant in many places for more than a century but remains in some locations despite the concerted efforts of colonial governments in the nineteenth and twentieth century to extinguish Indigenous rights (Harris 2001, Mack and Youngman 2020). By revitalizing Indigenous technologies and management systems communities are reconnecting salmon stewardship with harvest, Indigenizing education, and perpetuating culture through intergenerational knowledge transfer (e.g., Claxton 2015). In doing so, they are reawakening relationships to places and cultural practices that supported vibrant communities and healthy salmon returns since time immemorial. The long-term success of place-based salmon management depends on uplifting this holistic vision for community participation in stewardship and governance.

Reconciliation and a changing landscape of cogovernance in Canada

For many Indigenous people, colonization severed access to sustainable and socially just salmon fisheries. Generally, in Canada, access to fisheries resources was not granted to Indigenous nations from the government despite repeated requests (Harris 2001). This exclusion from fisheries resources and decision making drastically undermined traditional livelihoods and created food insecurity among First Nations people (Eckert et al. 2018, Lee et al. 2019). As a result, Indigenous peoples' ability to transmit the knowledge critical to traditional management of fisheries was harmed. In turn, the sustainability of salmon fisheries suffered as long-standing systems of Indigenous fishery management

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were replaced by industrial fishing fleets serving global markets (Higgs 1982, Newell 1993).

In addition to historic damage, contemporary salmon management policies have resulted in declining returns, further reducing First Nations' ability to perform a constitutionally guaranteed practice of harvesting salmon in Canada (*R v. Sparrow* 1 S.C.R. 1075 [1990]). Some settlements following litigation have resulted in financial compensation for a portion of these losses (e.g., *R v. Gladstone* 2 S.C.R. 723 [1996]), but rarely have the root causes of the damage—the imbalance of management authority between Indigenous people and the colonial state and the failures of current management systems—been addressed. To address these historic and ongoing injustices, colonial governments and First Nations are increasingly making agreements that contribute to reconciliation.

Effective resource management requires scientific, regulatory, political, and moral legitimacy (Pinkerton and John 2008), and new examples of fisheries reconciliation processes are emerging in Canada with the potential to strengthen the legitimacy of management frameworks. For example, Coastal First Nations, a group of nine nations in coastal BC, has recently negotiated a Fisheries Resources Reconciliation Agreement (FRRA) with Canada's Department of Fisheries and Oceans (CFN 2017). The agreement provides a process for participating nations to be true comanagers of fisheries, bringing together First Nations and DFO at regional tables and setting harvest management through a "strong collaboration" process. In addition, the participating nations will acquire commercial fishing licenses, and develop community-based commercial fisheries that support multispecies fisheries that are managed, permitted, and enforced under nation's fishing authority. This initiative will require access (licensing) reforms and has the goal of revitalizing local fleets and First Nations participation in fisheries. These agreements will likely make it easier to develop terminal harvest opportunities on the basis of observed in-season abundance.

Combined, these governance and policy advancements offer opportunities to support rebuilding salmon stocks and harvest in a socially just and sustainable manner. However, absent transformative changes in the modes of harvest and collaborative management processes for salmon, the opportunity presented by the FRRA may yield few benefits to communities. Although it is nonselective, mixed-stock fisheries remain the dominant mode of harvest, opportunities for sustainable salmon fisheries will very likely continue to dwindle under the weight of indiscriminate harvest of salmon populations and governance arrangements designed to enable extraction.

Returning to traditional scales and systems of management offers a positive step on the path of reconciliation. Although this process will not be the same for every nation, some likely commonalities and challenges emerge. First, depressed salmon stocks will need to be recovered to levels that enable long-term sustainable harvest opportunities. Second, expertise and interest in the use of terminal or selective fishing technologies will need to be rebuilt. Finally, fisheries managers will need to work with harvesters and community organizations to support implementation and management. In particular, revitalizing systems of contingent proprietorship whereby the individuals or groups interested in harvesting salmon are also responsible for monitoring escapement, managing fishery impacts, and redistributing some of their catch within their communities could empower local fishers or community organizations to help lead this transition (Greer 1993, Copes 2000, Johnsen 2009, Carothers 2011).

Finally, the reputation of many traditional fisheries technologies (e.g., weirs) have been tarnished by racist anti-Indigenous sentiment and legal frameworks, disrupting the transmission of cultural knowledge related to their use (Higgs 1982, Newell 1993, Harris 2001, Steel 2020). Correcting these harms requires that colonial management agencies acknowledge the efficacy of Indigenous salmon management and the harm that was done by banning these approaches. Thus far, the emergence of Indigenous leadership in monitoring and management of natural resources has been hindered by an imbalance of power in governance, and an unwillingness of governments to relinquish authority back to Indigenous communities (Thompson et al. 2020). By upholding the inherent rights of Indigenous people to manage natural resources within their ancestral territories and incorporating traditional knowledge and management systems into fishery management, colonial governments may begin to rectify that harm.

Biological realities, limitations and opportunities

The challenges facing salmon fisheries draw their origins in a multitude of historical and ongoing changes and are further compounded by the financial and logistical realities of managing salmon fisheries in remote regions of western North America. Climate change and habitat loss both pose existential threats to wild salmon populations, contributing disproportionately to their decline around the Pacific Rim (Lichatowich 1999, Gustafson et al. 2007, Katz et al. 2013). In recent decades wild salmon have experienced climate driven declines in survival at sea and in freshwater that have contributed to the collapse of many stocks that formerly supported major commercial fisheries (McKinnell et al. 2001, Peterman and Dorner 2012, Malick and Cox 2016). Declining abundance and productivity have led to lower sustainable harvest rates, limiting opportunities for commercial and subsistence fisheries (e.g., Fisheries and Oceans Canada 2019a). Marine heatwaves and drought are increasing in their frequency (Islam et al. 2017, Frölicher and Laufkötter 2018), causing acute short-term impacts on salmon survival (Rand et al. 2006, Daly et al. 2017). As anthropogenic climate change progresses, salmon returns are becoming more variable and less predictable (Grant et al. 2019).

Despite ongoing environmental changes and declining abundance, salmon populations remain resilient and often

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highly productive. In many cases, there are opportunities for sustainable harvest if fisheries can be downscaled to target specific healthy populations. In the face of growing uncertainty and unprecedented environmental changes, in-season monitoring to support adaptive management is essential, allowing fisheries to harvest during times of unexpected abundance and to reduce impacts when conservation warrants precaution (Mantua and Francis 2004, Schindler and Hilborn 2015). Fisheries targeting single stocks may be a particularly valuable management tool when the status of individual populations is variable and management resources are limited. In cases in which circumstances necessitate mixed-stock harvesting, reef nets, seine nets and fish traps—centuries old technologies with deep roots in western North America—are already enabling selective harvest. By allowing fishers to harvest abundant populations or hatchery-origin fish, and safely release nontarget species, these technologies hold the potential for much wider application in selective fisheries.

Fisheries targeting mixed and single stocks balance tradeoffs between conservation and harvest opportunity differently. In general, mixed-stock fisheries tend to produce larger and more stable catches through time (Nesbitt and Moore 2016, Freshwater et al. 2020). Paradoxically, the stability conferred by harvesting multiple populations comes at the cost to small or depressed populations that comigrate with larger more abundant populations, threatening the very biodiversity that underpins stable catches (Connors et al. 2020). In some notable instances, networks of locally interconnected terminal fisheries have alleviated conservation risks and produced stable harvest opportunities. The Bristol Bay sockeye fishery—the world's largest wild salmon fishery—is managed using terminal fishery openings targeting specific population groups that meet in-season escapement targets (Hilborn 2006, Schindler et al. 2010). Similarly, most traditional First Nations' fisheries targeted fish returning to a single population, but the impact of natural fluctuations in abundance were damped by social connections, and kin-based networks of sharing and redistribution across villages and family groups (Suttles 1968, Trosper 2002, Prince 2011). Therefore, rebuilding networks of terminal fisheries that couple harvest and monitoring could increase salmon fishing opportunities, generate in-season information on escapement, and reduce conservation risks, while supporting resilient portfolios of salmon harvest.

Conclusions

Approaches to harvest and governance that are grounded in Indigenous knowledge can promote selective fisheries, local leadership of monitoring and management, and more equitable fishing opportunity for Indigenous and non-Indigenous communities alike. Adopting approaches grounded in traditional Indigenous management systems can catalyze long-needed transformations in salmon fisheries toward locally sustainable fishing opportunities (Greer 1993, Pinkerton 1999, Healey 2009). Numerous contemporary and historical examples of community-run fisheries have demonstrated the potential for local governance to maintain productive fisheries (Pinkerton and Weinstein 1995, Leal 1998, Pinkerton and John 2008, Johnsen 2009, Bavinck et al. 2015), and a growing body of evidence suggests that by integrating traditional and local knowledge into monitoring and management, fisheries can achieve greater social–ecological resilience (Berkes 2003, Lee et al. 2019, Salomon et al. 2019). Reconnecting salmon harvesting with stock assessment using terminal and selective in-river fisheries can unify monitoring, management, and harvest under the umbrella of local management, and encourage fisher participation in resource stewardship. This would bolster the legitimacy and resilience of fisheries management by emphasizing the observations and values of local communities, generating much needed biological data, and supporting governance frameworks that empower local decision-making (Moller et al. 2004, Augerot and Smith 2010, Angel 2017, Thompson et al. 2019).

There is an urgent need to realign the scales of fisheries with biologically relevant scales (e.g., salmon populations or watersheds) to reduce conservation risks, create opportunities for sustainable harvest, and support salmon-dependent species and ecosystem processes (Healey 2009, Ward et al. 2009, Gayeski et al. 2018b, Freshwater et al. 2020, Walsh et al. 2020). However, realignment of harvest toward greater terminal or in-river harvest will be of limited benefit if mixed-stock harvest rates remain high and fish are intercepted before reaching terminal fisheries, and terminal fisheries are not a panacea for sustainability if in-river fisheries overharvest returning salmon (Freshwater et al. 2020). For many species, allocation decisions driven by the PST remain a hindrance to recovery and limit the potential for transformation toward more locally managed fisheries. Therefore, mixed-stock ocean fisheries will likely need to forgo some harvest opportunity if the biological and social benefits of terminal and selective fisheries are to be realized (Connors et al. 2020). Including Indigenous people and local communities in future PST negotiations will therefore be essential, so that management of Pacific salmon fisheries can reflect their needs, aspirations, and understandings.

In the absence of transformation, salmon managers will continue to face a set of wicked tradeoffs posed by mixed-stock fisheries, where harvesting abundant salmon contributes to the long-term erosion of the biodiversity that underpins future fishing opportunity (Connors et al. 2020). Fortunately, solutions to these problems are not out of reach, and there is growing momentum toward transformative changes in the way that salmon are caught and managed. From weir and seine fisheries in Babine Lake, and nascent trap fisheries on the lower Columbia and Skeena Rivers, to selective reef net fisheries in the Salish Sea, these examples create growing momentum toward the revival of Indigenous harvest technologies that supported sustainable fisheries management over thousands of years.

We suggest that Indigenous salmon management practices offer lessons and options for fostering resilient salmon

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fisheries as socioecological systems. Salmon possess biological traits that confer a remarkable ability to cope and recover from change (Waples et al. 2008, Healey 2009, Schindler et al. 2010). However, salmon are a part of a rapidly evolving socioecological system that has, at times, shown low resilience as evidenced by collapsed populations and fisheries (Gustafson et al. 2007, Bottom et al. 2009, Walters et al. 2019). Stories of Indigenous mismanagement or periods of scarcity, and contemporary examples of dysfunctional cogovernance do suggest the importance of not overeulogizing Indigenous management. However, from an empirical perspective, Indigenous salmon fisheries persisted for thousands of years, which speaks to their overall long-term resilience (e.g., Cannon and Yang 2006, Campbell and Butler 2010). Indigenous salmon management systems exhibit many of the principles that can promote resilience in social–ecological systems (Biggs et al. 2015). For instance, by fishing and managing at the scale of a single river traditional fisheries maintained biological diversity and limited the geographic scope of harvest impacts, garnered broad participation, and created diverse interconnected systems of governance. Indigenous fishery management is also grounded in multigenerational understanding of the links between salmon, people, and ecosystems, promoting adaptive learning that has fostered resilient human–salmon relationships for thousands of years.

Amid rapid and deep-rooted changes in ecosystems and fisheries, 10,000 years of Indigenous stewardship knowledge and growing scientific consensus tell us that revitalizing Indigenous systems of harvest and resource governance should be an urgent priority. Broader application of terminal and selective fishing technologies can help rebuild resilient locally managed salmon fisheries, and in doing so contribute to long-needed shifts in the balance of power, legitimacy, and opportunity in salmon fisheries. With humility and in a spirit of collaboration let us work together to bringing the story of salmon fisheries full circle, supporting the revitalization of Indigenous management systems that formerly supported sustainable fisheries for millennia. In doing so we will move closer to a goal shared by many Pacific Northwesterners; that wild salmon remain at the foundation of North Pacific cultures and ecosystems for generations to come.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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Marine heatwaves exacerbate climate change impacts for fisheries in the northeast Pacific

William W. L. Cheung[1*] & Thomas L. Frölicher[2,3]

Marine heatwaves (MHWs) have occurred in all ocean basins with severe negative impacts on coastal and ocean ecosystems. The northeast Pacific 2013–2015 MHW in particular received major societal concerns. Yet, our knowledge about how MHWs impact fish stocks is limited. Here, we combine outputs from a large ensemble simulation of an Earth system model with a fish impact model to simulate responses of major northeast Pacific fish stocks to MHWs. We show that MHWs cause biomass decrease and shifts in biogeography of fish stocks that are at least four times faster and bigger in magnitude than the effects of decadal-scale mean changes throughout the 21st century. With MHWs, we project a doubling of impact levels by 2050 amongst the most important fisheries species over previous assessments that focus only on long-term climate change. Our results underscore the additional challenges from MHWs for fisheries and their management under climate change.

Marine heatwaves (MHWs) - persistent extremely warm ocean temperatures - are already impacting ecosystems worldwide[1–5]. Impacts from MHWs include range shifts of marine fishes and invertebrates[6–9], bleaching of coral reefs[2], mass mortality of kelp forest[4,10] and other coastal vegetation[11] and reduction in reproductive success and survivorship of marine animals[12]. Long-term ocean warming since the early 20th century due to human-induced increase in greenhouse emissions has led to widespread increases in MHW frequency, intensity and duration[13]. Globally, the frequency of MHWs has been doubled since 1982[14], and is projected to increase further under continued global warming[5,14,15].

In 2013, a large MHW in the northeast Pacific appeared off the coast of Alaska and subsequently expanded south to Baja California. Th s specific MHW, commonly known as the "Blob"[16], persisted through to the end of 2015 and was the largest MHW globally since 1982[17] with sea surface temperature (SST) anomalies of over 6 °C. Th s warm Blob affected ecosystems from the California Current in the South to the Gulf of Alaska and the Bering Sea in the North[9,18–20]. The anomalously high temperature enhanced the stratifi ation of the upper ocean, leading to a decrease in nutrient supply to the surface ocean and causing a decrease in net primary production and community production[21,22]. Observational studies have reported ecological changes in the Northeast Pacific region, such as shifts in the horizontal and vertical distributions of marine species[8,19], as well as changes in pelagic micronekton and macrozooplankton communities and their species richness[18,23]. Such changes impacted also human activities such as fisheries[19]. Towards the end of 2019, a new MHW has emerged in the North Pacifi [24], raising concerns that a similar MHW as the Blob in 2013–2015 may reappear in the near future. Due to the already low numbers of Pacific cod (*Gadus macrocephalus*) and the potential reappearance of the Blob, the United States' federal cod fishery in the Gulf of Alaska closed for the 2020 season as a precautionary measure[25]. Th fisheries closure underscores the potential high impacts of such MHWs not only on marine ecosystems, but also on social-economic systems such as fisheries.

Simulating ecological changes of fish stocks and fisheries using modelling approaches can help elucidate and attribute the relative contribution of MHWs to observed changes in ecosystems[26] and assess future ecological risks under alternative scenarios of climate change[27]. However, projections of ecological impacts of MHWs have focused mainly on sensitive biogenic habitats such as coral reefs and intertidal systems[28,29]. In contrast, previous impact assessments on fish stocks and fisheries focused mainly on decadal-scale changes in mean conditions under climate change while the additional impacts of MHWs are more uncertain. Improved understanding of

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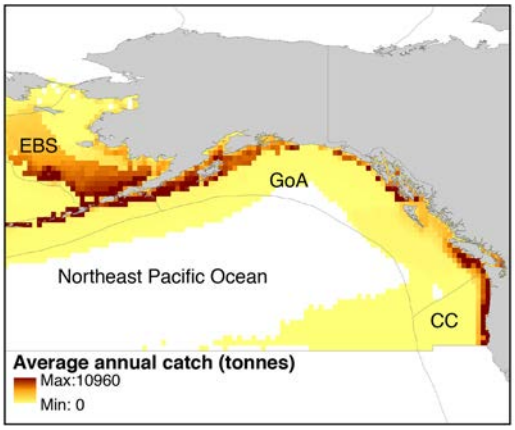


Figure 1. Average annual fisheries catches of the 22 studied fish stocks from 1981 to 2015 in the northeast Pacific Ocean and the three large marine ecosystems therein. Catches data were obtained from the Sea Around Us fisheries database (www.seaaroundus.org)[55]. The boundary of the northeast Pacific Ocean is based on the United Nations' Food and Agriculture Organization Statistical Area 67. The large marine ecosystems include: EBS - Eastern Bering Sea, GoA - Gulf of Alaska, and CC - California Current.

the futures of living marine resources will help inform dependent human communities, sectors and governance institutions to develop more effective climate-adaptation and risk-reduction measures.

Here, we aim to test the hypotheses that MHWs will add to the impacts of changes in mean ocean conditions under climate change, leading to additional anomalous shifts in biomass, distribution and potential catches of fish stocks in the northeast Pacific regions. Previous studies have applied species distribution models to project the effects of changing long-term mean ocean conditions on spatial distribution, abundance, community structure and the potential biomass production of fishes and invertebrates in this region[27,30,31]. In this study, we extend such modelling approaches to examine the consequences of MHWs on fish stocks and fisheries. Our analysis focused on the northeast Pacific Ocean and the Large Marine Ecosystems (LMEs) therein where most fishing took place (Fig. 1). We used the United Nations' Food and Agriculture Organization (FAO) Statistical Area (Area 67) to delineate the northeast Pacific region. Th s region includes three LMEs[32]: (a) Eastern Bering Sea, (b) Gulf of Alaska and (c) California Current. We examine the additional risk of MHWs on fish distribution[biomass] and and potential fisheries catches and explore whether and how the projected impacts of MHWs add to the decadal scale changes in mean ocean conditions. We also discuss the implications of the fi dings for ecosystem-based fisheries management.

We analyzed projected changes in annual mean Sea Surface Temperature (SST) in the northeast Pacific Ocean using a 10-member ensemble simulation of the Earth system model version 2 developed at the Geophysical Fluid Dynamics Laboratory (GFDL ESM2M[33–35]; see Materials and Methods). Each ensemble simulation was run over the 1950–2100 period under the same external forcing of historical changes before 2005 and Representative Concentration Pathway 8.5 (RCP8.5) thereafter. The RCP8.5 scenario represents a pathway of greenhouse gas concentrations for which radiative forcing reaches approximately 8.5 Wm^{-2} by 2100. We simulated changes in abundance and distributions of exploited fish stocks that are highly important to fisheries in the northeast Pacific region (Fig. 1) We included a total of 22 fish species that were reported in the fisheries statistics in the northeast Pacific region (www.seaaroundus.org). These species were important to fisheries in this region as they contributed up to 80% of the total observed catches from 2006 to 2015 (www.seaaroundus.org). We used the dynamic bioclimate envelope model (DBEM)[36,37], which is a spatially-explicit species distribution-population dynamic model, to simulate dynamical changes in biomass, and potential fisheries catch for each species on a 0.5° latitude × 0.5° longitude grid of the world ocean (see Methods for details). To identify MHWs, we calculated anomalies between the annual mean SST simulated by each of the individual 10 ensemble members and the ensemble-averaged SST (Fig. 2). We calculated four impact indicators to examine the ecological responses of fish stocks and their implications for fisheries during a MHW. These indicators are: (1) total biomass, (2) latitudinal centroid (average of the coordinates of grid cell weighted by the species' biomass), (3) depth centroid (average of bathymetry of grid cell weighted by the species' biomass), and (4) maximum catch potential [catch at fish stock-specific fishing mortality rate (F) that achieves maximum sustainable yield (MSY) i.e., $F = F_{MSY}$].

Results

We identifi d amongst the ten ensemble member simulations in total 149 MHWs in any of the three LMEs from 1981 to 2100. During these MHWs, the SST anomalies (i.e. mean annual intensity) are on average 0.99 °C (5^{th} to 95^{th} percentile = 0.55–1.49 °C) higher than the ensemble-mean SST (Fig. 3A). In comparison, the simulated average rate of SST change across the LMEs is 0.23 ± 0.04 °C (standard deviation) per decade (Fig. 3B). Thus, the average MHW SST anomalies, which are estimated annually, are about four times the mean warming per decade in the northeast Pacific LMEs. The intensity of MHWs is higher in the high latitude LMEs, i.e., Eastern Bering Sea and Gulf of Alaska, relative to that in California Current (Fig. 3A), because the SST variability is larger in Eastern Bering Sea and Gulf of Alaska than in California Current. Since we focused on annual means in SST, the modeled SST anomalies in all three LMEs are in general smaller than the observed peak SST anomalies during the Blob.

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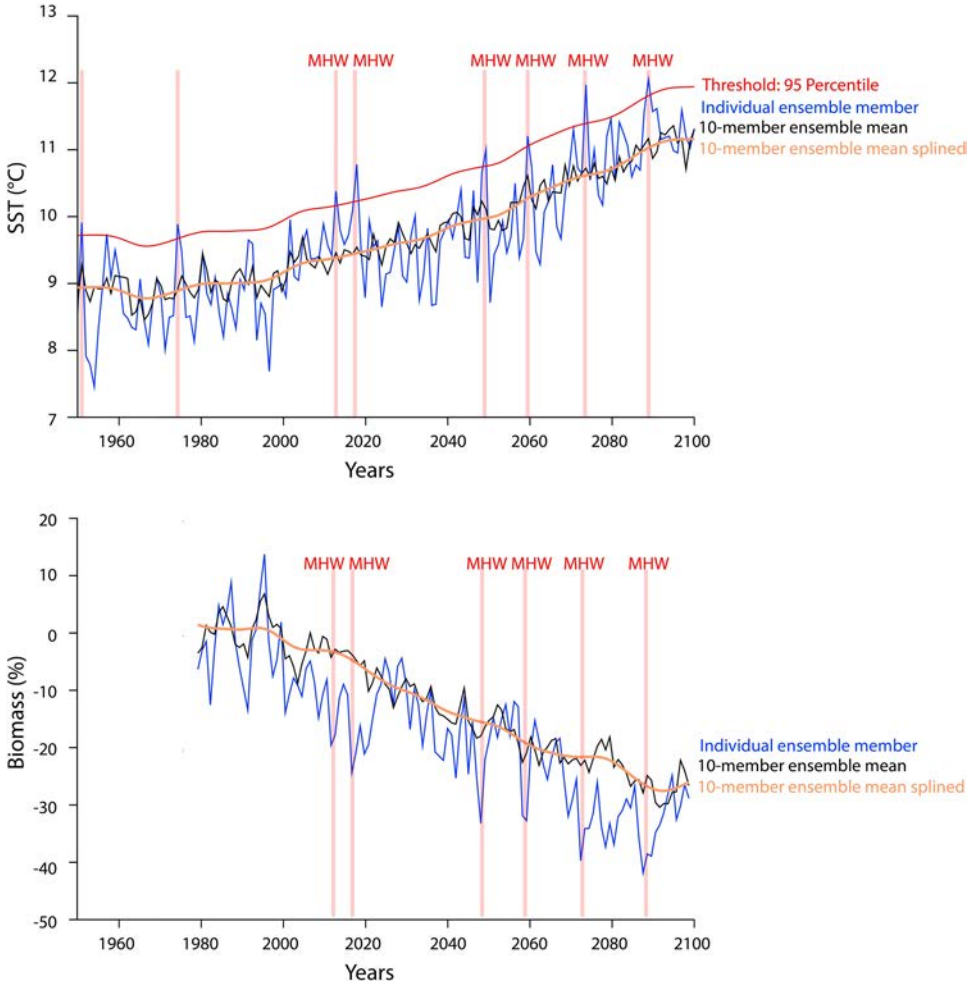


Figure 2. Schematic diagram explaining the characterization of Marine Heatwaves (MHWs) and their impacts on fish stocks. (**a**) The characterization of MHWs based on outputs from the 10 ensemble member projections of the GFDL ESM2M and (**b**) their impacts on biomass of the sockeye salmon (*Oncorhynchus nerka*) in the Gulf of Alaska large marine ecosystem. The red vertical bars in both panels indicate MHW events. Biomass changes are given as changes relative to 1986 to 2005.

The biomass of the 22 exploited fish stocks in the three northeast Pacific LMEs was projected to decrease by a median of −2.8% (5^{th} to 95^{th} percentile = −17.1 to 0.4%) during MHW events (Fig. 3C), with maximum decreases of up to 20%. Changes in maximum catch potential levels were almost the same as changes in biomass (Fig. S4–6). The biomass (and maximum catch potential levels; not shown) of almost all fishes in the California Current fish stocks were lower during MHWs for the majority of the fish stocks (median = −4.0%, 5th to 95th percentile from −18.3 to 0.0%). The direction of impacts of MHW on fish stock biomass in the Eastern Bering Sea (−0.8%, from −11.7 to 1.1%) and Gulf of Alaska (−3.0%, from −14.5 to 0.2%) were slightly more variable. These general decreases in biomass during MHWs added to the long-term climate change-induced changes in biomass. The decadal mean changes in biomass were projected to be more variable in the direction of changes than changes during the MHWs years across the LMEs (Fig. 3D). For the species with negative responses during MHWs, the decreases in biomass during MHWs were several factors higher than the rate of biomass decrease per decade from 1981 to 2100 under RCP8.5.

We also projected signature of MHWs on the biogeography of exploited fish stocks in the northeast Pacifi (Figs. 3E,G). 70% of the fish stocks showed a poleward shift in the latitudinal distribution centroids during MHWs (Fig. 3E). The direction of shifts in the Gulf of Alaska were projected to be more variable across species (median = −0.76 km, 5th to 95th percentile from −7.6 to 19.9 km) than those in Eastern Bering Sea and California Current, with around half of the species shifting southward. On average, fish assemblages in Eastern Bering Sea and California Current were projected to shift poleward at a rate of 9.5 km (−4.0 to 23.9 km) and 5.8 km (−5.1 to 22.0 km) per year, respectively, for each MHW event, with maximum shifts of over 30 km relative to the mean distribution. The pattern and magnitude of the latitudinal shifts of the fish assemblages were similar to the average decadal-scale shifts under climate change (Fig. 3F). Bathymetric shifts with MHWs were projected to vary more substantially across the stock-ensemble members, particularly in Eastern Bering Sea (−0.8, −6.7 to 24.1 m) and California Current (−4.1, −14.4 to 26.1 m) compared to Gulf of Alaska (1.6, −16.1 to 8.1 m); note

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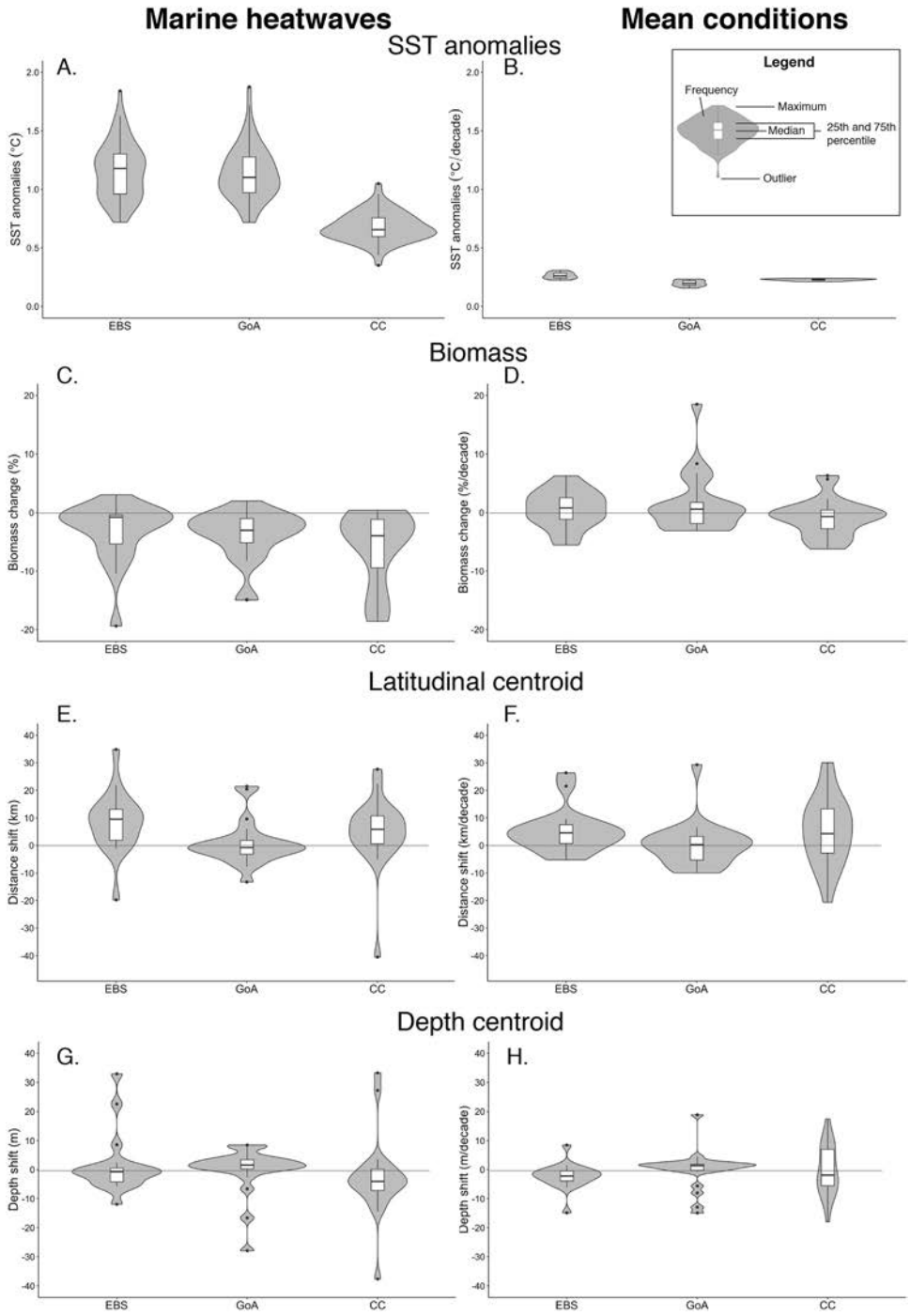


Figure 3. Projected changes in sea surface temperature (**A**,**B**) and the impact indicators (biomass, latitudinal centroid and depth centroid; **C**–**H**) of the 22 studied fish stocks in the three large marine ecosystems (Eastern Bering Sea - EBS, Gulf of Alaska - GoA, California Current - CC) of the northeast Pacific during MHWs (left panels) and due to long-term climate change from 1981 to 2100 (right panels). Changes in sea surface temperature and impact indicators during MHWs were expressed relative to the spline-smoothed ensemble-mean of the same time period. In contrast, long-term climate changes were calculated from linear regressions over the 1981–2100 period, with the rate of change (slope of the regression) expressed as change per decade. Negative depth centroid shifts in G-H indicate species' average distribution that were projected to be deeper.

negative values indicate shift to deeper waters). The pattern of shifts in depth centroids of fish assemblages were generally consistent between MHWs and long-term decadal-scale mean changes (Fig. 3G,H).

Amongst the 22 fishes, pelagic fish were projected to be most negatively impacted by MHWs, followed by Pacific salmon and groundfish (Fig. 4). Overall, almost all the studied pelagic fish showed signifi ant decrease in

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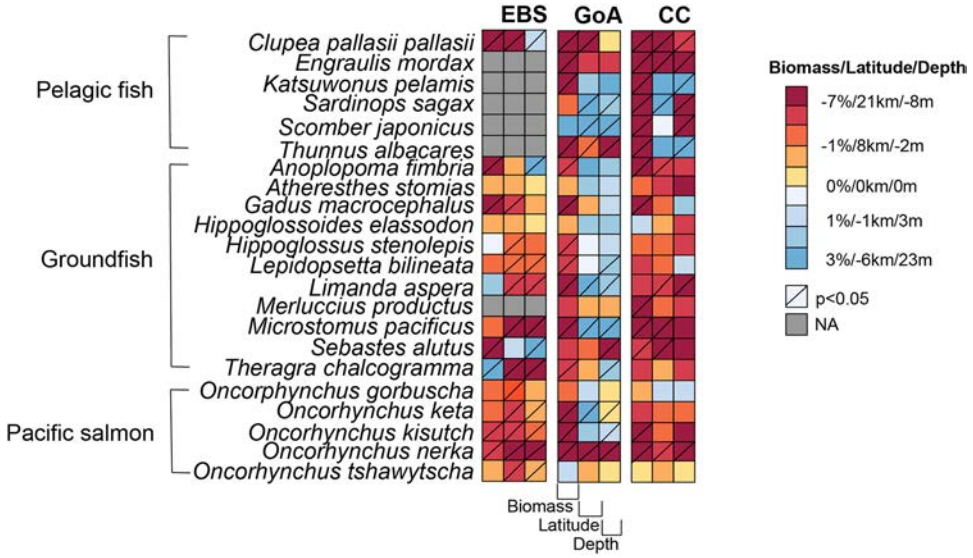


Figure 4. Projected mean changes in biomass, latitudinal and depth centroid of the 22 exploited marine fish stocks in the Eastern Bering Sea (EBS), Gulf of Alaska (GoA) and California Current (CC) during MHW years. NA - not available in catch record between 2006 and 2015.The different colour scales represent the projected changes in biomass, latitudinal centroid and depth centroid. Stripping of a cell represents changes at a signifi ant level of below 0.05.

biomass (more than 7%) under MHWs relative to the mean conditions, except Pacific sardine (*Sardinops sagax*) and Japanese mackerel (*Scomber japonicus*) that did not show signifi ant changes in Gulf of Alaska. Amongst the five studied Pacific salmon species, biomass of sockeye salmon (*Oncorhynchus nerka*) decreased most substantially and most consistently across LMEs under MHWs, followed by coho salmon (*O. Kisutch)*. For groundfish, biomass of Pacific cod (*Gadus macrocephalus*), sablefish *(Anoplopoma fimbria*) and Pacific ocean perch (*Sebastes alutus*) were projected to decrease signifi antly under MHWs in all LMEs. Only Alaska pollock in the Eastern Bering Sea increased signifi antly in biomass under MHWs amongst all the 22 species and LMEs.

For MHW impacts on species' biogeography, the distribution centroids of Pacific hering (*Clupea pallasii pallasii*) and sockeye salmon were projected to shift poleward in all three LMEs (Fig. 4). More fish stocks in Gulf of Alaska than in Eastern Bering Sea or California Current shifted signifi antly equatorward, or in variable directions amongst ensemble members under MHWs. Direction of shifts in depth centroid also often differed between LMEs for the same species. For example, Pacific Dover sole (*Microstomus pacificus*) was projected to shift poleward in Eastern Bering Sea and California Current, but equatorward in Gulf of Alaska and to deeper waters in Eastern Bering Sea, while shifted shallower in Gulf of Alaska (Fig. 4).

We chose Pacific cod, sockeye salmon and Californian anchovy that were of particular interest to fisheries and coastal communities in the northeast Pacific region to highlight how MHWs will exacerbate impacts from long-term climate change (Fig. 5). Firstly, these species will experience ocean warming as a result of both the mean increase in SST under RCP8.5 as well MHWs (Fig. 5A–C). Th s will greatly exacerbate the warming hazards to these species. Secondly, biomass of these three fish stocks dropped approximately 5% for Pacific cod in Eastern Bering Sea to 30% for sockeye salmon in Gulf of Alaska and California anchovy in California Current during MHWs in addition to the decrease due to long-term mean changes under RCP8.5 (5%, 25% and 10% by 2100 relative to 2000; Fig. 5D–F). Similarly, shifts in biogeography, as indicated by the latitudinal centroids of the three selected species (Fig. 5G–I), added to the effects of the shifts due to changes in mean ocean conditions by as much as 100 km poleward during MHWs (e.g., California anchovy in California Current). As such, biomass decrease and biogeographic shifts during MHWs early in the 21st century were projected to be at a similar level as the decadal-scale average changes by around the 2050 s. This also means that MWHs will exert large impact 'shocks' while fish stocks are already impacted by long-term mean climate change. For example, with both MHWs and changes in mean conditions, biomass of sockeye salmon was projected to drop by more than 40% by 2100 relative to 2000 under RCP8.5.

Discussion

Our fi dings provide theoretical support to the empirical observations from scientific surveys and anecdotal accounts from fishers that fisheries important fish stocks such as Pacific cod and sockeye salmon had been impacted by the 2013–2015 northeast Pacific MHW[19]. In addition, we offer new insights into the combined impacts of MHWs and long-term climate change on the species distribution in the northeast Pacific. Specifi ally, we show that MHWs can more than double the magnitude of the impacts on fish stocks by 2050 due to long-term climate change. Previous vulnerability and impact assessments have therefore greatly underestimated the risk to future fish stocks and fisheries in the northeast Pacific under climate change.

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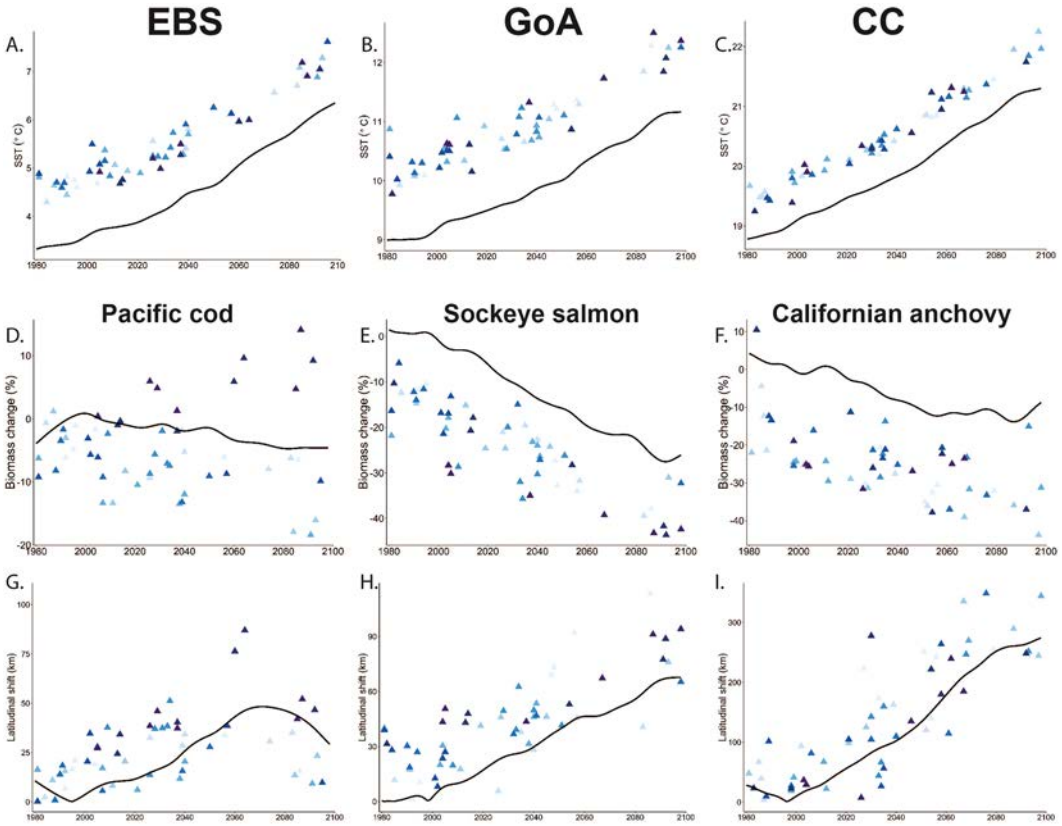


Figure 5. Projected time-series of changes in sea surface temperature (SST) (**A**–**C**), biomass (**D**–**F**) and latitudinal centroid (**G**–**I**): Pacific cod (*Gadus macrocephalus*) (**D**,**G**), sockeye salmon (*Oncorhynchus nerka*) (**E**,**H**) and Californian anchovy (*Engraulis mordax*) (**F**,**I**)) in the Eastern Bering Sea (EBS), Gulf of Alaska (GoA) and California Current (CC). The solid lines represent the average values across the 10 ensemble member simulations (smoothed with a cubic spline function); blue-colored triangles represent values during MHW years; the different intensity of blue color represents different ensemble member simulations (see Figs. S1–12 for results for all the large marine ecosystems and studied fish stocks).

Some fish stocks had already showed changes in biogeography during the recent Blob that are similar to the MHW impacts projected in this study. In Gulf of Alaska, analysis using data collected from scientific surveys showed that some groundfish species such as Pacific cod had shifted their distributions to deeper waters during anomalous warm temperature[8,9]. However, the directions of biogeographic shifts varied between species and across their life stages. Such shifts also differed between sub-regions due to different oceanographic conditions and bathymetric profiles[8]. These oceanographic and biological complexities could contribute to the large variability of our projected biogeographic shifts for groundfish between ensemble members.

Although shifts in biogeography associated with the Blob are more widely reported in literature[19], our results show that biomass decreases are more consistent in response to MHWs in the northeast Pacific relative to biogeographic shifts. Therefore, biomass of fish stocks may be a better impact indicator in detecting and assessing the impacts of MHWs as part of ecosystem-based management. However, as the magnitude of the projected biomass decrease and biogeographic shifts varied between species in our study, different sets of impact indicators that are species-specific can be used to more effici tly monitor and assess the impacts of MHWs.

The characteristic of the MHW impacts will result in a different set of challenges for management and conservation of living marine resources than those associated with the long-term mean change in climate. The rate of changes in biomass, potential catches and biogeography of fish stocks are much higher under MHWs than under long-term climate change. For example, in the California Current, Pacific sardine and California anchovy population are observed to show alternations of their abundance that are partly driven by changes in oceanographic regimes in the Pacific Ocean[38,39]. Particularly, warm regimes tend to favor sardine's recruitment and abundance while cool regimes favor anchovy. Thus, under decade-scale mean ocean warming, sardine was projected to increase in biomass while the opposite was projected for anchovy in the California Current. In contrast, poleward range expansion of sardine and anchovy was projected to result in long-term increase in their abundance in the Gulf of Alaska. However, the projected short-term rapid warming under MHWs pushed environmental temperature beyond those preferred by both sardine and anchovy, leading to a drop in their biomasses in both the California Current and Gulf of Alaska. Moreover, satellite data and model simulations suggest that MHWs are linked to and can be exacerbated by, multi-annual climate variability such as El Niño Southern Oscillation (ENSO), resulting in the particularly large and persistent biological impacts in the Northeast Pacific region from the Blob[13,19,40]. In any case, these complex biological responses of sardine and anchovy that inter-mixed between

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the effects of MHWs and decadal-scale warming therefore demand more rapid and short-term governance and adaptation responses such as alteration of fishing quota, shifts in fishing ground and targeted species[41]. The challenges from MHWs impact will thus put 'double strains' on sustainable management of living marine resources under climate change, pointing to the need for future research into the development of more robust adaptation and governance responses[42,43]. Previous studies have shown that global warming substantially increases the risks of MHWs to occur[14]. Our study additionally suggests that MHWs can strongly exacerbate the impact of decadal-scale mean ocean warming on fish stocks. A reduction of anthropogenic greenhouse gas emissions - the fundamental driver of global warming[44] – is therefore needed to limit the impacts of MHWs on fish stocks and fisheries[5].

Even though we consider the projected pattern of MHW impacts on fish stocks and the implications for understanding future risks on fisheries and their governance under climate change as robust, a number of caveats needs to be discussed. The global Earth system model used in this study (i.e. GFDL ESM2M) is able to adequately simulate mean states and trends in different marine heatwave metrics over the satellite 1982–2016 period[14]. However, the horizontal resolution (about 1°) of the ocean component of the Earth system model is too coarse to accurately represent some of the oceanographic dynamics in coastal and shelf seas such as upwelling or mesoscale eddy activity e.g.[45]. In addition, some of the biogeochemical processes in the high latitudes associated with sea ice are also not well resolved. The simulated net primary productivity in GFDL ESM2M, in particular, is highly uncertain[46], especially in regions with sea ice[47], because nutrient inputs during sea ice melt[48] or through rivers[49] are not included. The fish stock model assumes that historical species' biogeography refl cts their environmental niches[50]. Variations in the projected pathways of changes in biomass and biogeography of species in this study were partly caused by the differences in species' temperature preferences calculated from different Earth system model ensemble members e.g., the increase in biomass under MHWs for Pacific cod in one of the ensemble members (dark purple diamonds in Fig. 5G). The fish stock model also did not account for interspecific interactions or evolutionary adaptation to epigenetic responses to environmental changes[51]. For instance, we projected a positive impact of MHWs on Alaskan pollock (*T. chalcogramma*) in Eastern Bering Sea. However, previous studies have suggested that anomalous warm temperature affects the availability of preferred nutritious prey that reduced the survivorship and recruitment of pollock in the Bering Sea[19]. Moreover, we only examined climate projections following the 'no mitigation' high greenhouse gas emissions scenario (RCP8.5) and including an 'idealized' fishing scenario i.e., assuming all fishing is at level to achieve maximum sustainable yield of each fish stock. The effects of scenario uncertainties associated with different greenhouse gas emission and pathways of fishing effort and their management on the impacts of MHWs on marine ecosystems need to be explored further. Future research can build on the foundation laid by this study to incrementally address these uncertainties[52]. For example, the number of ensemble members, Earth system models and fish models may be increased to explore a wider range of model uncertainties. The analysis can also be repeated using high resolution Earth system models, and fish models with trophic interactions and/or eco-evolutionary dynamics.

Overall, this study underscores the importance of considering MHWs in assessing climate risks and impacts. Previous risk and impact assessment that focused on the effects of long-term changes in mean conditions under climate change may have largely underestimated climate risks on fish stocks and fisheries. Moreover, the rapid rate of change and the prevalence of impacts across fisheries important fish stocks in the northeast Pacific point to the need to examine whether climate adaptation, designed mostly for dealing with long-term mean changes, would be sufficient to reduce the additional climate risks from MHWs. Without appropriate mitigation and adaptation measures, MHWs may pose additional risks on the long-term viability of marine species and the sustainability of their fisheries, and the associated benefits to dependent human communities such as food, economic benefits and livelihoods[11]. Our results also provide a foundation for further modelling efforts and analysis to build on and systematically explore different dimensions of uncertainties.

Methods

Earth system model. We analyzed projected changes in annual mean SST in the northeast Pacific Ocean using a 10-member ensemble simulation of the Earth system model version 2 developed at the Geophysical Fluid Dynamics Laboratory (GFDL ESM2M[33–35]). The GFDL ESM2M is a fully coupled carbon cycle-climate model that consists of an ocean, atmosphere, sea ice, and land model, and includes land and ocean biogeochemistry. The nominal horizontal resolution of the ocean component is about 1° latitude × 1° longitude with 50 vertical levels[53].

Each ensemble simulation is run over the 1950–2100 period under the same external forcing of historical changes before 2005 and Representative Concentration Pathway 8.5 (RCP8.5) afterwards. The RCP8.5 is a high greenhouse gas emission scenario[54] that leads to a global atmospheric surface warming in ESM2M of 3.2 °C by 2081–2100 relative to preindustrial. All 10 ensemble members are run under the same external radiative forcing scenario, but are started from different initial conditions in January 1st of 1950. Spread in the ensemble members is generated by slightly perturbing the initial state of the Earth system at the start of each simulation. These initial perturbations cause each ensemble member to have a unique atmosphere and ocean state at each point in time, i.e. a different state of internal variability. As a specific example, the real ocean experienced an El Niño in 1997–1998. In the model, ensembles may have had a La Niña, El Niño or been neutral at this time.

Dynamic bioclimate envelope model. We simulated changes in abundance and distributions of 22 exploited fish stocks that are highly important to fisheries in the northeast Pacific region using the dynamic bioclimate envelope model (DBEM)[36,37]. The DBEM is a spatially-explicit biomass dynamic model. It is driven by changes in ocean conditions that are obtained from the Earth system model simulations described above. Variables of ocean conditions include temperature, dissolved oxygen concentration, salinity, sea ice extent, surface advection and net primary production. Variables for surface and bottom were applied to model pelagic and demersal species, respectively. The DBEM model simulates changes in annual average biomass and catch potential

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of marine fishes and invertebrates on a 0.5° latitude × 0.5° longitude grid of the world ocean. Movement of adults and pelagic larvae is calculated by sets of advection and diffusion equations with diffusion rates vary according to gradients of environmental suitability for each modelled species and ocean currents[36]. Fishing mortality (F) was set at the level to achieve maximum sustainable yield (MSY). The projected annual catch for each species is hereafter termed maximum catch potential.

Identifying MHWs in the northeast Pacific. To identify MHWs, we calculated anomalies between the SST simulated by each of the individual 10 ensemble members and the ensemble-averaged SST (Fig. 2). First, for each ensemble member simulation, we calculated the annual average SST in each of the three LMEs within the northeast Pacific region (as defi ed in Fig. 1) from 1950 to 2100 (blue line in Fig. 2a). Second, for each year, we calculated the average SST across the temperatures simulated from the 10 ensemble members; i.e. the ensemble-averaged SST (black line in Fig. 2a). Thi d, we applied a cubic spline (using the R function "smooth. spline" with smoothing parameter = 0.6) to the ensemble mean SST to further minimize the contribution of changes in temperature due to internal variability (orange line in Fig. 2a). Thus, the resulting SST series show the long-term changes in mean conditions only. For each LME in the northeast Pacific region, we identifi d MHWs as the positive temperature anomalies that were above the 95th percentile of temperature anomalies from 1950 to 2100 (red line in Fig. 2a). For every MHW identifi d from each ensemble member, we characterized its magnitude (SST anomalies relative to the smoothed ensemble mean values) and occurrence year.

Modelling ecological responses to MHWs. We included a total of 22 fish species that were reported in the fisheries statistics in the northeast Pacific region (www.seaaroundus.org). These species were important to fisheries in this region as they contributed up to 80% of the total observed catches from 2006 to 2015 (www.seaaroundus.org). We calculated four impact indicators to examine the ecological responses of fish stocks and their implications for fisheries during a MHW. These indicators are: (1) total biomass, (2) latitudinal centroid (average of the coordinates of grid cell weighted by the species' biomass), (3) depth centroid (average of bathymetry of grid cell weighted by the species' biomass), and (4) maximum catch potential (catch at $F = F_{MSY}$). We used outputs from DBEM to calculate these indicators for each LME. Since the projected relative changes in biomass and maximum catch potential are similar, we presented simulation outputs for changes in biomass only.

For each of the four impact indicators, we calculated the annual anomalies with procedures similar to those applied to SST (Fig. 2). Firstly, we applied DBEM to simulate changes in spatial distribution of biomass and catches from 1950 to 2100 under changes in ocean conditions projected from each of the 10 Earth system model ensemble members (blue line in Fig. 2b). Secondly, for each year, we calculated the average values simulated from the 10 ensemble members (black line in Fig. 2b) and smoothed the averaged series with a cubic spline filter (orange line in Fig. 2b). We then calculated the annual anomalies of each impact indicator from the difference between each ensemble member simulation and the detrended series. Finally, we recorded the ensemble member-specific annual indicator anomalies in the year when the temperature anomalies had been characterized as MHWs (red bars in Fig. 2b). We focused on analyzing the simulated impact indicators from 1981 to 2100 to ensure that the detected signals are not due to model initialization during the early period of the simulation.

We tested the statistical signifi ance of the effects of the occurrences of MHWs on the ecological impact indicators for exploited fish stocks in the northeast Pacific region using the glm function in R, with the occurrences of MHWs or non-MHW year as factor. The datasets for the information for accessing the projected temperature changes, MHWs and impacts on fish stocks are provided in the SI.

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Author contributions

Both W.L.C. and T.L.F. contributed to the conception and design of the work, the acquisition, analysis and interpretation of data, and the writing of the manuscript. W.L.C. conducted the study as a visiting scholar at the Oeschger Centre for Climate Change Research and the Climate and Environmental Physics Division of the Physics Institute of the University of Bern, Bern, Switzerland.

Competing interests

The authors declare no competing interests.

Additional information

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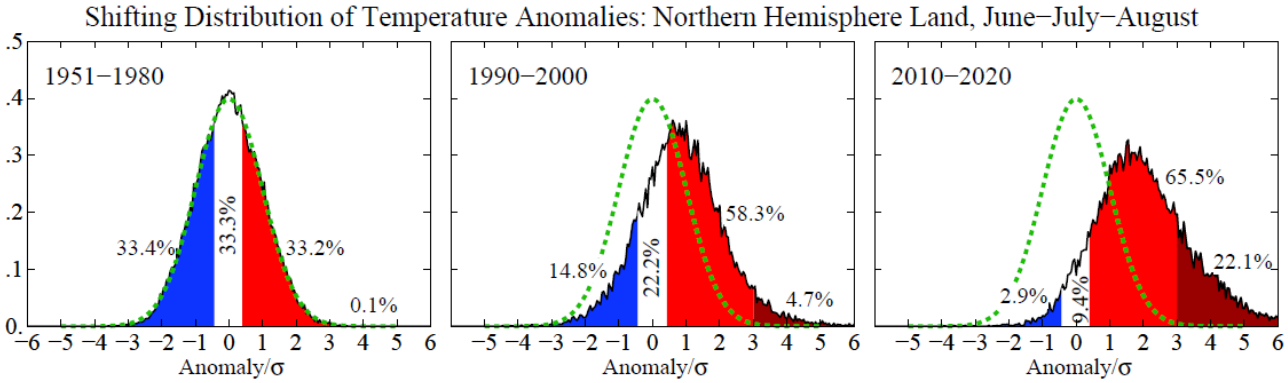


Fig. 1. The shifting bell curve for Northern Hemisphere land in the summer.

The Climate Dice are Loaded. Now, a New Frontier?

13 July 2023

James Hansen, Makiko Sato and Reto Ruedy

Andy Revkin recently asked whether the "climate dice" have become more "loaded" in the last 15 years. Climate dice were defined[1] in 1988, after we realized that the next cool summer may cause the public to discount human-caused climate change. The answer is "yes," the dice are more loaded as we will explain via the shifting bell curve (Fig. 1). The shift is large enough that most people notice the change, but that doesn't prevent a person with a bias from taking the cool June in the U.S. this year (Fig. 2) as proof that global warming predictions were wrong – and, of course, a loose cannon on Twitter has done just that. That's nonsense, of course. On global average, June 2023 was easily the warmest June in the historical record, as we will illustrate below.

What to do about loose cannons? Censor them? Bad idea. Censorship leads to enforced conformity, which has more serious consequences than loose cannons. Conformity leads to dogma,[2] which is anti-science. Science aims to compile real-world data and interpret it without prejudice, including its implications for policy. In a democracy, we must keep the public informed, which requires correcting disinformation. The aim is not to persuade a loose cannon – who likely has prior bias and is unpersuadable – but rather to educate those people who are open-minded.

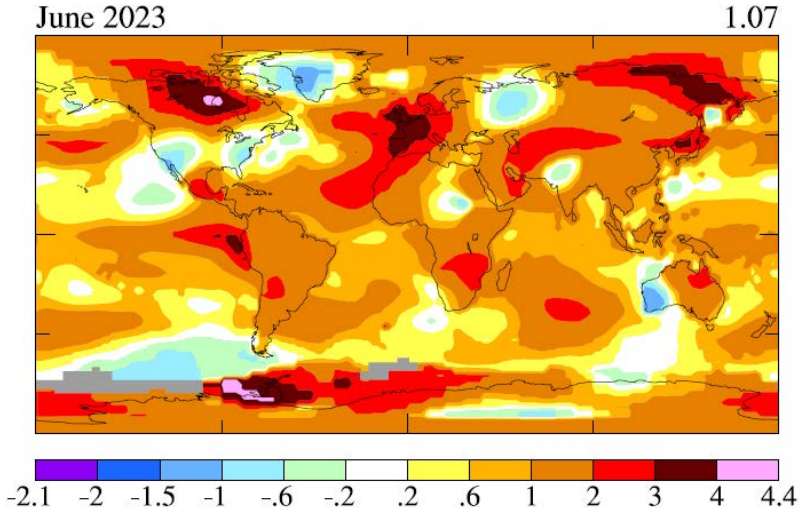


Fig. 2. Surface temperature anomaly (°C) in June 2023 relative to 1951-1980 June mean.

A 1-page description of the bell curves and climate dice is available as the author summary of our PNAS paper[3] on the topic. The variability of summer mean temperature in the base period (1951-1980, prior to the period of rapid global warming), is described by the bell curve on the left (Fig. 1). By definition, the one-third of summers closest to average temperature are the white, warmer summers are red and colder are blue, thus each color covering 2 of the 6 sides of the dice. By the last decade of the 20th century, red conditions were occurring 63% of the time on Northern Hemisphere land, which is almost the 67% needed to cover 4 sides. Twenty years later, the red area is 87.6%, five sides of the dice. So, the answer to Andy's question is: yes, one more side is red.

The more important point is the dark red area on the bell curve, the portion that exceeds three standard deviations. These are extremely hot summers that seldom occurred in the base period (less than 1% of the time). Chance of occurrence now is more than 20%, thus covering more than one side of the dice (one side is 16.7%). Increase of such climate extremes has the greatest practical importance. Moreover, the moisture extremes are more important than the temperature extremes.

In testimony to Congress in 1988 and 1989, and in a paper attached to the 1989 testimony, we noted that global warming causes wet places to get wetter and dry places to get drier. In places where the average precipitation changes little, we showed that wet times get wetter and dry times get drier. We also found that storms become stronger in a warmer world. We found that the "fuel" for storms, something called "moist static energy" – the sum of sensible heat, latent heat, and geopotential energy – increases in a warmer world. Moist static energy increases especially near the surface, so a warmer climate is prone to more powerful vertical convection that reaches greater altitude. In our climate model, doubled CO_2 caused the height of convective cumulus storm cells to increase several hundred meters. Higher absolute humidity and deeper penetration of moist convection cause a larger portion of the rainfall to occur in intense thunderstorms, as opposed to the gentler rainfall from large-scale stratiform clouds. Increased storm strength is not limited to thunderstorms. Kerry Emanuel of MIT used sea surface temperature increases from our $2\times CO_2$ experiment to estimate the effect on maximum intensity of tropical cyclones. Minimum sustained surface pressure fell from 880 mb to 800 mb and maximum potential wind speed increased from 175 to 220 miles per hour.

A new climate frontier? Suspicion that we are headed into new climate territory, not seen in the past million years,[4] is fueled by the present extraordinarily large Earth's energy imbalance (EEI). EEI (Fig. 3) is the proximate cause of global warming: as long as more energy is coming in than going out, we must expect global warming to continue. Given the acceleration of EEI in the past

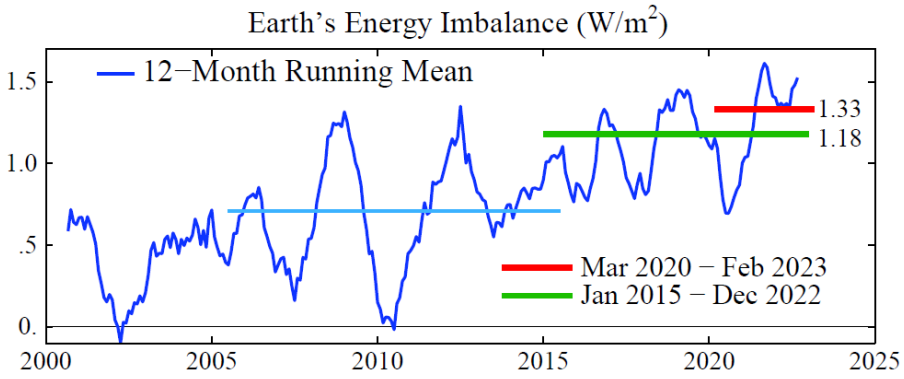


Fig. 3. 12-month running-mean of Earth's energy imbalance from CERES satellite data[5] normalized to 0.71 W/m² mean for July 2005 – June 2015 (light blue bar) from in situ data.[6]

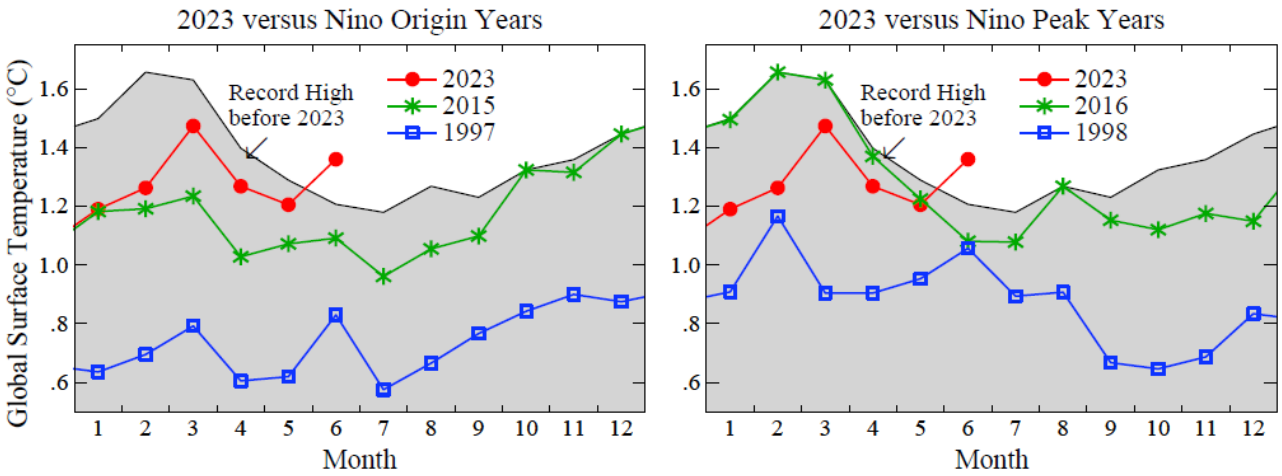


Fig. 4. Global temperature (relative to 1880-1920 mean) for the 1997-98 and 2015-16 super El Ninos with the budding 2023-24 El Nino. The two earlier El Ninos peaked in February of the second year. It is too early to tell how strong the current El Nino will be and whether it will peak in February 2024.

several years (Fig. 3), we anticipate an acceleration of global warming. Acceleration is difficult to measure because of the large interannual variability of global temperature associated with tropical El Nino/La Nina oscillations. If the newborn El Nino proves to be comparable to the prior two strong El Ninos (1997-98 and 2015-16), the 2023-24 global temperature will provide a measuring stick that helps determine whether the global warming rate is accelerating.

In the 18 years between the 1997-98 and 2015-16 El Ninos, global temperature increased 0.43°C, thus at rate of 0.24°C per decade, larger than the 1970-2010 global warming rate (0.18°C/decade), as has been pointed out.[7] For reasons discussed in the draft paper Global warming in the pipeline,[8] we anticipate acceleration of global warming to the rate shown by the yellow area in Fig. 5. In that case, the 2023-24 temperature curve (red curve in Fig. 4) is likely to fall substantially above the (green) curve for the prior El Nino and may set new global temperature records continually during the next 12 months. It seems that we are headed into a new frontier of global climate.

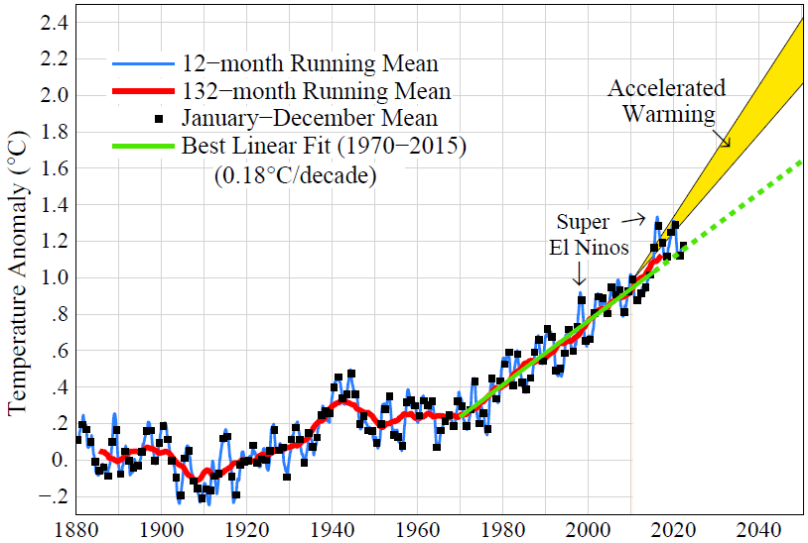


Fig. 5. Global temperature relative to 1880-1920. Edges of the predicted post-2010 accelerated warming rate (see text) are 0.36 and 0.27°C per decade.

[1] Hansen, J., I. Fung, A. Lacis, D. Rind, S. Lebedeff, R. Ruedy, G. Russell, and P. Stone: Global climate changes as forecast by Goddard Institute for Space Studies three-dimensional model. *J. Geophys. Res.*, **93**, 9341-9364, 1988.
[2] For example, belief that we can still solve the climate problem via just greater reduction of greenhouse gas emissions. Or belief that borrowing enough money from our grandchildren to build solar panels and windmills as fast as possible will significantly reduce global CO_2 emissions. Or that support for nuclear power is "not needed" because solar power is so cheap (Nuclear power is a needed carbon-free complement to renewables and viable scenarios for decarbonized electricity include an increasing role for modern nuclear power, but there is a total disconnect with financing (Bowen, M. and K. Guanio, 2023: A critical disconnect: Relying on nuclear energy in decarbonization models while excluding it from climate finance taxonomies, Commentary, Center on Global Energy Policy at Columbia University.).
[3] Hansen J, Sato M and Ruedy R 2012 Perception of climate change *Proc Natl Acad Sci* **109** 14726-14727 E2415
[4] Global warming of 1.2°C since 1880-1920 has brought global temperature to at least the level of the prior interglacial period, the Eemian, about 120,000 years ago. The Eemian was one of the warmest interglacials in the last million years.
[5] Loeb, N. G., Johnson, G. C., Thorsen, T. J., Lyman, J. M., Rose, F. G., & Kato, S., Satellite and ocean data reveal marked increase in Earth's heating rate, *Geophys. Res. Lett.* **48**, e2021GL093047, 2021.
[6] von Schuckmann K, Cheng L, Palmer MD *et al.* Heat stored in the Earth system: where does the energy go?, *Earth System Science Data* 2020;**12**:2013-41
[7] Grantham, J., The Race of Our Lives Revisited, GMO White Paper, August 2018.
[8] Global warming in the pipeline, draft paper, criticisms welcome

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RESEARCH ARTICLE

Requirements and availability of prey for northeastern pacific southern resident killer whales

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Data Availability Statement: The data underlying the results presented in the study are third party data, and available from the Chinook Technical Committee at the Pacific Salmon Commission (https://www.psc.org/about-us/structure/committees/technical/chinook/). To access the specific dataset related to this research, please contact the Chinook Technical Committee at the Pacific Salmon Commission at info@psc.org. Some data were also directly provided by Fisheries and Oceans Canada. We hereby confirm that the

Abstract

The salmon-eating Southern Resident killer whale (SRKW) (*Orcinus orca*) population currently comprises only 73 individuals, and is listed as 'endangered' under the Species at Risk Act in Canada. Recent evidence suggests that the growth of this population may be limited by food resources, especially Chinook salmon (*Oncorhynchus tshawytscha*). We present spatio-temporal bioenergetics model for SRKW in the Salish Sea and the West Coast of Vancouver Island from 1979–2020 with the objective of evaluating how changes in the abundance, age-structure, and length-at-age of Chinook salmon populations has influenced the daily food consumption of the SRKW population. Our model showed that the SRKW population has been in energetic deficit for six of the last 40 years. Our results also suggested that the abundance of age-4 and age-5 Chinook salmon are significant predictors of energy intake for SRKW. We estimated that the annual consumption (April-October) of Chinook salmon by the whales between 1979 and 2020 ranged from 166,000 216,300. Over the past 40 years, the model estimated that the contribution in the predicted SRKW diet of Chinook salmon originating from the Columbia River has increased by about 34%, and decreased by about 15% for Chinook salmon stocks originating from Puget Sound. Overall, our study provides an overview of the requirements and availability of prey for SRKW over the last 40 years, while supporting the hypothesis that SRKW were limited by prey abundance in the study period.

Introduction

The Northeastern Pacific resident killer whale population encompasses three genetically isolated sympatric assemblages: the Alaska residents (ARKW), the southern residents (SRKW), and the northern (NRKW) residents [1, 2]. The SRKW and NRKW are the two resident populations known to forage along the southern Coast of British Columbia during the summer

authors of this study did not have any special privileges to access those data.

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months. The SRKW are often found in waters off southern Vancouver Island and Northern Washington State, while the NRKW most commonly occurs in Johnstone Strait and Queen Charlotte Strait [3, 4]. The SRKW population has received attention in recent years because of its small population size (currently 73 individuals) and recent declines. Since 2008 it has been listed as endangered in both the US [5] and Canada [6]. Important aspects of large marine mammal biology that make killer whales at risk include their slow-reproduction rate [1], late sexual maturity [7], small population size [8], and low levels of genetic variation [1]. Understanding how those inherent traits increase the vulnerability of killer whale populations worldwide remains a challenge, as the status of most of the populations is still unknown [9]. Three additional factors have been identified as potential threats for SRKW, including vessel traffic and associated underwater noise [10, 11], toxic contaminants [12, 13], and declines in food resources [14, 15]. The historical range of the SRKW population is thought to extend from California to Haida Gwaii on the north coast of British Columbia [8, 16]. SRKW historically spent about 80% of their time in the Salish Sea during the summer months, where they travel extensively through Juan de Fuca, the Haro Strait, and the southern part of San Juan Islands [17]. In recent years sightings in British Columbia are closely tied with salmon runs from May to October at the southern end of Vancouver Island [3, 18].

SRKW are highly specialized salmonids predators with a strong selectivity for Chinook salmon, which represent up to 90% of their diet during the summer months [19–21]. Chum (*Oncorhynchus keta*) and coho (*Oncorhynchus kisutch*) salmon are considered secondary prey [19, 20]. Most wild Chinook salmon populations of the northeastern Pacific have recently experienced a decline in abundance and productivity [22–24]. In Puget Sound, it was shown that although the hatchery-produced population have been relatively stable over time and have exhibited increased rates of survival and productivity, wild Chinook population have been declining since the 1970s [25]. Chinook salmon were thought to be particularly abundant in Washington and Oregon States prior to the 1990s [26]. Despite a sharp decline in the 1990s, Columbia River Chinook have shown recent signs of recovery, annual runs exceeding a million fish in some years [27]. In the Strait of Georgia and along the West Coast of Vancouver Island, most conservation units (i.e.) have seen a decrease in spawner abundance since the mid-1990s [28]. Broad scale ocean and atmospheric variation such as the North Pacific Gyre Oscillation (NPGO) and the Pacific Decadal Oscillation (PDO) are thought to be the main drivers of productivity, while changes in abundance also are linked to other factors [23, 29]. Changes in population demographic (i.e. lower size-at-age, age-at-maturity, and fecundity) [22], assimilation of pollutants [30], degradation of freshwater habitats [31], increased predation [32], and selective fisheries exploitation for larger fish [22] are recognized as other contributing factors to the decline in Chinook salmon populations along the northeastern Pacific coast [22]. For instance the high natural mortality observed in juvenile Chinook salmon in the Salish Sea might also indicate increasing predation by growing populations of harbor seals and sea lions [33–36].

Currently, half of the Chinook salmon stocks in British Columbia are in the red status zone (i.e. spawning abundance is likely to be lower than the biological benchmark needed to sustain those populations) of the Wild Salmon Policy (WSP), which was implemented in 2005 by the Canadian government to promote wild salmon conservation [37]. Most stocks spawning in the interior of British Columbia have been listed as endangered or threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). In the USA, most Chinook stocks originating from the Columbia and Sacramento Rivers are currently listed as endangered or threatened under the Endangered Species Act (ESA) [38]. The decline in Chinook salmon populations has been suggested as the most important factor affecting the SRKW population demographics. Yet, evidences supporting this hypothesis are mostly limited to two

periods of prey shortages, the most recent of which being around the early 2000s [39]. Additional analysis is needed to understand the magnitude of food limitation and its impact on the SRKW population. Previous research showed that food limitation for SRKW might be associated with an increase in mortality [39], decline in reproductive success [15, 40, 41], and change in social network structure [42]. Other studies suggest that the interaction between prey shortage and the SRKW population limitation remains unclear and needs further investigations [41, 43].

The energy requirements of warm-blooded, large marine mammals are particularly high due to metabolic requirements of thermoregulation and the high bioenergetics costs of foraging [44, 45]. In addition to prey abundance, there is a need to consider the prey energy value and body conditions when assessing the potential impact of food limitation on SRKW. Between 1950 and 1975, the mean weight of Chinook salmon caught in the Canadian Pacific troll fishery decreased dramatically [46]. In the southern waters of British Columbia, this decrease in mean weight was roughly 45% from approximately 4.5–5.5 kg (10–12 lbs) to 2.7–3.1 kg (6–7 lbs), apparently stabilizing in the early 1960s [46]. Since then, there have been indications that changes to fishing regulations have helped increase the mean weight of some Chinook salmon stocks, though abundances have declined for stocks in the Salish Sea [47, 48]. Some evidence suggests that the mean size of fish in southern BC stocks remains low compared to historical levels though stock-specific length and weight-at-age data is sparse. A combination of declines in Chinook salmon abundance [28, 49], reduced numbers of older (i.e. larger) fish [22, 25, 50], and potential slower growth and reduced weight-at-age [47] would threaten the SRKW population, as their high degree of prey specialization makes them particularly sensitive to changes in prey availability and population structure [39]. In this context, understanding how the consumption of fewer and smaller fish could impact the SRKW ability to meet their energetic needs is essential to promote the recovery of this population.

To address this question, we built a size and age-structured population reconstruction model of Chinook salmon stocks in the Salish Sea and along the West Coast of Vancouver Island covering the last 40 years, along with a bioenergetics model for SRKW. The ultimate objective of this paper was to evaluate potential energy deficiency patterns for SRKW over the last 40 years, while (1) understanding how variations in Chinook salmon abundance and average body size have influenced the daily food consumption of the SRKW population, (2) evaluating how potential changes in the age-structure of Chinook salmon stocks available in the SRKW range might have impacted the amount of energy available and the demographic trend of the SRKW population, and (3) examining potential variations in Chinook salmon stocks-of-origin consumed by SRKW over the years.

Materials and method

The SRKW bioenergetics model was built to represent three seasons–spring (April/May), summer (June/July), and fall (August/September/October) from 1979 to 2020. The study area for our model includes the Salish Sea (Strait of Georgia, Puget Sound, and Juan da Fuca Strait) as well as the West Coast of Vancouver Island, where SRKW chiefly are spotted between April and October [51] (Fig 1). Our model does not include winter, as it remains unclear where SRKW occur during this period.

1. Prey parameters estimates

1.1. Chinook salmon abundance. In the early spring, SRKW are sighted most often in the western Strait of Juan de Fuca, and off SW Vancouver Island and the Olympic Peninsula, feeding primarily on spring-run Chinook salmon originating from the Columbia River and the

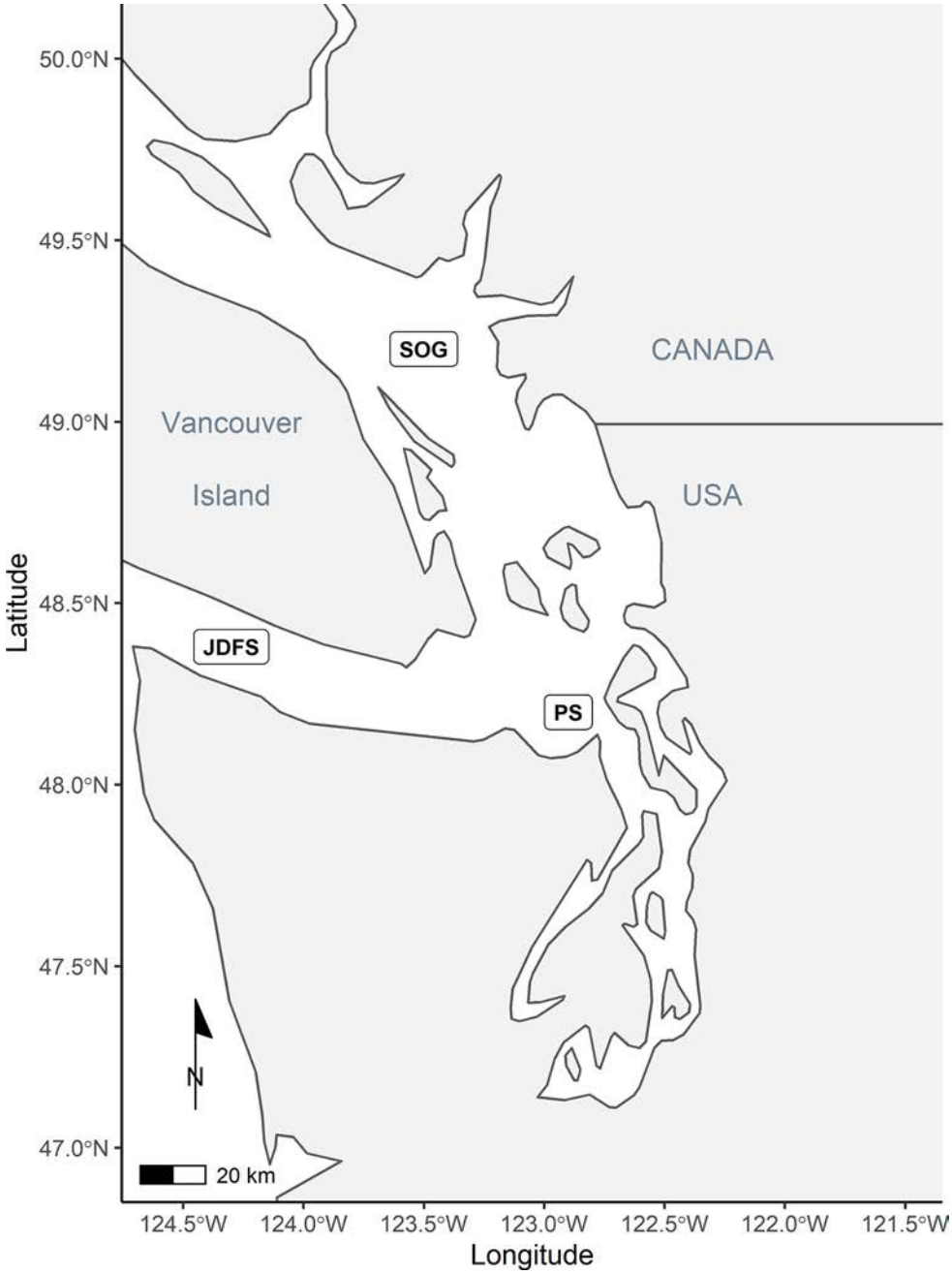


Fig 1. Map of the study area, including the Salish Sea (Strait of Georgia (SOG), Puget Sound (PS), and Juan da Fuca Strait (JDFS)), as well as the West Coast of Vancouver Island.

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upper portion of the Fraser watershed [20, 43, 51]. By June, SRKW spend the majority of their time in the southern portion of the Salish Sea, and are often sighted around the west coast of Vancouver Island, Juan Da Fuca Strait, San Juan Island, and Haro Strait [20]. During the summer months, Chinook salmon constitutes up to 90% of the SRKW diet, about 90% of which are summer-fall run originating from the Fraser River and travelling up the San Juan Islands between June and September [20, 44]. Adult SRKW exhibit strong prey selectivity and mainly feed on Chinook salmon aged from 3 to 5 years old, with age-4 fish being the most heavily

Table 1. List of the 30 Chinook salmon stocks of interest for SRKW.

Area	Stocks	ID	Run	Area	Stocks	ID	Run
FR	Fraser spring 1.2	FS2	spring	**WCVI**	WCVI wild	WVN	fall
	Fraser spring 1.3	FS3	spring		WCVI hatchery	WVH	fall
	Fraser summer 1.3	FSS	summer	**OC**	North Oregon migrating	NOC	fall
	Fraser summer 0.3	FSO	summer	**WC**	Washington wild	WCN	fall
	Fraser Chilliwack fall	FCF	fall		Washington hatchery	WCH	fall
	Fraser Harrison fall	FHF	fall	**CR**	Cowlitz fall-Tulle	CWF	fall
SoG	Middle Georgia Strait	MGS	fall		Cowlitz spring	CWS	spring
	Lower Georgia Strait	LGS	fall		Wells Summer	SUM	summer
PS	Nooksack fall	NKF	fall		Mid-Columbia Brights	MCB	fall
	Nooksack spring	NKS	spring		Lyons Ferry fingerling	LYF	fall
	PS yearling	PSY	fall		Priest Rapid	URB	fall
	PS wild	PSN	fall		Bonneville Lower River	BON	fall
	PS fingerling	PSF	fall		Willamette spring	WSH	spring
	Skagit	SKG	fall		Spring Creek	SPR	fall
	Snohomish	SNO	summer				
	Stillaguamish	STL	fall				

The 'ID' refer to the 'model stock acronyms' used in the PSC model, and in this paper. 'Run' refers to the seasonal timing of the spawning migration for each stock. 'Stocks' are shown by 'Area' of origin, which include the Fraser River (FR), the Strait of Georgia (SoG), Puget Sound (PS), the West Coast of Vancouver Island (WCVI), Oregon Coast (OC), Washington Coast (WC), and the Columbia River (CR).

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represented in their diet (which can represent up to 50% of their Chinook salmon catches) [19, 43]. Although age-2 Chinook salmon constitute about 25% of the SRKW in the winter months, the whales appear to predominantly target older age classes of Chinook salmon in the summer months [19, 43]. For this reason, younger Chinook salmon age classes (younger than 3 years old) were not included in our model. Previous studies have used genetic methods to identify the Chinook salmon stocks targeted by SRKW between May and October [20, 43, 52]. Following those findings, we included 30 Chinook salmon stocks of interest in our model (Table 1).

The method described below in our reconstruction model yield ranges of annualized Chinook salmon numbers-at-age estimates for mature or fish nearing maturity (at least 2 years of ocean age, Ocean Age 2+). In total, 30 stocks were included given that their migratory route out of the Salish Sea as juveniles and back as adults requires them to pass through at least the southwestern portion of the study area (i.e. Southwestern part of Vancouver Island, Juan de Fuca Strait).

The PSC is an international organization formed to support implementation of the Pacific Salmon Treaty between Canada and the United States. The Chinook Technical Committee (CTC) of the PSC publishes annual public reports on Chinook salmon catch and escapement, Coded-wire-tag (CWT) exploitation rate analysis, and PSC Chinook Model calibrations. An advantage of the CTC Model is the large breadth of integrated data. The PSC expends a large effort to integrate coded-wire-tag (CWT) release and recovery data as well as catches from Canadian and American fisheries both inside and outside the Salish Sea for each stock and age class. The modeling method used in the CTC model is a combination of backward and forward cohort analysis, which relies on various statistics, including the base period CWT data, Canadian and American fisheries catch data, Chinook salmon non-retention data, estimates of fisheries and gear-specific catchability, escapement and non-terminal run data, maturation rate and adult equivalent data, hatchery releases and recoveries, spawner-recruit parameters, and

proportion non-vulnerable estimates) [53]. Age 2+ fish (Gilbert and Rich format) have a much larger ocean distribution than the study area, with a notable proportion of fish from the Salish Sea being caught in northern Alaskan fisheries [53–56]. Modeled estimates of total cohort, escapement, catch by fishery-at-age were directly provided by the Pacific Salmon Commission (PSC) Chinook Technical Committee (CTC) for our 30 stocks of interest [53]. It should be noted that no uncertainties estimates were associated with those data.

Summing the PSC's estimates of total escapements and catch from fisheries occurring within the Salish Sea yields a minimum abundance-at-age for each stock *s* at the start of each year within the study area, using:

$$N_{s,a,y,A} = C_{s,a,y,A} + E_{s,a,y} \quad (1)$$

where $N_{s,a,y,A}$ is the minimum abundance of fish originating from stock *s* and age *a* transiting through the study area *A* during year *y*. $C_{s,a,y,A}$ is the total catch of fish at age *a* originating from stock *s* from all fisheries operating in the area *A*. $E_{s,a,y}$ is the escapement estimate for age *a* fish originating from stock *s* in year *y*. Assuming accurate catch reporting and escapement estimates, $N_{s,a,y,A}$ represents a minimum bound on the number of fish in each age class passing through our study area each year.

Predation mortality of mature and immature fish in each cohort also undoubtedly occurs in the study area. We used the static estimates of age-specific natural mortality rates from the CTC model to expand the minimum estimate of mature fish abundance and in transit to their spawning grounds within the study area [53]. The assumed natural instantaneous mortalities were 30% for age-3 fish ($m = 0.36$ year^{-1}), 20% for age-4 fish ($m = 0.22$ year^{-1}), and 10% for age-5 fish ($m = 0.1$ year^{-1}). As these PSC natural mortality estimates already included predation mortality, we estimated the Chinook consumption by SRKW for the different stocks from 1975 to 2020. Most consumption estimates were lower than 10% and were then considered small enough not to substantially impact the initial stock abundance calculations.

Because of a lack of information allowing us to divide catch between mature and immature fish, all catch within the study area was assumed to be of mature fish returning to their spawning grounds. Immature fish were assumed to experience predation mortality over the full year (m_a) and escapees and fish caught in fisheries were assumed to experience predation mortality over two months prior to spawning ($m_a/6$). The equation used to expand catch and escapement in the study area was:

$$N_{m,s,a,y,A} = \frac{C_{s,a,y,A} + E_{s,a,y}}{e^{-ma/6}} \quad (2)$$

where $N_{m,s,a,y,A}$ is the abundance of mature fish N_m originating from stock *s* and age *a* transiting through the study area *A* during year *y* (prior to fishing and predation mortality), and where *m* is the natural instantaneous mortality-at-age. This method implicitly assumes that natural mortality occurs prior to fisheries mortality which was deemed acceptable for our purposes given that terminal run fisheries mortalities are generally higher than ocean fisheries mortality on Fraser River stocks. Another advantage of back-calculation is it allowed us to include only those fisheries catches that occurred in the study.

Only a portion of a cohort spawns each year (estimated in the CTC model using maturation schedules, but these were unavailable at the time of writing). In lieu, the CTC model provides an estimate of total cohort size, $N_{s,a,y}$ which was used here to back-calculate the number of

immature fish N_i at age a originating from stock s in year y as:

$$N_{i,s,a,y} = N_{s,a,y} - N_{m,s,a,y} \quad (3)$$

However, the CTC model estimates of abundance-at-age, N_a, (i.e. a 'cohort') were sometimes *lower* than the catches for that age class in the same year, C_a–i.e. for some years, the values calculated by subtracting age-specific catches from age-specific abundance were negative. In this situation, the cohort size estimates provided by the PSC were used instead. This abnormality might be explained by an unusual method for calculation of the total cohort size used in the CTC model. To calculate abundance of an age class where fisheries occur early in the year, a common method is:

$$N_{a+1} = s(N_a - C_a - S_a) \quad (4)$$

where the abundance in the next age class, N_{a+1}, is the abundance from the previous year multiplied by survival rate, s (i.e. $s = 1$-M where M is the finite mortality rate) minus the catches, C_a, and spawners, S_a, from the previous year. Thus, the survival rate is applied only to the fish remaining after harvest and excluding the fish that spawned. Using the same equation as above, the equation used in the CTC model can be rewritten as:

$$N_{a+1} = sN_a - C_a - S_a \quad (5)$$

The survival calculation in the CTC model is therefore applied to the cohort *prior* to all fishing and spawning, not after. We expressed concern to PSC on this matter. The data provided did not include the base year catch and survival estimates, and other parameters, so it was not possible to re-do the cohort reconstruction. As such, the CTC total cohort size was assumed to be biased low.

Spawning fish are not present for the entire year, so spawn timing data and spatial distribution information was used in calculation of numbers-at-age for each season in the Salish Sea and along the West Coast of Vancouver Island. The marine distribution of maturing Chinook salmon is believed to be significantly greater than the Salish Sea and the west coast of Vancouver Island, and generally thought to vary by population [56]. We found no evidence that a significant proportion of Chinook salmon originating from the Columbia River basin and the outer coast rear in the Salish Sea, so the relative proportion of immature Chinook salmon for those stocks was not accounted for. Shelton et al. (2019) investigated marine distributions of fall-run Chinook salmon on a seasonal basis, and concluded that fall-run Chinook salmon originating from the Fraser River and Puget Sound spend more time rearing in the Salish Sea than the spring- and summer-run populations [55]. For spring and summer run immature Chinook, we estimated that 5% of each cohort was present in the study area in all months based on an estimate that the study area represents approximately 5% of the marine range of the species, combined with stock-specific marine distributions summarized in Brown et al. 2019 [56]. We relied on the analysis of Shelton et al. (2019) for estimates of seasonal proportions of Fraser- and Puget Sound- origin fall-run immature Chinook salmon present within the Salish Sea and applied these estimates to arrive at a proportion of all immature fish $N_{i,s,a,y,A}$ at age a originating from stock s and present in the study area A in year y (Table 2):

$$N_{i,s,a,y,A} = N_{i,s,a,y} \times P_{i,s,a,y,A} \quad (6)$$

where $P_{i,s,a,y,A}$ is the proportion of immature fish $N_{i,s,a,y,A}$ present in the study area A. Given that the total cohort size is estimated in the CTC model with natural mortality accounted for, no expansion for predation mortality was applied.

Table 2. Estimated seasonal proportions $P_{i,s,a,y,A}$ of the fall and spring and summer runs immature Chinook salmon residing in the Salish Sea.

Stocks	Run	Spring	Summer	Fall
FR	spring	0.05	0.05	0.05
FR	summer	0.05	0.05	0.05
FR	fall	0.35	0.35	0.4
PS	spring	0.05	0.05	0.05
PS	summer	0.05	0.05	0.05
PS	fall	0.05	0.05	0.05
SOG	fall	0.35	0.35	0.4

The stocks are originating from 3 main areas: Fraser River (FR), Puget Sound (PS), and the Strait of Georgia (SOG).

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To estimate seasonal presence for spawning fish, we used peak run timing for Fraser and Strait of Georgia stocks [57, 58] and Puget Sound stocks [59] and subtracted two weeks to account for travel time through the Salish Sea. We used these estimates as a multiplier to arrive at the proportional seasonal abundance P_s of mature fish originating from those stocks and travelling to their spawning grounds (Table 3). For all Chinook salmon originating from the Columbia River Basin and the Oregon/Washington Coast, we relied on 2 area-specific indices (Salish Sea (Salish) and Southwest Vancouver Island (SWVI)) provided by NOAA [60]. It is important to mention that those indices were calculated from the Chinook FRAM model, which has slightly different time-steps than our model (one-month difference). It is also important to consider that we used those estimates as a proxy for spring- and summer-run, as most of those area-specific indices were originally computed for fall-run Chinook stocks [60].

Using the relative proportion of each stock present in the Salish Sea and along the West Coast of Vancouver, we estimated the relative contribution of each stock in the predicted SRKW diet between 1979 and 2020, assuming that the whales did not exhibit any preference for specific stocks. We found no studies estimating the relative proportion of spring and summer run mature Chinook salmon found within the Salish Sea and West Coast of Vancouver Island from April to October. For these populations, we ran our models under three different scenarios of seasonal distribution of those stocks in the study area (Table 4).

Table 3. Estimated seasonal proportions P_s of the fall run and migrating spring and summer mature Chinook salmon present in the Salish Sea and along the West Coast of Vancouver Island in the spring, summer, and fall.

Area	Stocks	spring	summer	fall	Area	Stocks	spring	summer	fall
Fraser	FS2/FS3	0.8	0.6	0	PS	SNO	0.6	0.8	0.3
Fraser	FSO/FSS	0.6	0.7	0.3	WCVI	WVH/WVN	0.055	0.07	0.24
Fraser	FCF/FHF	0	0.3	0.7	OC	NOC	0.09	0.075	0.07
SoG	MGS/LGS	0	0.3	0.7	WC	WCN/WCH	0.14	0.07	0.15
PS	NKF/SKG/STL	0.51	0.5	0.47	Lower CR	CWF/BON/SPR	0.21	0.19	0.1
PS	PSY	0.09	0.075	0.07	Middle CR	SUM/MCB/LYF	0.18	0.14	0.11
PS	PSN	0.2	0.12	0.17	Upper CR	URB	0.2	0.18	0.1
PS	PSF	0.17	0.17	0.17	CR spring	CWS/WSH	0.17	0.17	0.17
PS	NKS	0.8	0.6	0					

Fall-run Chinook salmon abundance (all stocks) and spring and summer-run abundance estimates of southern stocks (i.e. WVN, WVH, NOC, WCN, WCH, BON, CWF, SPR, SUM, MCB, LYF, URB, CWS, WSH) are based on area-specific indices provided by NOAA and Shelton et al. (2019), whereas spring and summer Chinook salmon abundance estimates for stocks originating from the Fraser River, Puget Sound, and the Strait of Georgia (i.e. FS2, FS3, FSO, FSS, NKS, SNO) are computed with Scenario 2.

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Table 4. Relative seasonal proportions P_s of migrating spring and summer Chinook salmon stocks originating from the Fraser River, Puget Sound, and the Strait of Georgia.

Run	Spring run Chinook salmon			Summer run Chinook salmon		
Season	Spring	Summer	Fall	Spring	Summer	Fall
Scenario 1	0.8	0.6	0	0.6	0.8	0.2
Scenario 2	0.6	0.5	0	0.5	0.7	0.3
Scenario 3	0.5	0.3	0	0.3	0.5	0.4

The relative seasonal proportion of the stocks (i.e. FS2, FS3, FSO, FSS, NKS, and SNO) was computed under three different scenarios. The results of this paper are presented for Scenario 2, as we found little sensitivity of our model to variations in abundance estimates for those different scenarios. The values are expressed as relative proportion of the stocks. Note that they do not add up to 1 as some fish might stay in the area for several weeks and be available to SRKW over several seasons.

https://doi.org/10.1371/journal.pone.0270523.t004

1.2. Chinook salmon length-at-age and energetic value estimates. Length-at-age models for Fraser River Chinook salmon stocks from 1979 to 2020 provided by the PSC were used in our model [61]. The mean Von Bertalanffy growth parameters from this statistical model were used here.

Chinook salmon have high energy densities (average of 1,724kcal.kg^{-1}), but exhibit important variations in body sizes and energy content among Northeastern Pacific populations [62]. Yet, there is a paucity of information regarding variation of mass and lipid content in salmon populations. In this context, the linear regression model developed by O'Neill (2014) to predict the relationship between fish length (in mm) and total energy content (kcal.fish^{-1}) for Chinook salmon was used, such that:

$$\text{Kcal.fish}^{-1} = 0.000011(\text{fish fork length})^{3.122} \quad (7)$$

Mass-at-age was calculated using length-weight equations for Chinook salmon from an empirical study of lab and pen-raised Strait of Georgia Chinook [63].

1.3. Chum and coho salmon. In late September and October, SRKW also prey on large Fraser runs of coho and chum salmon [43]. The Fraser River is home to the largest run of chum salmon in British Columbia [64]. Fraser River chum salmon all migrate from September to December through Johnstone Strait, Juan da Fuca Strait, and the Strait of Georgia to reach their spawning grounds in the lower portion of the Fraser River [64]. In fact, coho and chum salmon may constitute between 20% and 50% of the SRKW diet during this period, and previous studies suggest that age-3 coho salmon and age-4 chum salmon are predominantly targeted [19, 43].

In the fall and early winter, coho salmon are migrating in high number to their spawning grounds in the interior Fraser River watershed [65]. Estimates of numbers of returning adult coho salmon in the Salish Sea and through the Juan da Fuca Strait were calculated using escapement numbers, historical catches, and CWT survival rates for the Strait of Georgia and the Fraser River. Escapement data were extracted from the publicly accessible database NuSEDS (i.e. New Salmon Escapement Database System) for streams in the Strait of Georgia and the Fraser River region, and expanded by the proportion of streams surveyed each year [66]. The escapement numbers were added to the historical catches reported in the public Pacific Fisheries Catch Statistic Database, and fitted to the total survival rates which were obtained from a coastwide database of tag releases and recoveries maintained by the Pacific Salmon Commission [67–69]. To obtain pre-harvest coho abundances, the escapement estimates were expanded by ratios of catch to escapement based on coded wire tagging recovery data. Coho salmon catch:escapement ratio estimates have varied from year to year depending on tag expansion assumptions, but have generally been consistent in terms of overall

exploitation rates, especially after the major decrease that occurred in 1997 when retention of coho was largely stopped as a conservation measure [67]. It is important to note that some of those databases contain estimates of highly variable quality, and that some information was missing for some streams in recent years. For chum salmon, we used estimates of catch and escapement provided by the Fraser and Interior Area Stock Assessment Program and computed by the Department for the Fisheries and Oceans (corrected for changes in sampling effort) (Mike Hawkshaw, personal communication). The catch data was compiled by various catch programs, primarily validated landings at processing plant (Mike Hawkshaw, personal communication).

2. Predator parameter estimates

As energetic requirements for SRKW are impossible to accurately measure in the field, we used the Daily Prey Energetic Requirement (DPER) estimates for SRKW developed by Noren in 2011 [45]. Those DPER estimates are based on field observations of different activity states for SRKW, and account for a digestive efficiency of 84.7% [70]. As energetic needs are proportional to individual body mass, we used births and deaths data collected by the Center for Whale Research to estimate the age- and sex- structure of the SRKW population from 1979 to 2020 [71] (Fig 2). Calves younger than 1 year old were not included in our analysis, as they do not feed on solid food during the first year of their life [71].

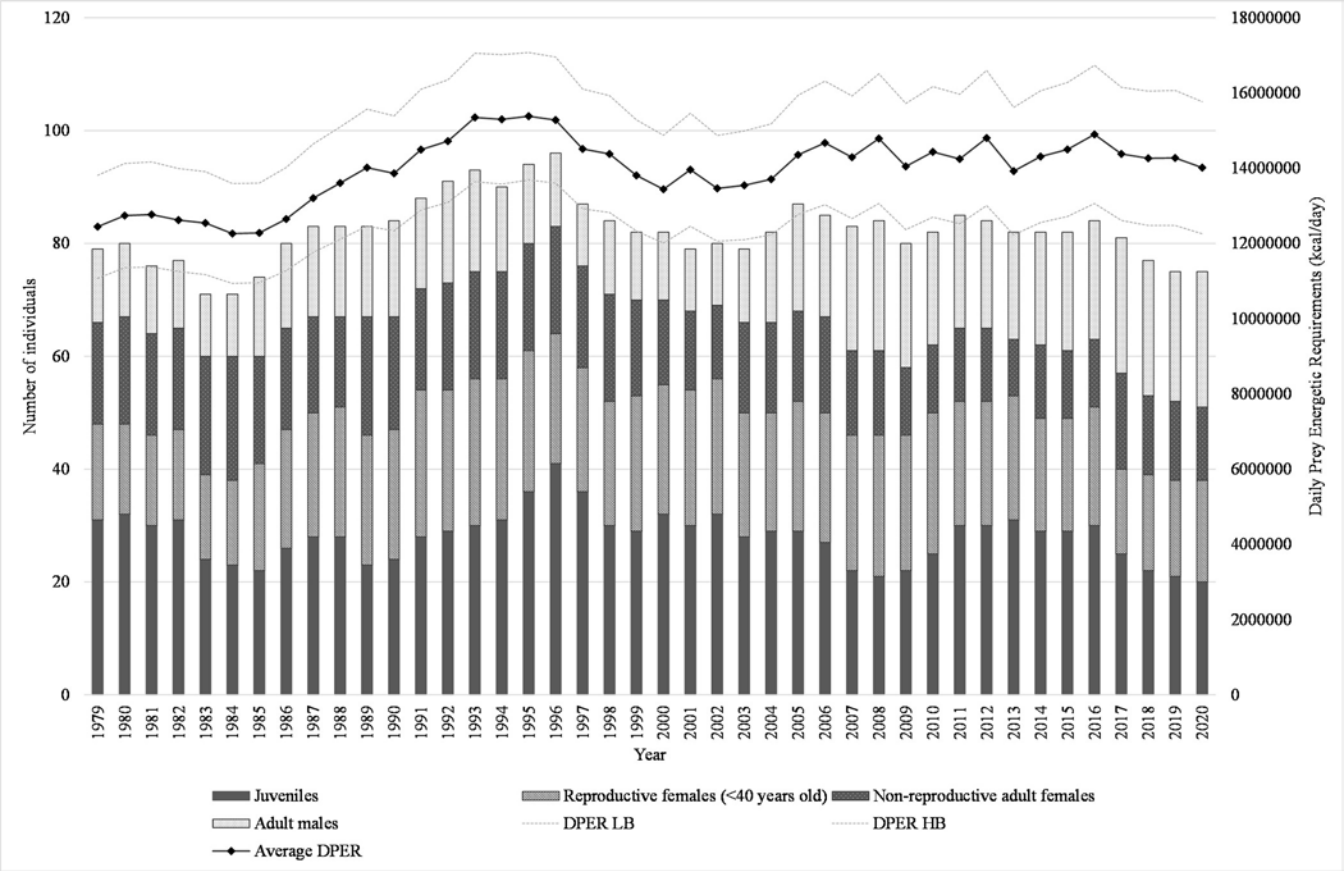


Fig 2. Number of individuals (stacked columns) and associated average daily prey energetic requirements (solid line) for the SKRW population from 1979 to 2020. The dashed lines represent the higher and lower bounds of the DPER estimates.

https://doi.org/10.1371/journal.pone.0270523.g002

For each year, we estimated the DPER of every whale individual based upon previous estimations of mass-at-age [45]. Following the method developed by Noren in 2011 [45], we assumed that the body mass of SRKW between 1 and 12 years of age was similar for males and females, and increased at a constant rate of 183.4 kg.year^{-1} (to reach a body mass of 2298.6 kg at 12 years of age). It was assumed that both males and females level their body growth and food consumption by 20 years of age to reach terminal body masses of 3,338kg and 4,434kg, respectively [45]. Between 12 and 20 years of age, the body mass of females was assumed to increase at a constant rate of 107 kg.year^{-1}, while males grew at a constant rate of 244 kg.year^{-1}. For each year, lower and upper bound DPER estimates were calculated for every whale individual using Noren's equations [45]:

$$\text{(a) Low bound DPER : } 413.2{*}\mathrm{M}^{0.75} \quad \text{(b) High bound DPER : } 495.9{*}\mathrm{M}^{0.75} \tag{8}$$

Where M is whale body mass (in kg), and DPER in expressed in kcal/day.

3. Prey-predator dynamics: The Holling disc equation

The multi-species disc equation developed by Holling predicts a type II functional response, where the prey consumption rate of a predator rises as prey density increases before levelling off as predators become limited by their capacity to process food (handling time). This equation was used in our model to predict the relationship between the SRKW rate of food consumption and the relative density of the different age classes of Chinook, chum, and coho salmon. This model allowed us to estimate the average daily prey intake by SRKW, as well as the annual consumption of Chinook salmon by SRKW in the Salish Sea and along the West Coast of Vancouver Island between 1979 and 2020. Although it is known that SRKW share their prey (especially adult females), we were able to treat each whale individual as a single predator without changing the prey handling time [19].

The Holling disc equation is routinely used to predict multispecies diet patterns in ecosystem modelling. According to the Holling disc equation, the total number of preys eaten per predator daily P_t can be predicted as:

$$P_t = \sum_{i=5}^{i} P_i = \sum_{i=5}^{i} ((a_i N_i T_t)/(1 + \sum a_i N_i h_i) \tag{9}$$

where for each prey i, P_i is the total number eaten per day, N_i the estimated abundance available to predators, a_i the rate of effective search, and h_i the handling time per prey.

To use the Holling disc equation, we first needed to calculate the Holling disc equation parameters values needed to predict the observed diet composition in some reference years for which we have estimates of total prey abundance N_i by prey type and relative diet proportions of those prey types in the predators' diet. We used Ford and Ellis (2006) estimates of all prey types i in the SRKW diet during those reference years (here 2000–2004) to calculate the disc equation parameter values (i.e. rate of search efficiency a_i and handling time h_i) needed to predict the observed diet composition during those years (Table 5). To do so, we assumed that $T_{t,}$ which represents the total time where SRWK were 'reactive' to prey, was equal to 21 hours/day [45]. T_t can be written as:

$$T_t = T_s + \sum h_i P_i \tag{10}$$

where T_s was defined as the time actively searching for prey, and equal to 5 hours/day [45]. We assumed that the handling time h_i of each prey type i was proportional to prey weight W_i, so

Table 5. Base parameters used to calibrate the Holling disc equation.

	Age 3	Age 4	Age 5	Chum	Coho
Diet proportion *(in biomass)*	0.101891	0.424545	0.297182	0.070909	0.08
Prey abundance ***N*** *(in numbers)*	551903	309695	41916	321030	2455706
Mean length *(in cm)*	769.3913	841.0689	882.7972	700	650
Weight *(in kg)*	6.777113	8.098663	8.922202	4.3	3.5
Average energy *(in kcal.fish^{-1})*	11270.53	14883.9	17312.93	8390.518	6657.454
Age proportion	1.240471	5.168629	3.61804	0.863283	0.97396
Handling time ***h*** *(in hours)*	1.209285	1.445099	1.592048	0.767278	0.624528
Rate of effective search ***a*** *(in prey abundance/hours)*	4.50E-07	3.34E-06	1.73E-05	5.38E-07	7.93E-08

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that:

$$h_i = k_i W_i \tag{11}$$

Under this assumption and by converting the previous equations, the weight coefficient k_i was calculated to estimate the handling time h_i per prey type i so that:

$$k_i = T_h / \sum P_i W_i \tag{12}$$

Where T_h represents the total prey handling time, which can also be written as:

$$T_h = T_t - T_s \tag{13}$$

The predator rate of search efficiency a can be defined as the area searched by a predator per unit of time. The kill rate of a predator depends on the searching efficiency, which itself logically varies with prey density N_i. The predator rate of search efficiency can thus be expressed as:

$$a_i = P_i / N_i T_s \tag{14}$$

Similarly to the other base parameters of the Holling disc equation, the rate of search efficiency a_i was calculated using the number of prey type P_i eaten between 2000 and 2004 as well as their overall abundance estimates N_i over those reference years [19]. It is impossible to estimate the sensitivity to variations in the Holling disc equation parameters other than to provide results for a range of reasonable increment in critical parameters. In the case of the Holling disc equation, it is expected that the model would likely show small sensitivity to any parameters except T_s, as this base parameter is used to calculate estimates of the rate of search efficiency a_i from the diet data. To address this uncertainty, we ran our model under two scenarios of T_s = 3h and T_s = 7h (±20%), and provided an estimate of the annual Chinook salmon consumption by SRKW and seasonal DPER differential for each scenario.

There is a paucity of information on the average daily food weight consumption for wild resident killer whales. The average daily energetic requirements of our SRKW population between 2000 and 2004 were about 171.245 kcal.day^{-1}, and the average prey energy content was 13.740kcal (estimated by multiplying each relative prey proportion in the SRKW diet by their average energy content). Based on those estimates, we assumed that a SRKW individual consumed about 12 fish.day^{-1}, or about 102 kg.day^{-1}. Those estimates are about 54% higher than previous calculations on captive killer whales, which could logically reflects higher energy expenditure associated with swimming, hunting, and socializing in the wild [45, 72]. Based on our calibration for the reference years, we were able to predict the consumption of each prey i

by SRKW in the spring, summer, and fall between 1979 and 2020. Logically, the overall daily energy E_t gained by the SRKW population was defined as:

$$E_t = (\sum_{i=5}^{i} P_i E_i) N_p \quad (15)$$

Where E_i is the energy content of each prey i and N_p the total number of predators.

It is important to note that the big uncertainty in these calculations is the base time T_s spent searching for prey each day, which might vary with factors like diurnal behavioral changes and obligatory time spent socializing. It is difficult to be more precise because even if the whales were followed closely over time, it would be hard to determine whether they would be reactive to prey at any given moment should they encounter one during other activities, like socializing or "resting". Although hard to quantify, this limitation could cause substantial uncertainty in the a_i ratios, along with uncertainty about diet proportions of prey of different sizes/ages/stocks.

To determine how the SRKW population was able to meet its energetic needs over the last 40 years, we compared the energetic differential between the DPER (low, high, average) and the average energy ingested per individual. We also used a logistic regression to understand which factors (i.e. abundance-at-age, length-at-age) could best predict the likelihood of the SRKW population meeting its energetic needs from April through October each year assuming the prey density dependence functional response relationship described below. In order to understand whether food limitation could influence the demographics of the SRKW population, we compared the birth rate (i.e. number of births/number of reproductive females), death rate (i.e. number of deaths/number of individuals in the population), as well as the annual net population change (birth rate–death rate) between years where the model predicted that the SRKW population met its DPER and years where it did not. We used graphical representations and a Wilcoxon rank-sum test to evaluate the presence of an energetic consumption influence on the SRKW population demographics. Our entire model was built on R (R Core Team 2013, version 1.4.1103).

Results

Overall, the model sensitivity to changes in spring and summer stocks' spatio-temporal distribution was considered small enough not to affect the results significantly. Between scenarios 1 and 3 (see Table 4), the overall trend of variations in average daily prey energetic requirement differentials remained comparable, with a maximum difference of 4143 kcal, or about 2.4% of the average DPER for a SRKW. Similarly, the difference between the annual Chinook salmon consumption by SRKW under those two scenarios was about 5,817 fish, which only represents about 2.5% of the total annual consumption of Chinook salmon by SRKW. No major difference in relative stock contribution into the predicted SRKW diet was found when running the model under the three different scenarios. We estimated that the overall predictions of our model did not significantly differ under our three scenarios, and chose to present the results of our model under scenario 2.

The data provided confirmed that the overall abundance of all Chinook age classes available to SRKW decreased over the study period (Fig 3). When comparing abundance-at-age numbers between 1979 and 2020, we found that the overall age-3, age-4, and age-5 fish abundance decreased by 39.7%, 20.9%, and 25.8%, respectively. The data also showed that the average abundance-at-age was the lowest during the mid-1990s, before increasing to higher levels around 2010 (Fig 3). The average length-at-age also slightly decreased for all ages of Chinook salmon targeted by SRKW, especially since 2000, by about 3cm (age-3), 7cm (age-4), and

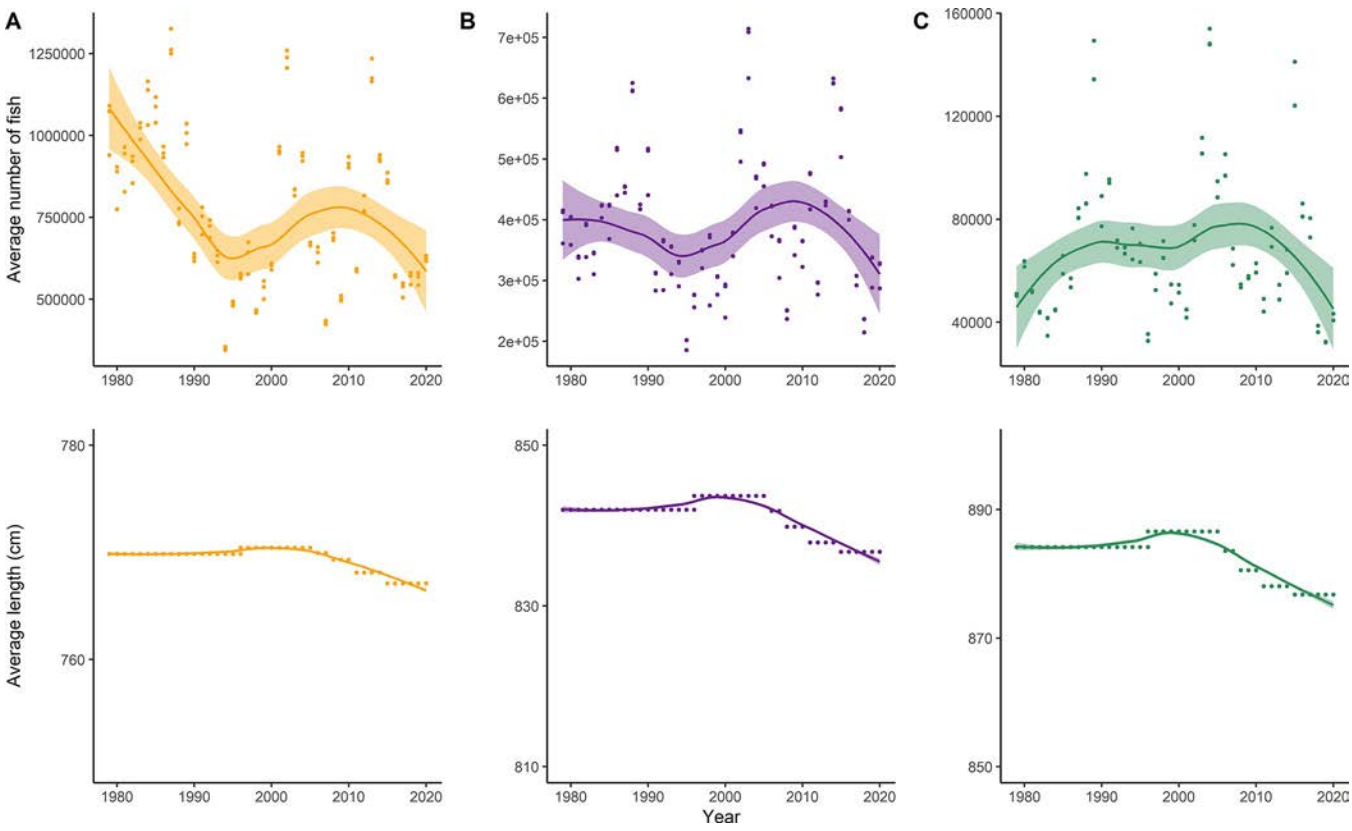


Fig 3. Average trend of abundance (top) and length-at-age (bottom) for age-3 (A), age-4 (B), and age-5 (C) Chinook salmon available to SRKW from 1979 to 2020 during the months April-October.

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10cm (age-5). For an age-5 Chinook salmon, a 10cm decrease in fish size would represent a difference of about 220kcal per fish.

Altogether, our model estimated that the uncertainty of our model associated with reasonable variations in the time during which SRKW were actively searching (i.e. T_s) was relatively minimal. When running the model under $T_s = 5 \pm 20\%$, we found that the average difference in the annual Chinook consumption was about 4748 fish, or ~22 fish per day for the whole SRKW population.

Using our base value of $T_s = 5$h, we estimated that the seasonal Chinook salmon consumption by SRKW from April to October varied between about 216,300 and 166,000 fish.yr^{-1} between 1979 and 2020 (Fig 4). It is worth highlighting that the trend observed regarding the annual Chinook salmon consumption by SRKW reflects temporal variations in Chinook salmon abundance as well as changes in the size of the SRKW population. The estimated highest consumption was in 1993, whereas the estimated lowest consumption was in 2018. The model predicts that consumption by SRKW of Chinook salmon belonging to the stocks in the model dropped substantially twice over the study period. A 22% decrease in Chinook salmon consumption was observed between 1993 and 1999, whereas consumption dropped by 18.4% between 2015 and 2020. Our model showed that chum salmon consumption by SRKW oscillated between 53,887 and 4,710 fish per year (highest level in 1998 and 1999), while coho consumption varied between 6,115 and 382 fish only. Our model predicted that SRKW consumed more chum salmon in the fall than age-3, age-4, and age-5 Chinook salmon separately in 1998 and 1999.

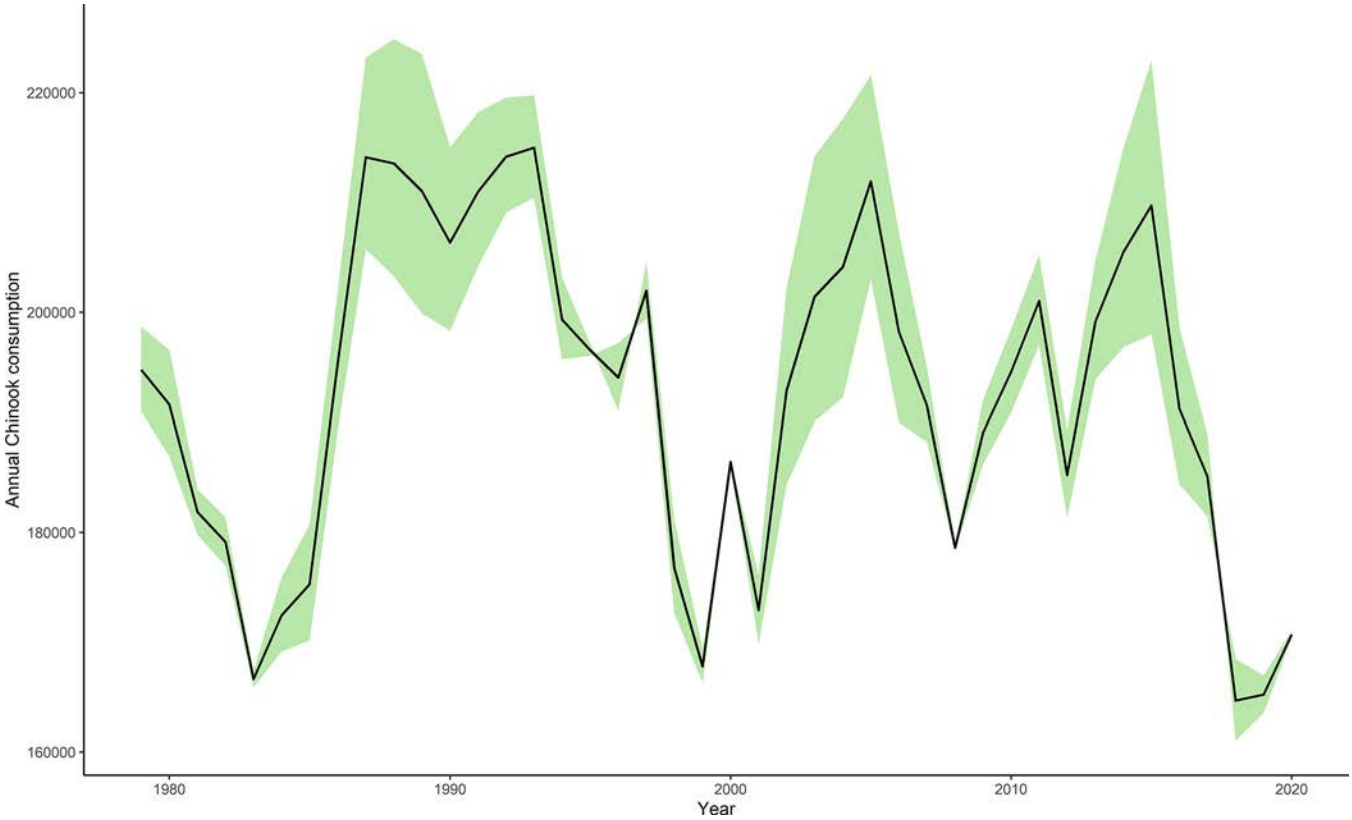


Fig 4. Estimated annual (excluding November-March) consumption of Chinook salmon (in number of fish) from April to October in the SRKW range from 1979 to 2020. The black line represents the predicted annual Chinook salmon consumption for T_s = 5h, whereas the green area represents the estimated Chinook salmon consumption for T_s = 5h±20%.

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Although SRKW appear to not be limited by prey for most years, our model predicted they were in average energetic deficit in all three seasons for four years between 1979 and 2020 (2008, 2018, 2019, 2020) (Fig 5). When considering high bound DPER and low bound DPER, SRKW were in energetic deficit in all seasons for 19 years and one year, respectively. When combining all three seasons over the last three years of the model, the average energetic differential was -28.716 kcal, which represents about 16.7% of the average adult killer whale DPER. Moreover, while the average number of fish eaten per whale individual decreased by only 3.5% before and after 2017, the average decrease in weight eaten was twice as important (-7.65%). Additionally, the results of our binomial logistic regression suggested that the abundance of age-4 and age-5 Chinook salmon were the most important factors determining whether SRKW met their DPER, with p-values equaling 0.00930 and 0.00086 respectively. Our model also revealed seasonal variation in whether DPER's were met, with SRKW consistantly consuming less energy in the spring and summer than during the fall. Over the last 40 years, the model predicts that SRKW have been in average energetic deficit during the spring or summer for four additional years. By combining the average energetic differential between the three seasons, we estimated that the SRKW population was in overall energetic defficiency with respect to the stocks and species included in the model for six of the last 40 years (1983, 2008, 2012, 2018, 2019, 2020).

Our model indicated that the average birth rate and net population change were slightly higher in years during which SRKW met their DPER, while the death rate was slightly higher

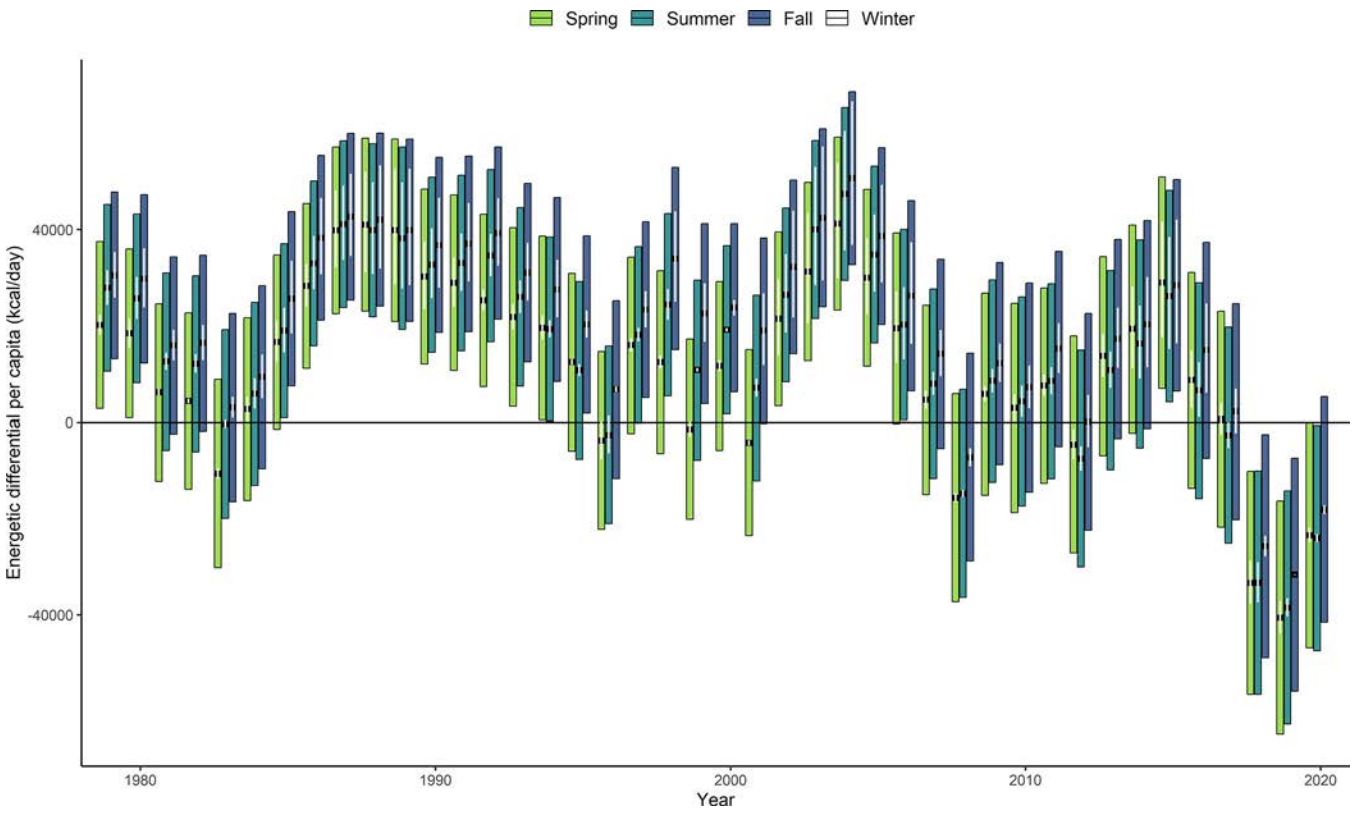


Fig 5. Energetic differential (kcal/day) between the energy ingested and the average DPER per whale individual. Each individual bar represents the highest and lowest DPER bound estimated by Noren et al. (2011), while the thick black dot represents the average DPER differential. The energetic differential was estimated in the spring, summer, and fall between 1979 and 2020. The white vertical lines represent the average DPER differential estimates when running the model with T_s = 5h±20%.

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in years during which SRKW did not meet their DPER (Fig 6). However, no significant results emerged regarding those differences. In all cases, the statistical weight of our results needs to be interpreted with caution with such a small population size. It is also important to note that the overall trend in births, deaths, and annual net population change was similar under all three scenarios.

Our model found substantial inter-annual variation in the relative proportion of different Chinook salmon stocks consumed by SRKW (Fig 7). Chinook salmon originating from the Fraser River, the Columbia River, and Puget Sound made up the majority of the predicted SRKW diet from 1979 to 2020, representing an average of 82% over the years. The relative proportion of stocks originating from the Columbia River increased substantially from 1979 (~27% of the SRKW diet) to 2014 (~61% of the SRKW diet). Conversely, the relative proportion of stocks originating from Puget Sound decreased after 1986 (representing an average of ~33% of the diet prior to 1986, against ~18% from 1986 to 2020) (Fig 7).

For the Fraser River, the relative contribution of FCF (age-3 and age-4) and FSO (age-4 and age-5) has increased in all seasons over the last 40 years. For instance, age-4 fish originating from FSO represented less than 4% of the predicted SRKW diet in 1979, against about 18% in 2019. Conversely, the relative proportion of other stocks in the SRKW diet consistently decreased from 1979 to 2020. Age-4 fish originating from FHF declined consistently in the summer and the fall, representing about 7.7% of the SRKW in 1979 against 2.3% in 2020. All stocks originating from the Fraser River or the Strait of Georgia showed a highest contribution

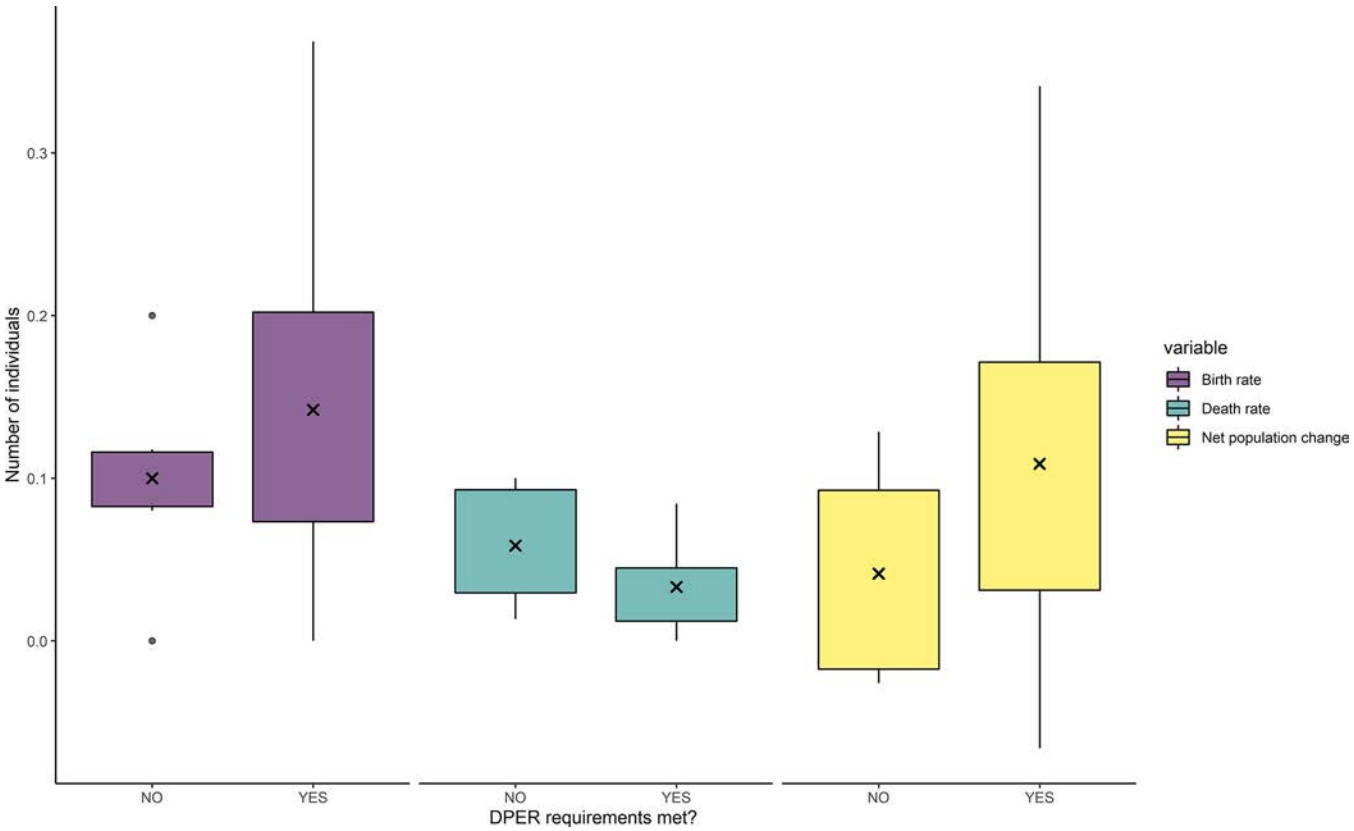


Fig 6. Whisker plot representing the number of births, deaths, and net population growth compared between years where SRKW did not meet their DPER (during at least one season over the year) and years where DPER were met in all seasons. The cross represents the mean.

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in age-4 fish, whereas the highest contribution from the West Coast of Vancouver Island stocks (both hatchery and natural populations) were age-5 Chinook. Finally, most of the stocks originating from the Fraser River, Strait of Georgia, or West Coast of Vancouver Island showed a peak in their relative SRKW diet contribution over some years, mainly around the early 1990s (WVH, FS3) or the early 2000s (FCF, FSS, WVN) (Fig 8).

The relative SRKW diet contribution of a majority of stocks originating from Puget Sound decreased substantially between 1979 and 2020. Averaged across all seasons and fish-at-age, a decrease was observed for NKF (-78%), PSN (-71%), PSY (-77.6%), SKG (-62%), and SNO (-76%). Except NKF, all those stocks combined already represented a small portion (<15%, all ages included) of the modeled SRKW diet in 1979. Conversely, the contribution of fish originating from PSF have consistently increased between 1979 and 2020 (+63%). Chinook salmon originating from the Washington and Oregon Coast (NOC, WCH, and WCN) represented in average 12.7% of the SRKW between 1979 and 2020. For the Columbia River, age-5 only Chinook salmon originating from URB represented about 11% of the predicted SRKW diet since 1990 (Fig 9).

Discussion

Our model predicted that the SRKW population has been in energetic deficit for six of the last 40 years, notably from 2018 to 2020. Several previous studies have highlighted positive correlations between Chinook salmon abundance and SRKW body condition [73], survival rate [39],

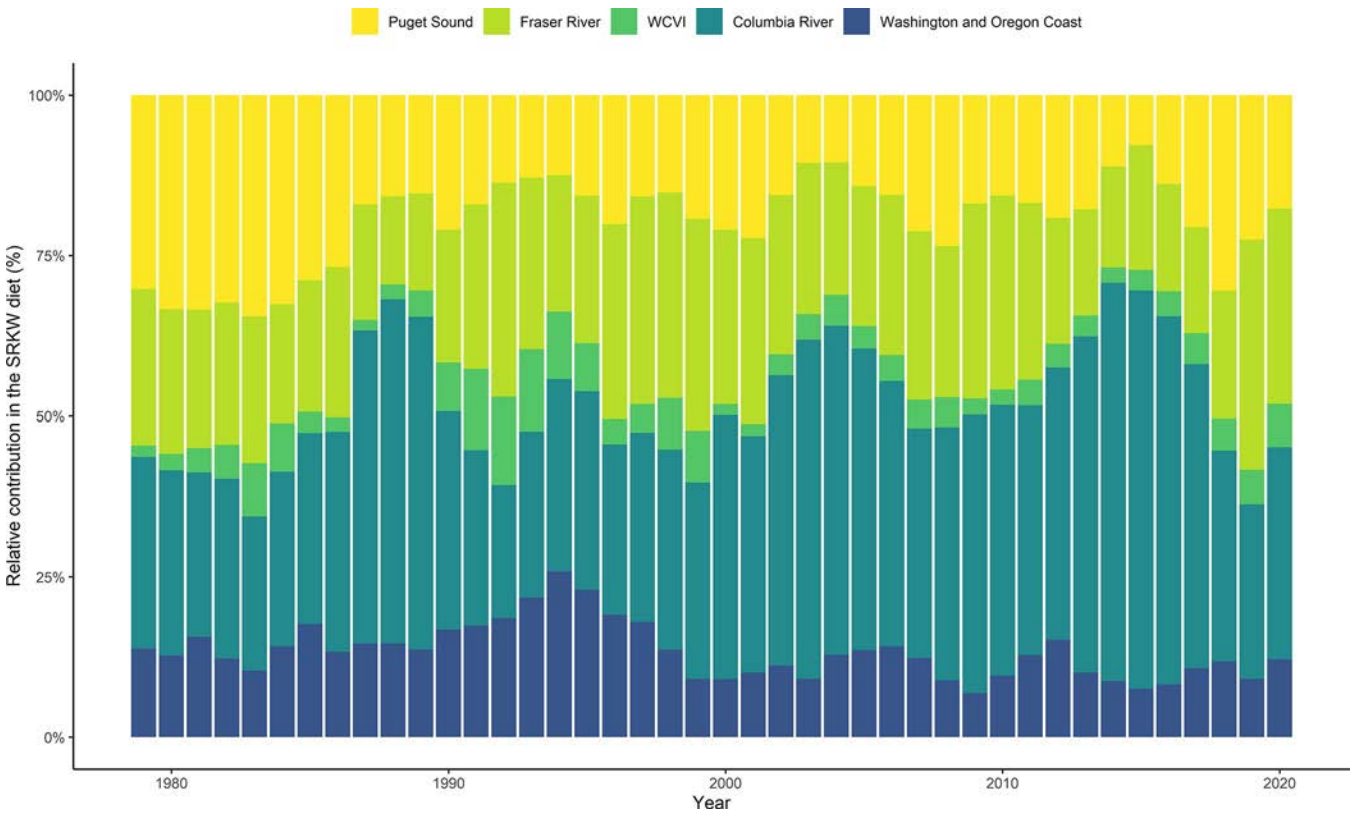


Fig 7. Estimated relative proportion (in %) of different stocks in the predicted SRKW diet from 1979 to 2020. For clarity, the stocks were split into five geographical areas: Puget Sound (NKF, NKS, PSY, PSN, PSF, SNO, SKG, STL), Fraser River (FS2, FS3, FSS, FSO, FCF, FHF, LGS, MGS), WCVI (WVN, WVH), Columbia River (URB, SUM, MCB, CWS, CWF, WSH, LYF, SPR, BON), and Washington Coast and Oregon Coast (WCH, WCN, NOC).

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and fertility [40]. Although our analysis did not permit to support those findings with certainty, our model suggests that SRKW could have a higher birth rate and net population and a lower mortality rate in years during which their DPER was met. Those results suggest that nutritional stress could influence the reproductive ability and survivorship of the whales during years of low prey abundance [19, 40]. Previous studies suggested that such pattern could reflect a trade-off between using energy for other physiological needs than reproduction when resources are scarce [40]. For example, the potential energetic cost associated with swimming further distances to find scattered preys would likely represent an additional metabolic cost and energetic expenditure for SRKW [45]. High death rate also occurred in years during which SRKW met their DPER (1996, 1998, 2001, 2006, 2010, and 2016), but some of those adult individual deaths appeared to be driven by factors unrelated to nutritional stress, such as blunt force trauma (individual 'J34'), fungal infection (individual 'L95'), or separation from the rest of the pod (L98) [71]. Over most of the years where SRKW did not meet their DPER, the population has also exhibited a high calf' mortality rate (at least 50% of the calves dying during their first year of life) and/or a low birth rate. Unfortunately, the low statistical power of our analysis on such a small population did not allow us to identify a significant relationship between energetic differential and those factors.

Our model also predicted that SRKW consistently consumed less calories in the spring than during the fall. This finding supports previous research showing that SRKW body condition is usually at his lowest level before summer, and confirms that SRKW could undergo a more acute nutritional stress during the spring. Moreover, our results support the hypothesis that

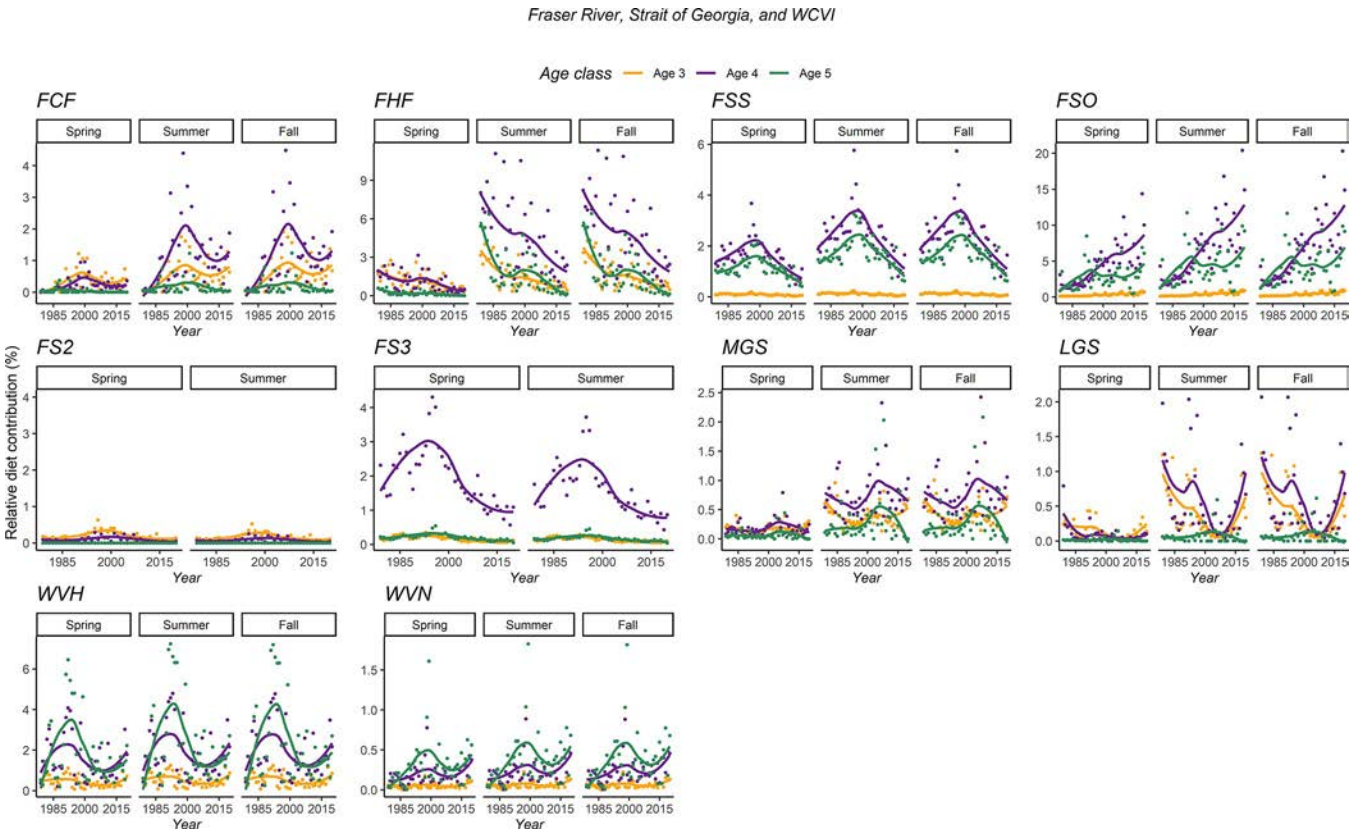


Fig 8. Estimated relative proportion of age-3, age-4, and age-5 Chinook salmon in the SRKW diet from 1979 to 2020. The stock IDs refer to the PSC model, and all stocks are originating from the Fraser River, Strait of Georgia, and West Coast of Vancouver Island.

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SRKW might not have enough resources in the spring months in the Salish Sea, therefore spending less time in this critical habitat during this season [74]. Interestingly, our model predicted that SRKW would consume more Chum salmon than any age classes of Chinook salmon during years where their usual Chinook salmon preys were at low levels. This result indicates that SRKW could switch to alternative targets when the abundance of their primary prey decline, which could promote resilience of the population. Although scientists have agreed that SRKW are highly specialized on Chinook salmon, our predictions are in line with recent evidence suggesting that SRKW exhibit seasonal variation in their diet [43]. In this context, future conservation and fisheries management decisions aiming at protecting food resources targeted by SRKW should focus on the recovery of different Pacific salmon, including chum salmon. One major caveat of our model is that e the salmon abundance data used only concern a subset of Chinook stocks, and likely do not include all the fish available to SRKW [53]. For instance, SRKW have been shown to also feed on Chinook stocks originating from the Central Valley or Klamath River (California) during the early Spring [43]. We assume that the Chinook stocks that are not included in this model follow the same population trends as our reference stocks, as they are likely subject to the same natural mortality, fishing pressure, and predation rate. Therefore, we believe that the overall trend in energetic differential for SRKW would remain the same even if those additional stocks were included.

Our model also revealed that age-4 and age-5 Chinook salmon abundances were significant predictors of energetic shortages for SRKW. This finding is not surprising, as older fish would provide more calories to SRKW, which appear to preferably target those Chinook salmon age

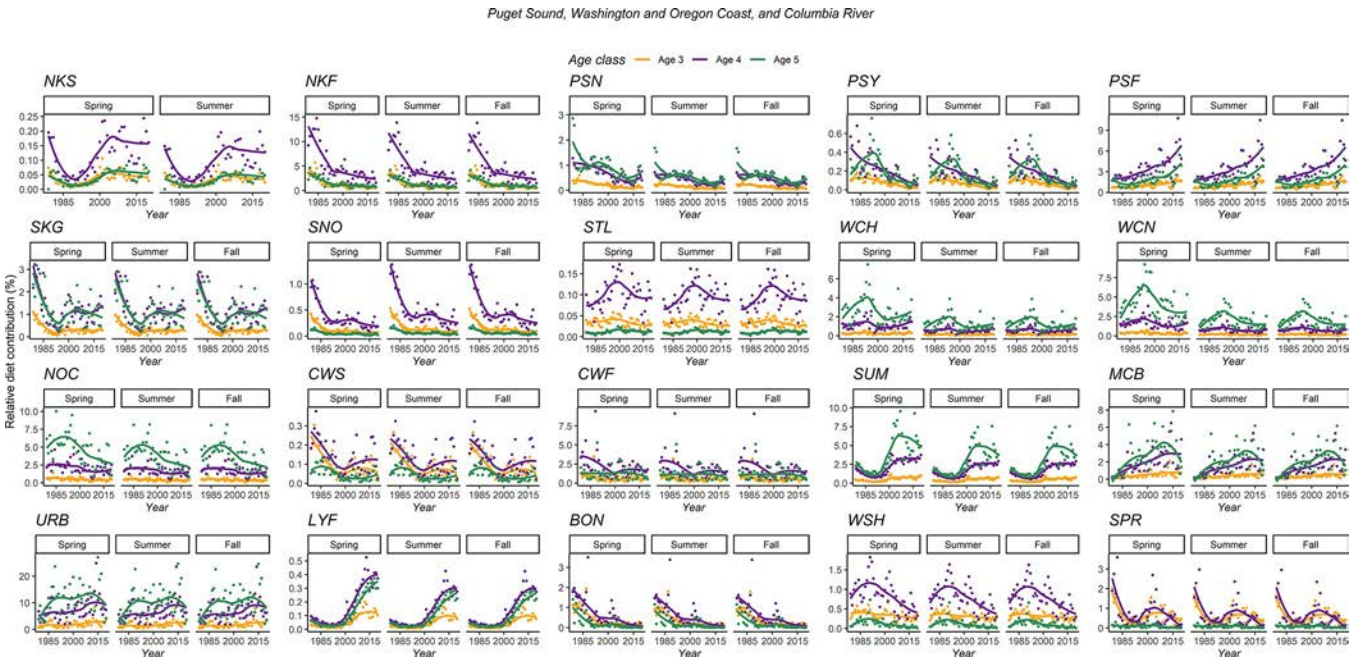


Fig 9. Estimated relative proportion of age-3, age-4, and age-5 Chinook salmon in the SRKW diet from 1979 to 2020. The stock codes refer to the PSC model, and all stocks are originating from Puget Sound, Oregon and Washington Coast, and the Columbia River.

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classes independently of their relative abundance [19]. Age-4 Chinook salmon have been harvested in equivalent or higher numbers than age-3 Chinook salmon since the early 2000s [53]. Over the last 20 years, an annual average of 83,590 age-4 Chinook salmon was harvested by both marine commercial and First Nation marine fisheries in the Salish Sea and along the West Coast of Vancouver Island. According to our model's predictions, these catch levels are equivalent to the average annual number of age-4 Chinook salmon (~85,900) that SRKW would have consumed over those years. Our model's predictions thus reinforce the importance of implementing size-specific selectivity for Chinook salmon fisheries operating along the Northeastern Pacific Coast, as well as the use of fishing techniques promoting the survival of larger individuals. Although increasing Chinook salmon abundance for older age classes could promote the recovery of the SRKW population, one important limitation of our model was that we could not account for prey accessibility when considering prey intake rate by SRKW. For instance, previous studies have shown that underwater noise pollution associated with vessel traffic could negatively affect the foraging behavior of resident killer whales, which could further reduce their search rate of efficiency and prey consumption rate [11]. Resident killer whales also travel significantly more in the presence of boats, likely increasing their average DPER [11]. Evaluating how such physical disturbances could influence SRKW foraging abilities is essential to differentiate the relative importance of prey abundance and prey availability on the SRKW prey energetic intake.

Our model predicted that SRKW have consumed in average between 216,000 and 166,000 Chinook salmon annually between 1975 and 2020. This estimate is slightly lower than Chasco et al. (2017), who predicted that SRKW could consume the equivalent to 190,000 and 260,000 Chinook salmon annually in the Salish Sea. This difference is not surprising, as Chasco et al. estimated SRKW Chinook consumption over all seasons, and assumed that SRKW were to meet their DPER. Between 1979 and 2020, our model predicted that SRKW consumed an average of 193,103 Chinook salmon (including all age classes), while an average of 458,669 were

harvested by marine fisheries in the Salish Sea and along the West Coast of Vancouver Island over those years. Although Chinook salmon fisheries in marine waters have been drastically reduced since 2000s, the annual average number of adult Chinook salmon harvested by fisheries between 2010 and 2020 was 198,530 while about 187,200 fish were consumed annually by SRKW during this period. Our model thus suggests that SRKW have been consuming slightly less adult Chinook salmon than fisheries have harvested. Although the retention of Chinook salmon is already not permitted for most of those fisheries, our research further highlights the need to implement and reinforce the use of size-selective fishing gear in the area. On the other hand, several recent studies have demonstrated an increasing pinnipeds' predation pressure on Chinook salmon [32, 35, 36]. For instance, the harbor seal population in the Salish Sea is thought to have been at carrying capacity (~50,000 individuals) since the mid-1990s, and each seal is estimated to consume a daily average of 0.02 adult Chinook salmon [75, 76]. In 2020, our model predicted that SRKW would consume about 800 adult Chinook salmon per day, against 1,000 for harbor seals based on those previous estimates. Our results thus support the need for promoting Chinook salmon population recovery, and highlights the necessity of considering both predation and fisheries pressures on those populations when implementing future conservation goals.

Finally, our model predicted that the overall relative contribution of stocks originating from the Columbia River in the modeled SRKW diet has increased over the last 40 years, while the contribution of stocks originating from Puget Sound has decreased. When presenting those results, we assume to reflect abundance variations of different Chinook salmon stocks available to SRKW, which might partially explain why SRKW have been seen less frequently in the Salish Sea in recent years [74]. Chinook stocks of the Salish Sea have been reduced by about 60% since 1984, and SRKW could logically be feeding upon other more abundant Chinook salmon stocks passing through different areas [77]. This is the case for Columbia River Chinook salmon, which are usually caught off the west coast of Vancouver Island and rarely migrate inside the Salish Sea [55]. Our model also predicted that the SRKW consumption originating from Puget Sound slightly raised around the late 1990s, which is in line with the highest number of sightings of SRKW in the area during those years [51]. Both results support the hypothesis that SRKW occurrence patterns could be driven by food resource abundance and availability. Some stocks—URB, MCB, SUM (Columbia River), FSO (Fraser River), PSF (Puget Sound), WCN and NOC (Washington and Oregon Coast)—showed a high contribution in age-4 and age-5 Chinook salmon in the predicted SRKW diet. As older fish are critical to SRKW meeting their DPER, it appears essential that future Chinook salmon fisheries conservation initiatives direct their efforts towards specific stocks and specific age classes. Altogether, our model provides an overview of prey availability for SRKW, and partially supports the hypothesis that the SRKW population could be limited by food resources. Regarding future research, Furthermore, the use of this model could be useful to evaluate the energy balance of other salmon-eating killer whale population, such as the NRKW. Such future research could help determine whether the differences in prey availability are indeed a plausible cause of the difference in growth trajectories among different resident killer whale populations.

Furthermore, evaluating to which extent external physical disturbances could affect the foraging abilities of SRKW is critical to identify whether SRKW could still fail to meet their daily prey energetic requirements under more favorable prey abundance scenarios. Finally, it will be key to understand how changes in fisheries harvest practices and marine mammals' predation pressure could influence the abundance of prey available to SRKW.

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Methodology: Fanny Couture, Greig Oldford, Carl Walters.

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Validation: Carl Walters.

Visualization: Fanny Couture.

Writing – original draft: Fanny Couture.

Writing – review & editing: Greig Oldford, Villy Christensen, Lance Barrett-Lennard, Carl Walters.

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ARTICLE

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Climate change threatens Chinook salmon throughout their life cycle

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Widespread declines in Atlantic and Pacific salmon (*Salmo salar* and *Oncorhynchus* spp.) have tracked recent climate changes, but managers still lack quantitative projections of the viability of any individual population in response to future climate change. To address this gap, we assembled a vast database of survival and other data for eight wild populations of threatened Chinook salmon (*O. tshawytscha*). For each population, we evaluated climate impacts at all life stages and modeled future trajectories forced by global climate model projections. Populations rapidly declined in response to increasing sea surface temperatures and other factors across diverse model assumptions and climate scenarios. Strong density dependence limited the number of salmon that survived early life stages, suggesting a potentially efficacious target for conservation effort. Other solutions require a better understanding of the factors that limit survival at sea. We conclude that dramatic increases in smolt survival are needed to overcome the negative impacts of climate change for this threatened species.

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Widespread declines of wild salmon[1–5] have negatively affected fisheries, cultural heritage for indigenous tribes[6], and other marine species, including endangered Southern Resident Killer Whales[7]. Currently, the majority of Atlantic and Pacific salmon and steelhead (*Salmo salar* and *Oncorhynchus* spp.) in the conterminous U.S. are threatened with extinction[8]. Over the past century, declines were driven by overfishing, migration barriers, water diversions, habitat loss, salmon farms, and hatcheries, as well as regime shifts in marine ecosystems[9]. Retrospective analyses also show strong relationships between climate indices and salmon performance[10,11]. Looking toward the future, indirect and qualitative assessments point to anthropogenic climate change as an additional overriding threat for salmon in the North Atlantic and California Current[12–15]. How to mitigate this threat is therefore a primary concern among conservation organizations and management agencies.

Previous population models that have used global climate model (GCM) projections have focused on drivers in freshwater life stages only (e.g., stream temperature, winter flooding, and drought)[16–18]. While these are useful for evaluating restoration actions within those contexts, they completely ignore the large impacts of climate change on the marine stage. On the other hand, GCM projections related to marine survival have been used primarily to inform niche-based models that forecast future habitat for salmon generally rather than for specific populations[19,20]. Although marine climate indices such as the Pacific Decadal Oscillation (PDO)[21] and Atlantic Multidecadal Oscillation (AMO)[4] have been tightly linked to survival, they cannot readily be used in projections of future climate because these phenomena are not consistently reproduced in GCM projections for complex reasons[22,23]. To produce a novel, robust analysis of climate change impacts, our analysis focused on climate drivers with more reliable performance in GCM projections that were also closely correlated with fish survival.

A more general limitation of previous models has been a failure to account for large-scale climate forcing that affects multiple life stages and food webs simultaneously, potentially compounding climate effects across developmental stages. Accounting for the correlation structure of climate effects over the full life cycle is especially important for migratory species with complex life histories[15,24]. We acknowledge that relationships between survival and climate are often nonstationary[25], so we made the correlation structure of environmental drivers explicit and flexible enough to incorporate future change. This is a new approach to downscaling climate projections in multiple environments.

These limitations contribute to three main reasons why existing approaches for modeling biological impacts of climate change are inadequate for informing or evaluating potential management actions for salmon conservation. Similar limitations apply to other species that are migratory or have complex life histories.

First, proposed management actions are usually focused on conditions in freshwater, but accounting for "carryover" effects from freshwater to marine life stages is essential for the evaluation of such actions. Carryover effects occur when the previous history of an individual affects its performance in a subsequent life stage[26]. For example, the timing of migration from freshwater to the ocean and back to freshwater are key determinants of salmon survival in other life stages, and one of the most climate-sensitive traits[27–30]. Migration timing is also a key element in multiple management actions, especially those involving the hydrosystem[31] and fisheries[32]. Therefore, quantification of carryover effects that will be affected by climate change is essential for evaluating the net benefit of proposed actions to protect endangered species.

Second, present models of survival in the salmon marine stage rely on climate indices, which cannot be linked directly to global climate model (GCM) projections. Therefore, it is impossible to conduct formal analyses of how alternative carbon emission scenarios or other anthropogenic actions to mitigate climate change might affect the timing of declines in marine survival. Nor is it possible to quantify uncertainty in modeled projections across GCMs and thus take full advantage of the *Coupled Model Intercomparison Project*, which represents the major advances of global climate modeling in recent decades[33,34].

Third, approaches that are currently available to account for climate impacts on freshwater and marine life stages use independent downscaling methods for the two environments. Terrestrial downscaling methods usually employ statistical or dynamical downscaling of temperature and precipitation, which are then fed into hydrological models. Statistical downscaling is an efficient way to explore many alternative climate projections and characterize model uncertainty at many steps in the modeling chain[35]. In contrast, a common approach to marine downscaling is to integrate GCM output into regional ocean models (ROMS), which in practice are only available for very few GCM projections[34]. As a result, these methods often rely on projections from different GCMs and are not consistent in characterizing potential model biases, and thus uncertainty in climate projections. Moreover, these multiple GCMs are not temporally linked, which impedes the ability to account for carryover effects from one life stage to the next[36].

We attempted to address each of these difficulties by developing a modeling approach with flexible and explicit mechanisms to account for the correlation structure among all climate drivers. We also used a multimodel approach to indirectly account for the change in the relationship between climate drivers and ecological responses. Finally, we allowed the initiation timing of juvenile and adult migration to vary with environmental conditions, which subsequently affected both smolt and adult migration survival. Timing also affected the probability that juvenile fish would be transported; transport by barge through the hydrosystem is a mitigation action that has fixed start and stop dates each year. Three factors—migration timing, hydrosystem operations, and transportation—subsequently affected arrival timing at the Columbia River estuary, which in turn affected ocean survival. Although details of the migration models are unique to this system, the need to account for carryover effects and the correlation structure of climate drivers in multiple environments is widely shared by migratory species.

We used a stochastic, age-structured life-cycle model[37,38] with both density-dependent and density-independent climate effects. Survival of Chinook salmon (*O. tshawytscha*) was forced by environmental drivers, while future climate trends were based on ensemble projections from GCMs (Figs. 1 and 2 and Supplementary Data 1). We used a simulation framework to explore model assumptions and quantify different aspects of model uncertainty, including the functional form of the model, covariate selection, and life-stage-specific sensitivity.

We applied the model to eight populations within the Snake River spring/summer Chinook salmon Evolutionarily Significant Unit (ESU). This ESU migrates downstream from natal headwater streams in central Idaho, passing eight major hydroelectric projects on the Snake and Columbia Rivers to reach the northeastern Pacific Ocean (Fig. 3). After 1–4 years of ocean rearing, individuals return to freshwater and migrate upstream for a single spawning opportunity.

We simulated population time series for these exclusively wild populations, whose recent 15-year geometric mean spawner abundance ranges from 45 to near 600[39,40]. The model reconstructed historical population dynamics closely for most

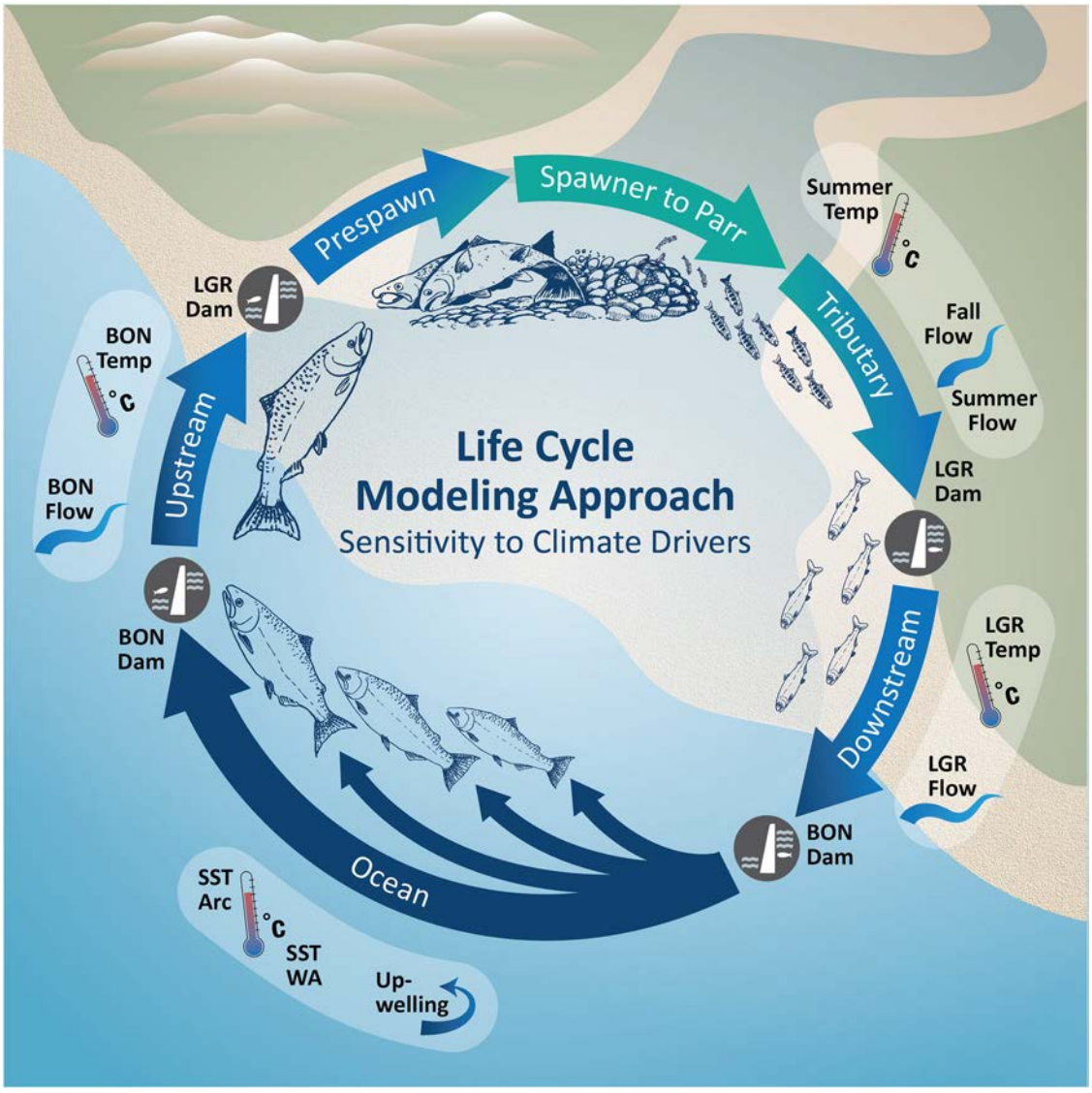


Fig. 1 Life-cycle model diagram. Diagram showing the life stages and climate drivers that influenced each stage. The freshwater stages include upstream migration and holding, spawning, rearing in tributaries, and migrating downstream. Migration routes pass through the Columbia River hydrosystem, bracketed by Lower Granite Dam (LGR), and Bonneville Dam (BON). Freshwater stages were influenced by stream flows (Flow) and temperatures (Temp). The marine stage, which has variable duration represented by multiple arrows, was influenced by ocean temperatures across the northeastern Pacific (SSTarc) and along the Washington coast (SSTwa). Other influences on ocean productivity are represented by Upwelling. Figure courtesy of Su Kim (NOAA Fisheries) and salmon illustrations by Blane Bellerud (NOAA Fisheries).

populations based on Kolmogorov–Smirnov diagnostics. This model has been relatively stable when confronted with new data over the last 10 years, a period during which it has been used operationally by the National Marine Fisheries Service[40]. Our updated version of the model is similar in general characteristics to that used by Crozier et al.[37]. However, the updated version imposes climate influences in more life stages and has stronger validation based on data from over one million individually tagged fish (Supplementary Methods and Supplementary Table 1).

We compared multiple alternative covariates in survival models, acknowledging that the best predictor might change over time and thus might track different temporal trajectories[25]. Notably, we have found that sea surface temperature (SST) is an important component of most relevant indices. This is not surprising, because SST reflects complex interactions between atmospheric forcing, wind strength, upwelling, and mixing of ocean layers, all of which affect ecosystem productivity throughout the California Current[41]. Although the response of these processes to greenhouse gas forcing will vary, SST will likely continue to be an important indicator.

Results

Populations declined dramatically in a warming climate. Chinook salmon migration timing did shift earlier in response to warmer freshwater conditions. However, the timing shift did not prevent large-scale population declines under either the RCP 4.5 or 8.5 scenarios. Population abundances diverged quickly under the two climate scenarios compared with baseline conditions, which were represented by a stable climate (Fig. 4). Recent population dynamics and historical population modeling are detailed in "Methods".

With a warming climate, deterministic declines inevitably lead to extinction unless some ecological, evolutionary, or climatic rescue

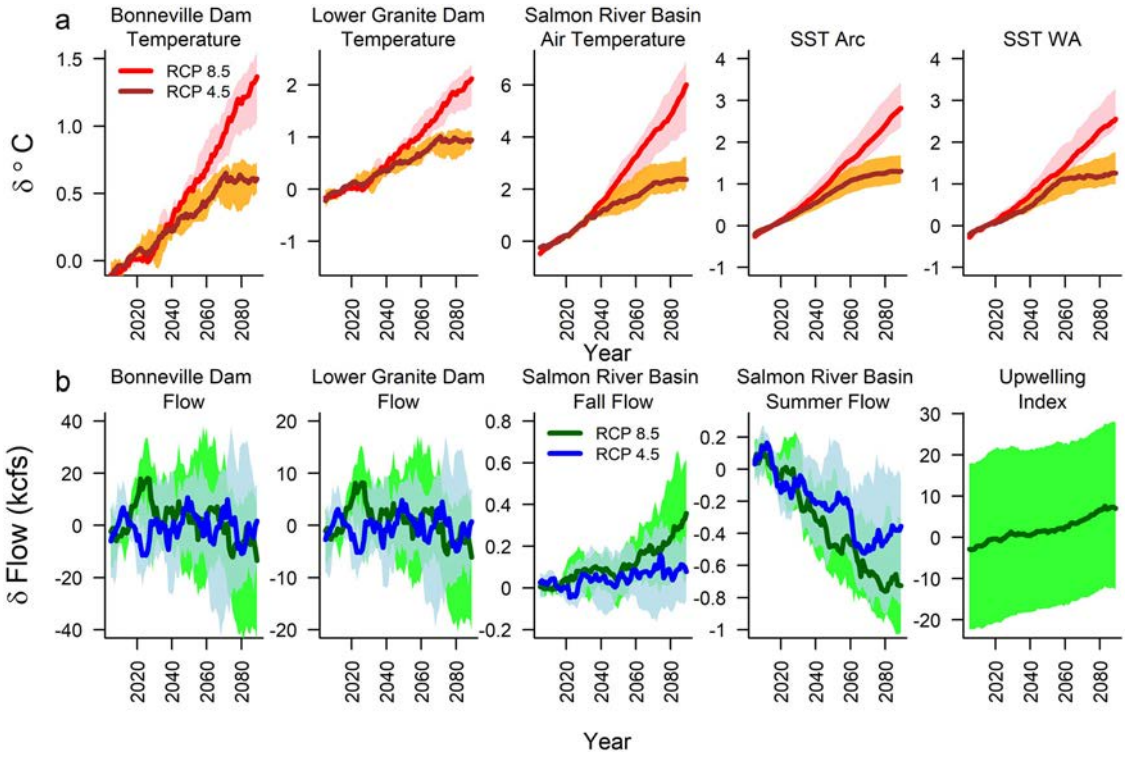


Fig. 2 Trends from global climate model projections used in climate scenarios. Global climate model projections are shown for each covariate that influenced population outcomes. Lines show median projections across climate models for two representative concentration pathways (RCPs), while shading shows the range across projections from the 25th to 75th quantiles. **a** Temperature covariates are shown in red for RCP 8.5 and brown for RCP 4.5, while **b** flow covariates are shown in green for RCP 8.5 and blue for RCP 4.5. For sources, see Supplementary Table 1. Note that the coastal upwelling index has different units from other covariates[112].

effect occurs[42]. Climate trajectories did level off in the second half of the 21st century under the RCP 4.5 scenario. This leveling reduced rates of population decline; however, most populations had already reached very low abundances at that point.

For practical purposes in salmon management, populations that have fewer than 50 spawners on average for 4 years in a row are considered to be at extremely high risk of extinction from chance fluctuations in abundance, depensatory processes, or the long-term consequences of lost genetic variation[43,44]. The evolutionary theory behind this threshold applies to isolated populations, and these populations are not truly isolated. So some small populations may be sustainable within a larger metapopulation. Nonetheless, when the majority of populations within an ESU pass this threshold, the ESU itself is at high risk. This ESU is already threatened with extinction because of historical declines[39]. Thus, although the 50-spawner threshold is somewhat arbitrary, it is a useful metric for demonstrating the severity of declines across all simulations. We assessed the first year (if any) in which a population in a given simulation fell below a quasi-extinction threshold of adult abundance (QET50). The QET50 is passed when the running mean of spawners, measured at the spawning stream, drops below 50 individuals over any 4-year period[45].

The proportion of all simulations in which a population dropped below QET50 increased dramatically under a warming climate compared with a detrended climate (Fig. 5). Under the representative concentration pathway (RCP) 8.5, ensemble-mean projection, even the largest populations (Bear Valley Creek and Secesh River) fell below QET50 in over 75% of simulations by 2060. Under RCP 4.5, the same milestone was passed a decade later.

Similar results with alternative model covariates. We conducted sensitivity analyses to characterize how extinction risk varied depending on covariates included in the model, and the extent to which impacts at different life stages predicted population-level response.

Alternative marine and freshwater covariate models had relatively little effect on overall patterns (Fig. 6). Resulting from the high importance of SST in model comparisons, all three models included combinations of basin-wide and coastal SST indices, which drives much of the overall effect on survival. Freshwater models differed in whether fall (Models 1 and 3) or summer (Model 2) flows limited smolt productivity. We considered both because the data were consistent with both models. Populations fared slightly worse in summer flow models because projected decreases in summer precipitation, increases in evaporation, and reduced groundwater storage cause summer flows to decline (Fig. 2). In contrast, fall precipitation (and hence fall flow) is projected to either stay the same or increase (Fig. 2). Models that included stronger increases in upwelling (blue, Q75 compared with Q25 in Fig. 6) were more optimistic because upwelling is positively associated with salmon survival. Nonetheless, negative effects from SST still drove most populations extinct within the century (Fig. 6).

Marine life stage most vulnerable to warming. The impact of climate change on freshwater life stages was not always negative but rather depended on population-specific and model-specific sensitivity. In the headwaters, the fall flow model produced a net benefit to parr-to-smolt survival, whereas the summer flow model lowered survival in the juvenile rearing stage (red and blue vs. yellow boxes in Fig. 7), but produced no difference in effects at other life stages. Thus, if climate change affected only the early rearing period and no other stage, there could be a mix of responses across populations depending on local limiting factors

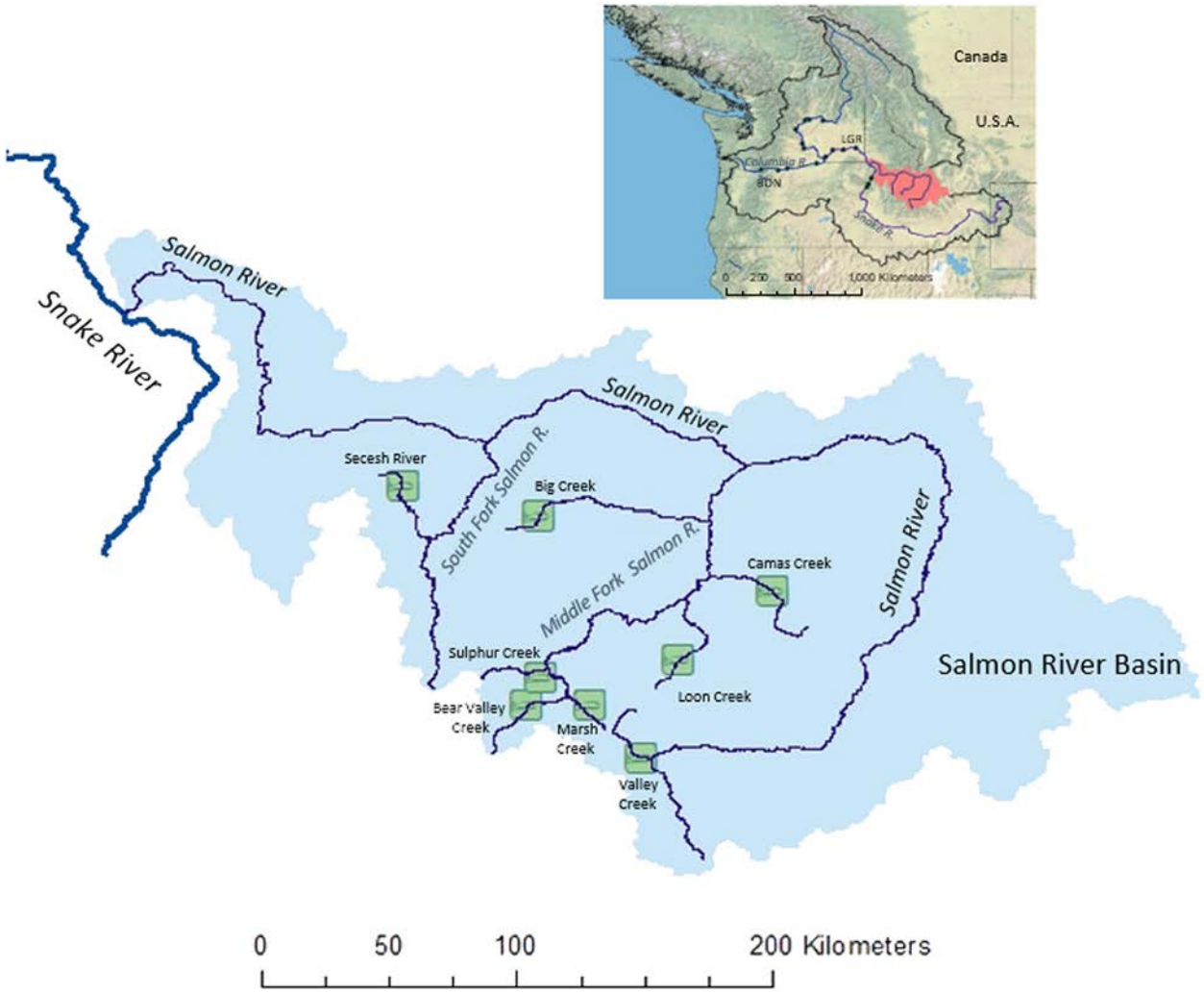


Fig. 3 Map of study populations. Chinook salmon populations included for modeling (green boxes in the lower map) are named by their natal stream in the Salmon River Basin. Insert above shows Columbia River Basin (black outline), with locations of the Salmon River Basin (red), Bonneville Dam (BON), and Lower Granite Dam (LGR).

such as summer vs. fall flow, similar to the conclusions of Crozier et al.[37].

Our model predicted that smolts would shift migration timing to arrive about 4.5 days earlier at Lower Granite Dam. This shift did indeed reduced temperature exposure in this life stage. Nonetheless, temperature effects on the juvenile migration still grew over time and reduced populations by about 18% on average from the 2020s to the 2060s.

Climate impacts were most dramatic in the marine stage, where survival was reduced by 83–90% (Fig. 7). This occurred despite the fact that smolts arrived at Bonneville Dam about 6.5 days earlier, indicating an earlier initiation of the marine stage, which generally improves marine survival[46].

Adult Chinook were also predicted to shift migration ~4 days earlier in response to warmer mainstem conditions with lower flows[47]. But again, this timing shift was not enough to prevent mortality from increased heat exposure. During the adult migration, populations that returned to spawning areas in summer (Secesh River and Valley Creek) were more affected by temperature than those that returned in spring, with net declines of up to 17% by the 2060 s. Still, the declines we found in the mainstem were relatively small because of the early adult run timing of Snake River spring/summer Chinook compared with other run types or species that migrate during peak temperatures.

Discussion

Our analysis showed relative resilience in freshwater stages, with the dominant driver toward extinction being rising SST, which tracked a ~90% decline in survival in the marine life stage. This occurred despite an advance in smolt migration timing and other changes in hydrosystem management. The modeled carryover effects of changes in timing are likely to be adaptive, but inadequate as compensation for large declines in marine survival.

Our results indicate that as one symptom of a changing ocean, rising SST puts all of our study populations at high risk of extinction, despite actions within the hydrosystem to speed juvenile travel and increase in-river survival. Small populations had minimal demographic buffers against declining marine survival rates and quickly dropped below the quasi-extinction threshold in nearly all simulations (Fig. 5). Threats to our larger study populations caused even greater concern because they are the remaining strongholds, which provide genetic and demographic resilience for the spring/summer Chinook salmon ESU as a whole[48].

Although we have focused on details for certain populations, there is strong synchrony across all populations within this Chinook ESU[49] and more broadly across other salmon species throughout their southern distributions[50,51]. Such synchrony

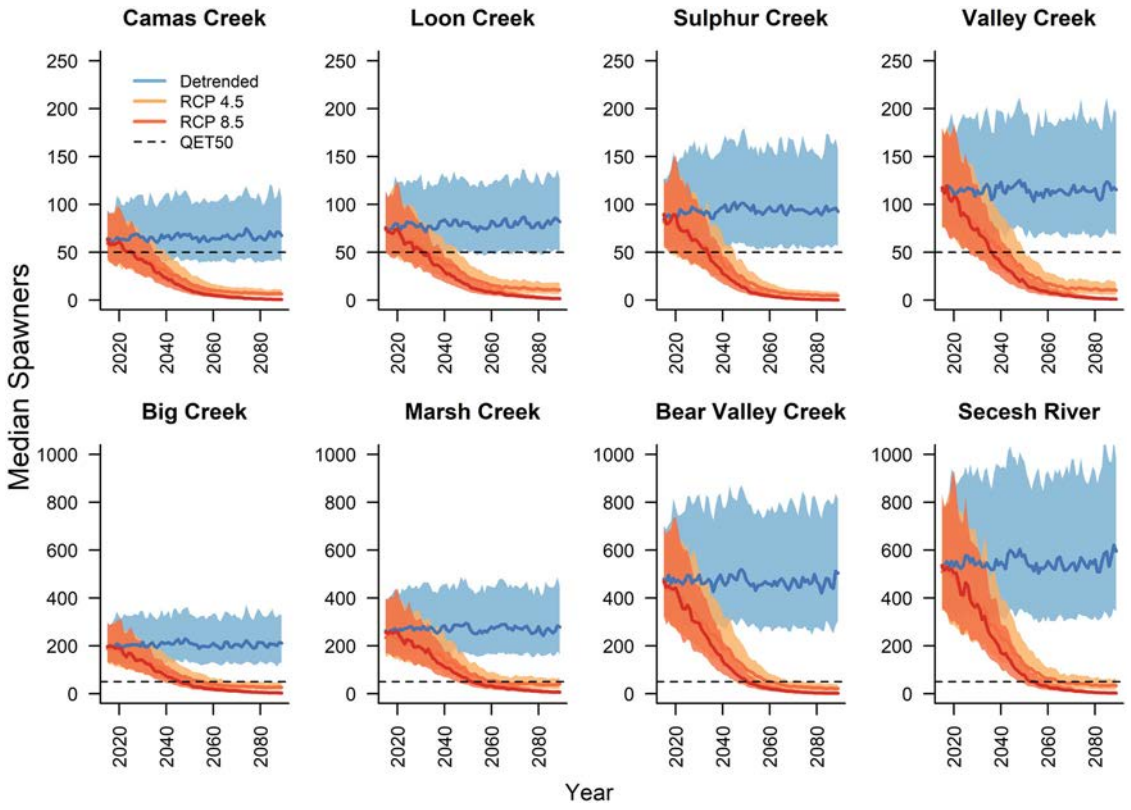


Fig. 4 Population abundance over time by population. Solid lines show the median while shading shows the interquartile range of population abundance across simulations for detrended (blue) vs. ensemble-mean global climate model projections for representative concentration pathways (RCP) 4.5 (orange) and 8.5 (red). Each panel shows a different population, ordered by present abundance. A reference abundance of 50 spawners, the quasi-extinction threshold (QET) is also shown (dashed horizontal line). Note the different *y* axes for small and large populations.

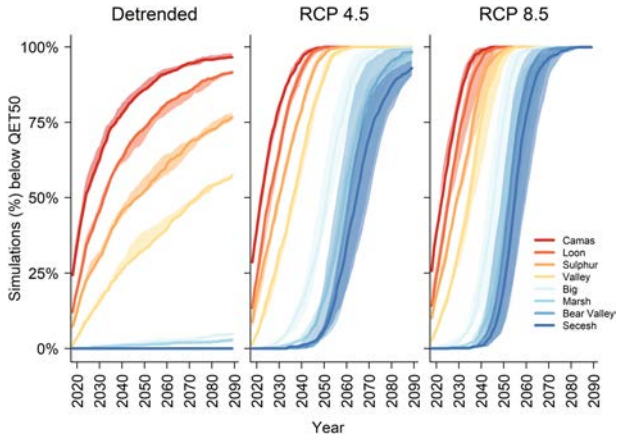


Fig. 5 Percent of simulations in which individual populations reached the quasi-extinction threshold. Time before most populations reached the quasi-extinction threshold (QET50) was longer in the detrended climate than in climate change scenarios RCP (representative concentration pathways) 4.5 and 8.5. For each climate scenario shown, solid lines reflect forcing by the median GCM projection, and shading reflects population responses across the interquartile range of projections.

suggests that the responses we found could represent a widespread phenomenon[52]. Salmon populations show coherence at many spatial scales, and synchrony has increased over time in both Pacific and Atlantic populations and in climate indicators[3,53,54].

Some Alaskan populations may fare better in response to ocean warming, but negative responses to warming in freshwater have been observed in other Alaskan populations, highlighting the benefits of examining the full life cycle[11,50,55]. And some studies have found similar declines in ocean survival over recent decades in southern and northern Chinook salmon[52]. Quantitative comparisons of combined climatic and anthropogenic influences, as well as more exploration of changing relationships among drivers, are needed to unravel the multiple pressures these populations face[4,56,57].

There are two main caveats to these modeled projections. First, the Northeast Pacific might not warm at the rate modeled, despite rising levels of atmospheric CO_2. Over the past century, global mean temperature has been a weaker determinant of SST than internal variability in the climate system, represented by strong changes in sea-level pressure and natural variability in ocean circulation[58]. How long this situation will continue is difficult to predict. Nonetheless, with the entire ocean warming at all depths[34], this signal will inevitably reach coastal waters.

A second possibility is that the Northeast Pacific will warm as modeled, but with some sort of ecological surprise[59] that will reverse the historical relationship between SST and salmon survival. Ocean temperature does not limit salmon through a direct physiological response, but rather through a combination of bottom-up and top-down trophic processes, which jointly regulate salmon growth and survival[60–62] and which explain the non-stationarity of statistical correlations[25]. Although warm conditions have been associated with lower-quality prey and more warm-water predators, it is possible that novel communities will arise with different responses to temperature, or that salmon will adapt to an altered food web in a positive manner. For example, salmon consumption rates could increase[63] with changes in the distribution of prey species[64]. Results from Model 3, in which marine survival was

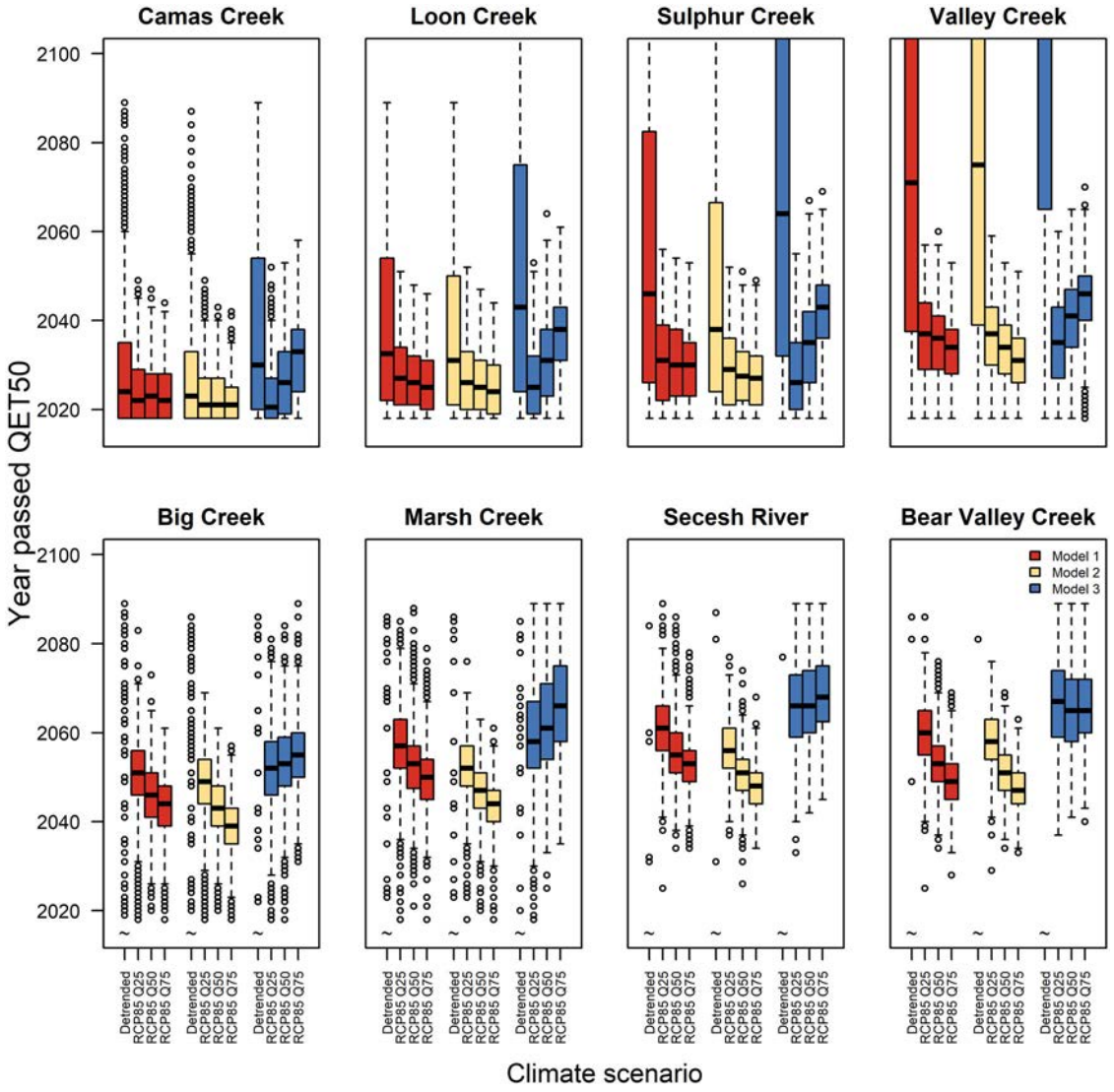


Fig. 6 Comparison of alternative models in the year each population met the quasi-extinction criterion. The year in which each population fell below the quasi-extinction threshold (QET50) for Model 1 (red), Model 2 (yellow), and Model 3 (blue). Model 1 covariates include sea surface temperature (SST), summer air temperature, and fall flow; Model 2 covariates include SST and summer flow; Model 3 covariates include SST, coastal upwelling, summer air temperature, and fall flow. Extinctions occurred earlier in scenarios with more warming (Q75) compared with less warming (Q25) in models that did not include upwelling (yellow and red) but later when more intense upwelling ameliorated SST effects (blue). However, in all models, extinctions occurred earlier in RCP 8.5 scenarios compared with a detrended climate. Note that larger populations (bottom row) often never dropped below QET50 in the detrended climate, indicated with ~. Boxes show the interquartile range across simulations, while whiskers extend to 1.5 times the interquartile range. Horizontal lines show the median values.

driven by upwelling, indicated that improved productivity in a warmer ocean could benefit salmon. Nonetheless, the benefit, in that case, was relatively small compared with overall negative effects. Further exploration using our model with a changing correlation structure over time could clarify additional possible trajectories and when they could be detected.

Other ecological surprises should also be considered, such as increases in competitors such as jellyfish[62] and Humboldt or market squid[65], either of which could reduce salmon survival in an altered ocean. Predators, which now concentrate on alternative prey, may change behavior when their preferred prey dwindle or shift distribution. Such behavioral change can either increase or decrease predation on salmon[66]. We recommend closely monitoring trophic interactions and salmon growth rates to detect such a possibility.

Finally, our model is conservative in that we have not accounted for any negative effects of ocean acidification. Declines of sensitive species could have a negative effect on salmon, especially salmon populations that rely more heavily on sensitive species[67]. We have assumed that ocean-stage salmon are relatively insensitive to pH, but if there are effects from ocean acidification, they will likely be negative[68,69].

Freshwater climate impacts in this study were also conservative in some respects. Specifically, we assumed linear responses to environmental variables, but actual physiological and ecological thresholds can create non-linear responses, meaning future temperature or flow impacts could have more severe effects. Furthermore, the primary covariate for juvenile survival in two of our models was fall flow, which was the covariate least sensitive to climate change[70]. Summer flow could also be (or become)

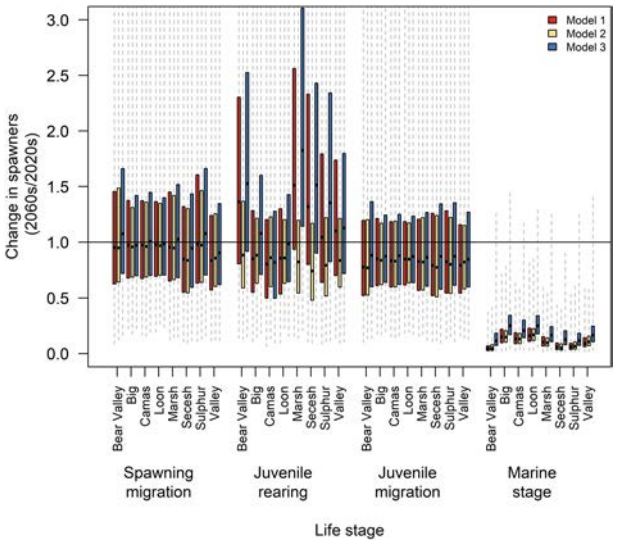


Fig. 7 Sensitivity analysis of the impact of climate change on individual life stages. Results from a three-by-four factorial experimental design examining relative loss in spawner abundance from 2020 to 2060 due to climate-change effects at four specific life stages. Net trends in population size are shown using the ratio of late abundance (2060–2069) compared with early abundance (2020–2029). Representative concentration pathway (RCP) 8.5 ensemble-mean climate trends were imposed at each life stage shown, with other life stages remaining under a detrended climate scenario. A value of 1.0 (horizontal line) indicates no change in spawner abundance. Boxes show the interquartile range across simulations, while the whiskers extend to the most extreme values of individual simulations. Horizontal lines show median values. Model 1 (red) covariates include sea surface temperature (SST), summer temperature, and fall flow; Model 2 (yellow) covariates include SST and summer flow; Model 3 (blue) covariates include SST, upwelling, summer temperature, and fall flow.

limiting (Model 2), and would cause a more negative response. More generally, the high-elevation, mostly-wilderness habitat of these populations is unusual for salmon in the region, and partially explains the relatively small effects of climate change on their freshwater life stages[71]. Other populations face more immediate impacts on freshwater productivity[16,72].

There is no easy way to completely mitigate for increasing SSTs that produce declines in marine survival of this magnitude. Additional changes to the juvenile transportation schedule or faster transit through the mainstem can still be explored, but improvements to survival through other mechanisms are needed. Ecosystem-based fisheries management attempts to consider the complex web of drivers for sustainability. These include both direct and indirect links to anthropogenic actions, as well as tracking of indicators in all sectors[73,74]. Conceptual models of factors that affect salmon marine survival show a large number of interacting processes[75,76]. Importantly, solutions involving management actions can be implemented in either the marine or freshwater realms.

In the marine realm, human activities can affect salmon survival through the harvest of salmon, their prey (sardine, anchovy, krill, juvenile rockfish, juvenile crab), predators (e.g., marine mammals), and competitors (e.g., hake, Pacific halibut, arrowtooth flounder). Changes in fisheries can consequently have positive or negative effects on salmon. Curtailed salmon harvest since the 1960s reduced one major source of direct mortality. Reduced harvest on top predators, however, led to rebounding marine mammal populations that now consume large amounts of salmon[61,77].

Sea-level rise combined with coastal development threatens complete loss of intertidal marshes in California and Oregon, as well as the majority of estuary habitat in Washington[78]. Such development will affect some salmon and their prey. Although the populations studied here generally spend relatively little time in the Columbia estuary, smaller, earlier-migrating individuals do utilize these estuary habitats[79]. As juvenile fish migrate earlier in the future, they might rely more on estuary habitat. Furthermore, other salmon populations depend heavily on estuary habitat for essential growth, and their success has been linked to estuary restoration actions[80].

Competition with hatchery fish interacts with climate effects to impact wild salmon in a complex manner[56] and is an area of active research. Reducing hatchery production could have positive benefits, especially for wild Alaskan salmon, which might then benefit from warmer conditions in some localities[11,55].

Other indirect anthropogenic effects on marine habitats are not well quantified and warrant more research. Increased awareness of the importance of forage fish for the entire food chain[81] has led to a ban on the development of new fisheries to exploit forage fish, demonstrating a proactive approach that should support salmon. But in sum, we lack key information on the full mechanistic basis of salmon marine survival, which limits the strength of end-to-end models for guiding management[82].

Efforts to mitigate carryover effects from freshwater that could affect marine survival in these populations have primarily focused on dams. Survival through Columbia and Snake River dams generally now meets recovery targets (>96%)[83], and cumulative mortality over 500 km of in-river migrating fish (~50%) is similar to that estimated for unregulated rivers of similar length (i.e., Fraser River[84]). However, slow travel time through slow-flowing reservoirs behind dams, combined with increased surface temperatures in these reservoirs[85], can potentially result in lower marine survival[86]. Mitigation efforts to increase smolt body size and advance migration timing could increase marine survival[46,87]. Restoration efforts in freshwater habitats, such as restoring floodplains, riparian planting to reduce stream temperature, reconnecting side-channel habitat[88], and supporting other natural processes in juvenile salmon rearing areas also enhance/restore freshwater salmon production.

Our models estimated strong density dependence at the parr-to-smolt stage, although it is not clear whether summer or winter habitat is constrained. Headwater areas are subjected to minimal anthropogenic impacts, but historical and current land use and irrigation withdrawals reduce habitat quality throughout the basin. Numerous actions have been identified in recovery plans and biological opinions that would improve rearing and migratory habitat in the mainstem Salmon River[40,89]. Our results suggest that at present, smolt carrying capacities are limited by flow more than temperature. Higher flows may create more habitat, improve connectivity, or decrease contact with predators. The predator community has also been affected by human impacts, from introduced sport fish (small-mouth bass and brook trout) to the creation of reservoir habitats extremely favorable to invasive fish species (e.g., American shad)[90].

Throughout salmon watersheds, improving and expanding access to rearing habitat should increase smolt abundance and body condition, resulting in improved population viability[91]. Intrinsic habitat potential is negatively correlated with present levels of disturbance, so restoring all critical habitat could yield substantial benefits. Specifically, the lower-elevation habitat that was historically highly productive has been preferentially lost. Improving individual fish growth by reducing contaminant loads[92], increasing floodplain habitat[91], and increasing habitat complexity, in general, could boost population productivity[93].

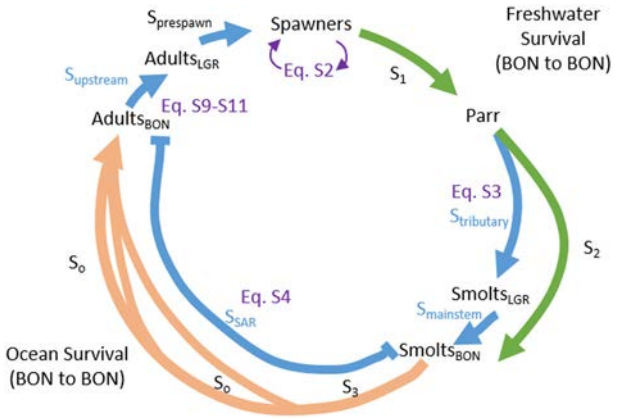


Fig. 8 Diagram of life-cycle model. Environmental covariate survival models that were fit directly to PIT-tag data are shown in blue ($S_{tributary}$, $S_{mainstem}$, S_{SAR}, $S_{upstream}$). Life stages and fitted transition parameters are shown in black, with associated equations for reference in the Supplementary Methods.

In conclusion, we have shown that prospects for saving this iconic keystone species in the conterminous U.S. are diminishing. Resilience to climate change depends on genetic and ecological diversity to adapt to environmental change. Many options have been considered over decades of dedication to salmon recovery, and improvements have been made. However, there are hard choices where human demands on land and water have come at the cost of wildlife.

The urgency is greater than ever to identify successful solutions at a large scale and implement known methods for improving survival. Management actions that open new habitat, improve productivity within existing habitat, or reduce mortality through direct or indirect effects in the ocean are desperately needed. We can find new ways to improve salmon habitats while maintaining other benefits for people, like reconnecting floodplains with rivers and natural marshes to recharge aquifers and mitigate flooding, storm surge, and channel erosion. Our modeling approach, which accounts for carryover effects across the life cycle, allows systematic exploration of alternative correlation structures among climate drivers and between climate drivers and ecological responses. This approach can provide a thorough accounting for uncertainty in climate projections and thus lay a path forward for evaluating the benefit of management actions protecting critical resources.

Methods

Data informing survival estimates. Spawner age and abundance estimates were compiled through large-scale collaborative efforts between states, tribes, and coordinating bodies[94–96]. Stage-specific survival estimates were obtained from multiple sources[97–100], originating from tagging and detection records downloaded from PTAGIS.org, a regional collaborative database (Supplementary Table 2). We used detection records only of fish identified as wild from known population sources. No hatchery fish were released in any of the streams supporting populations included for this analysis. Environmental covariates used in the model included air temperature, streamflow and temperature, SST, and coastal upwelling (Supplementary Table 3).

For the smolt-to-adult analysis, we considered data for all out-migrating yearling spring/summer Chinook salmon tagged in the Snake River Basin detected from 2000 to 2015 at Bonneville Dam—the furthest downstream dam on the Columbia River. We marked a fish as having survived the marine stage if it was detected at Bonneville Dam (or farther upstream) as an adult. The data included (i) the last detection date at Bonneville Dam as juveniles, (ii) transportation classification (transported or in-river), and (iii) whether the fish was detected in the Columbia River as an adult. Fish were identified by Columbia Basin Research (CBR) as having migrated volitionally or having been transported by barge. All PIT-tag files are available on the CBR website (http://www.cbr.washington.edu/dart/cs/data/nmfs_sar/). We excluded all fish with an unknown rearing type (i.e., hatchery versus wild), geographic regions with fewer than 200 individuals (over the 16 years), those fish released or tagged below the confluence of the Snake and Columbia Rivers, and fish that returned to spawn in less than 1 year. In addition, we excluded fish that passed Bonneville Dam prior to April 9th or later than July 8th (<0.14% of the total observations), because there was insufficient data to inform the temporal autocorrelation at the margins of the migration period. In total, there were 122,415 wild individuals for the SAR analysis.

Life-cycle model structure. We employed a stochastic, age-structured model modified from previous life-cycle models[37,38,101]. The model as depicted in Fig. 8 has five annual time-steps, based on the typical maximum 5-year generation time of Snake River spring/summer Chinook salmon. These time-steps correspond approximately to life-stage transitions.

The first time-step ("spawner to parr" stage) spans spawning (August/September), incubation, and early parr rearing. Survival through the second timestep (S_2) includes both tributary rearing ($S_{tributary}$) from summer (July or August) to the following spring when migrating juveniles pass Lower Granite Dam (April/May), and continue ($S_{mainstem}$) through the Snake and Columbia River hydrosystem.

The third timestep includes ocean entry (May/June) and the first winter and spring in the ocean. Some Chinook salmon return to spawn in their third year (jacks), but most females and mature adult males stay in the ocean for one or two more years, during which ocean survival is represented as S_o. The number of fish in the ocean each year is a latent variable, fit by detections of survivors when they re-enter freshwater ("smolt to adult return," or S_{sar}). Upstream migration survival through the hydrosystem ($S_{upstream}$) and from Lower Granite Dam to spawning areas ($S_{prespawn}$) are captured in the fourth or fifth timestep. Older females tend to lay more eggs, which is reflected in the fecundity parameter, F_5.

To calculate "effective spawners," we combined different age classes that returned to spawn in the same year as the weighted sum of three (weight = 0), 4- (weight = 1), and 5-year-old fish (weight = F_5). This sum was estimated by an expansion of the number of redds (nests) counted during spawning surveys[45].

Statistics and reproducibility. We fit the life-cycle model in two steps. First, we fit individual life-stage relationships with covariates using a variety of methods for different life stages to generate a posterior distribution for stage-specific parameter estimates. In addition to these parameters, the life-cycle model introduced some additional parameters that could not be directly fit to the data. We, therefore, conducted a second step to calibrate the life cycle model using the Approximate Bayesian Computing approach[102,103]. All analyses were conducted in RStudio (ver. 1.3.1073) using R (ver. 3.6.2)[104].

In the calibration step, we simulated population time series under recent climatic conditions using the life-cycle model. We compared the resulting spawner and smolt time series to those observed and ranked parameter sets by deviance from a Kolmogorov–Smirnov test. We selected the top 0.2% of 500,000 sets of parameter combinations (Supplementary Fig. 1). All resulting parameter sets met the criterion of producing a spawner distribution that was not statistically different from the observation dataset (P value > 0.05 from Kolmogorov–Smirnov test). This process maintained the appropriate correlation structure within each parameter set.

Spawner to parr (S_1) and parr to smolt ($S_{tributary}$) stages. We fit adult recruits per spawner for eight populations in a hierarchical Bayesian framework using multiple likelihood equations. These equations reflected stages that could be compared directly with data. Briefly, we fit a two-stage Gompertz function[105] (see Supplementary Methods) to solve the two stages simultaneously, combined with independently estimated survival rates for later stages. Individual population coefficients (productivity and capacity parameters for both stages as well as coefficients for temperature and flow) were assumed to be random samples from an underlying normal distribution[106] (priors shown in Supplementary Table 4).

To determine the best environmental covariates, we compared the estimated predictive error of alternative models using a leave-one-out, cross-validation method for Bayesian models using the LOO package[107]. Because of correlations among the climate variables tested, multiple models had similar support from the data (Supplementary Table 5). Our primary objective was to identify divergence in potential responses to climate change. Therefore, we selected two models with covariates that showed differing trajectories with climate change (Fig. 2). Model 1 included summer air temperature and fall streamflow, while model 2 included summer streamflow only.

Juvenile survival through the Columbia River hydrosytem ($S_{mainstem}$). We estimated juvenile survival from Lower Granite to Bonneville and arrival day at Bonneville Dam using the COMPASS model[108]. In the COMPASS model, equations for each dam and riverine reach used measured hourly flow, temperature, and spill to predict fish survival and migration rate. Dams had additional equations to determine the proportion of fish that passed using the spillway, turbine, or bypass system as a passage route. The COMPASS model also tracked the proportion of fish loaded into barges for transport and release downstream from the hydropower system.

Smolt-to-adult return (S_{sar}). We used a mixed-effects logistic regression model to determine the effects of ocean entry date and environmental covariates on the probability that an individual fish would return as an adult to Bonneville Dam. The model[109] included random effects of day and day-by-year interaction, which followed an auto-regressive process. Using Akaike Information Criterion, we selected variables with high importance based on model weights, which included a large-scale measure of SST (SSTarc) and a more local, coastal measure of SST (SSTwa), as well as spring upwelling. We applied separate models for fish that had migrated through the mainstem river vs. those that had been transported (Supplementary Table 6).

Adult upstream survival ($S_{upstream}$). For the adult upstream survival model, we used generalized additive mixed models (GAMMs) to evaluate the effects of both anthropogenic and environmental covariates on spring/summer Chinook salmon survival[47]. To run the model in simulation mode, all the non-environmental covariates (fisheries catch, proportion transported as juveniles) had distributions similar to those during the baseline period of 2004–2016. Survival from the hydrosystem to spawning streams ($S_{prespawn}$), was held constant due to lack of appropriate data with which to fit a relationship.

Calibration step. The model included a set of maturation parameters that could not be estimated directly from the data. Therefore, we treated them as tuning parameters for the life-cycle model as a whole. These parameters partitioned total smolt-to-adult survival (SAR) into age-specific survival rates (S) and propensity to return at a given age (b) as follows:

$$S_{SAR} = \frac{b_3 \times N_3 + b_4 \times N_4 + N_5}{N_2} \quad (1)$$

where b_3 denotes the proportion of all 3-year-old fish (N_3) that returned as jacks, b_4 is the proportion of all 4-year-olds (N_4) that returned to spawn, and N_5 is all 5-year-old fish. We calculated the number of fish in each age class as follows:

$$N_3 = S_3 \times N_2 \quad (2)$$

$$N_4 = (1 - b_3) \times N_3 \times S_0 \quad (3)$$

$$N_5 = (1 - b_4) \times N_4 \times S_0 \quad (4)$$

where S_3 denotes the survival rate of all smolts (N_2) over the first winter in the ocean and S_0 is the survival rate over subsequent years at sea. Fish that stay in the ocean longer have additional mortality, but there is a fecundity advantage (F) for older spawners because larger fish have higher fecundity. In the model, the effective number of spawners reflects the age distribution of female spawners, which return as either 4- or 5-year olds, with the latter having a fecundity advantage. A percentage of fish returned as 6-year olds, but it was so small that we pooled them with the 5-year olds.

We fit the tuning parameters (S_0, b_3, b_4, and F_5) using a modified Approximate Bayesian Computing approach[102,103]. We applied this method by first generating a prior distribution for each parameter. The priors for parameters that range between 0 and 1 (S_0, b_3, b_4) had a beta distribution centered on the mean and included the full range used by Zabel et al.[38] (Table 1). For F_5, we used the normal distribution with mean from Kareiva et al.[98] with sd = 0.1. These values were randomly combined with the freshwater parameter sets to create 500,000 combinations of all ten parameters.

We ran the life-cycle model to tune each population using each of these parameter sets in a different simulation. The life-cycle model was forced by historical meteorological conditions from 2000 to 2015 (Supplementary Table 3). For juvenile mainstem survival, we used COMPASS reconstructions of juvenile migration that incorporated actual river management practices. Note that historical river management was extremely variable over the juvenile migration stages and not comparable to the conditions we projected in climate simulations. In particular, transportation rates were higher, the spill was lower, and dam-passage survival was lower than in the corresponding actions proposed by the U.S. Army Corps of Engineers et al.[110] in their environmental impact statement. We ran the SAR model in retrospective mode, which used the fitted estimates of historical random effects and observation error. We simulated other life stages in the calibration as we would in future projections.

We ran 500,000 iterations with different parameter combinations through the historical reconstruction. We selected this number to produce at least 1000 sets of parameter values for each population that produced spawner distributions similar to those observed (Fig. 9). Parameter values from the top 0.2% of these parameter sets are shown compared with their prior distributions in Supplementary Fig. 1. The resulting models produced Kolmogorov–Smirnov P values from 0.16 to 0.76, each of which rejected the null hypothesis that modeled and observed time series came from different distributions ($P < 0.05$).

Climate scenarios

Detrended climate simulations. In creating future climate scenarios, our aim was to maintain the statistical properties of the environmental data driving survival in various life stages. Large-scale oceanic and atmospheric drivers affect marine and freshwater environments simultaneously. To account for this, we estimated an unstructured covariance matrix for all the freshwater and marine environmental covariates using the *Template Model Builder* (TBM) libraries for R[111]. We used a multivariate state-space model

$$\mathbf{x}_t \sim \mathrm{MVN}(\rho^x \mathbf{x}_{t-1}, \mathbf{Q}) \quad (5)$$

$$\mathbf{y}_t \sim \mathrm{N}(\mathbf{x}_t, 0.001) \quad (6)$$

where x_t was a vector of environmental processes at time t, ρ^x was the correlation between vectors from successive time-steps, and Q was an unstructured covariance matrix. For n covariates, the number of estimated correlation coefficients in the unstructured covariance matrix was equal to $0.5 \times n \times (n-1)$. Observation error for the observation model was fixed at 0.001, essentially implying that covariate data were measured without error.

Climate change scenarios. Our objective was to specifically explore how the relationships among various climate drivers interacted with population dynamics to shape population trajectories. To do this, we first simulated 1000 time series of 75 years of detrended environmental conditions that followed the model-fits of the covariance relationships in the historical record (Supplementary Fig. 2), although different matrices were generated for different models.

Second, we added offsets to these detrended simulations according to GCM projections. Each offset (trend) consisted of a single time series added to all 1,000 detrended simulations. Then, for each climate scenario, we input the resulting combinations of detrended-plus-offset environmental conditions into the life-cycle model as forcing factors.

For each model/population/climate scenario, we ran 1000 iterations. Climate trends were created from the median (GCM_{50}) and interquartile range across 10–80 GCM projections, depending on the covariate (Supplementary Table 1). We tracked geometric mean population abundance in 10-year intervals. We also assessed the first year (if any) in which a population in a given simulation fell below a quasi-extinction threshold of adult abundance (QET50). The QET50 was passed when the running mean of spawners, measured at the spawning stream, dropped below 50 individuals in any 4-year period[45].

We explored projected climate trends from two carbon emissions scenarios, representation concentration pathway (RCP) 4.5 and 8.5[112,113]. For marine variables, we used time-series output from GCMs directly. For freshwater variables, we used output that had been statistically downscaled and then processed through hydrological and stream temperature models[70,114,115]. For each variable, 10–80 time series per emissions scenario were available (Supplementary Table 1).

We used four steps to extract the relevant trends from GCMs. First, we calculated the variable mean (e.g., the average for a given month) over a baseline period centered on 2015 (2005–2025) within each time series individually. Second, we calculated anomalies from the 2005–2025 baseline period within each time series. Third, we created a 20-year running mean of anomalies for each time series. We smoothed each of these individual time series using a 20-year running mean to reduce interannual variation that was already accounted for by the TMB model. Fourth, we calculated the 25th, 50th, and 75th quantiles across all time series for each covariate in each year from the smoothed anomalies.

We repeated this process for each climate scenario, producing the trends shown in Fig. 2. These trends represented the spread across climate models of the low, medium, and high rates of change in each covariate. The smoothed trends were nearly linear because decadal and sub-decadal variability averaged out across models for most variables. However, decadal patterns were still apparent in the smoothed trends for flow, due to its very high natural variability as well as the few GCMs driving flow projections.

Although temperature and flow are physically linked (air temperatures are input into the hydrological models, and both air temperature and flow are input into stream temperature models) we found the trends for temperature were much more linear than those for flow. Thus, there was no consistent relationship between them (i.e., the rank order of temperature projections was not strongly correlated with the rank order of flow projections). We, therefore, treated the temperature and flow offsets as independent, and retained decadal variation in flow, which was low relative to annual variation. Exploration of alternative methods indicated this choice did not influence population responses.

Thus, in summary, we added each climate trend to the raw simulation of a detrended climate produced by the covariance model. All new time series retained the autocorrelation, variance, and covariance of the historical environment with forcing from greenhouse gas emissions added.

Life-cycle model simulations. Running the model in simulation mode was relatively straightforward for stages that had been fitted on an annual timestep (S_1 and $S_{tributary}$) because they only required an annual input of environmental conditions. However, submodels for upstream and downstream survival required daily environmental inputs. We, therefore, ran a separate step to produce survival estimates from numerous representations of daily time series, which were then grouped by annual spring mean temperature and flow. For each annual timestep, we sampled randomly from the appropriate disaggregated submodel output (Supplementary Methods).

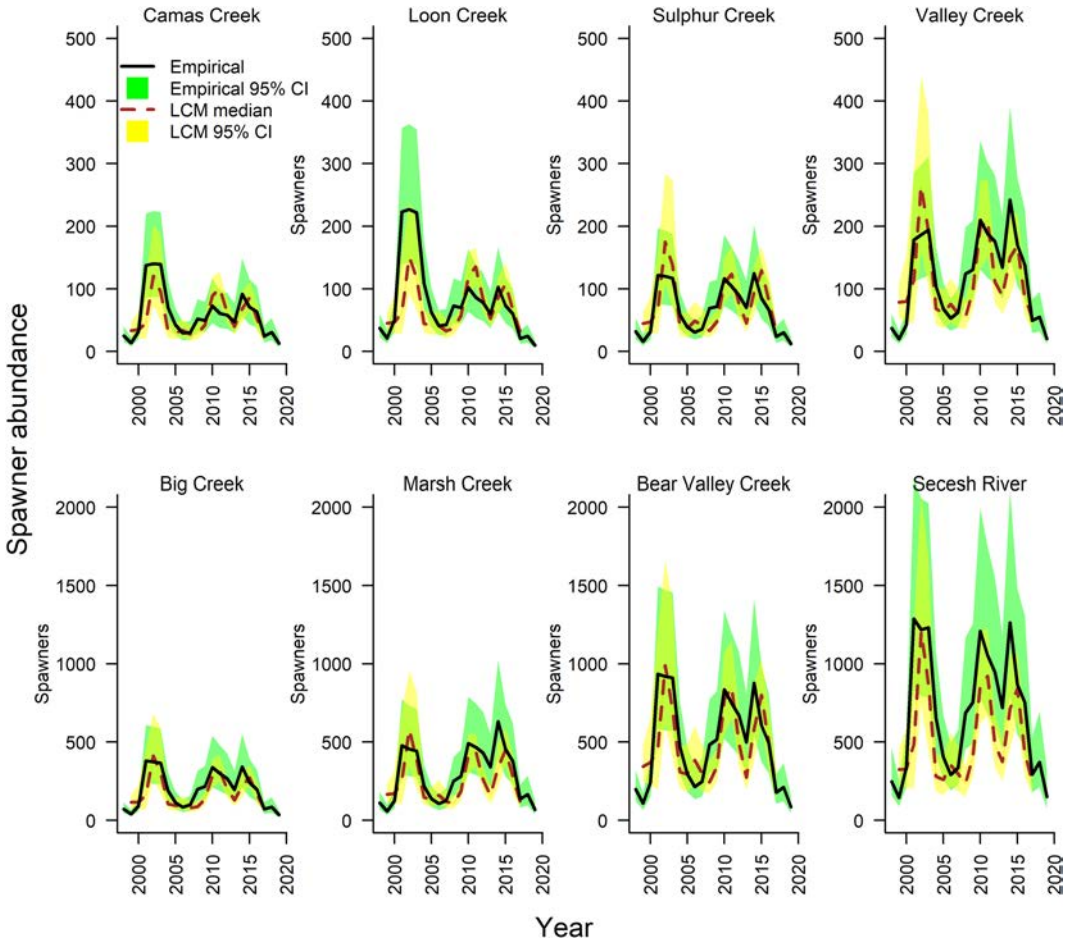


Fig. 9 Historical time series of spawner abundance. Heavy lines (black) show empirical estimates modeled from redd-count data for population status reviews, using methods described in ref. [39]. Broken lines (red) show median abundance from life-cycle model (LCM) simulations. The empirical estimates account for observation error and include 95% confidence limits, shown in green, while the 95% bounds from the life-cycle model are shown in yellow.

We ran the life-cycle model from 2015 to 2089, applying climate trends to the detrended climate for each environmental covariate on an annual timestep. We repeated 1000 iterations for each population, per model, and climate scenario. Our first results stemmed from a single combination of freshwater and marine covariates (Model 1: summer temperature + fall flow for freshwater, SSTarc in winter for transported fish, and SSTarc in winter + SSTwa in summer for in-river fish to show the full-time series of population response to climate scenarios (Figs. 4 and 5).

Sensitivity analyses. In our first sensitivity analysis, we compared population outcomes from Model 1 with a different freshwater covariate model (Model 2: summer flow + Model 1 marine covariates). Finally, we exchanged the marine covariates in Model 3: summer temperature + fall flow for freshwater, SST*wa* in summer for transported fish, and SST*arc* in spring + spring upwelling for in-river fish (Fig. 6). Thus, we explored all combinations of the top two models for freshwater and marine stages, respectively.

In our second sensitivity analysis, we applied climate trends for the ensemble mean of RCP 8.5 to one life stage, while the other life stages experienced a detrended climate (Fig. 7). We cycled through survival for parr-to-smolt stage ($S_{tributary}$), downstream migration ($S_{mainstem}$), smolt-to-adult return ratio (S_{sar}), and upstream spawning migration ($S_{upstream}$). In each case, we reported the extent of population decline as the ratio of geometric mean population size in 2060–2069 divided by mean abundance in 2020–2029. We ran 1000 simulations per life stage and calculated the mean change in abundance for each population.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All of the raw PIT-tag data used in this analysis are publicly available for download from PIT Tag Information System (www.PTAGIS.org). All survival estimates made from the raw data are published in other sources, listed in Supplementary Table 2. Redd counts are available upon request from the Idaho Department of Fish and Game (IDFG.idaho.gov) for all but one population, and from the Nez Perce Tribe for the Secesh River population (https://www.cbfish.org/Document.mvc/Viewer/P165414). Population estimates from redd counts were published by Ford, et al.[39] and are available at https://www.webapps.nwfsc.noaa.gov/apex/f?p=261:HOME:::::#. Environmental data are all publicly available from sources cited in Supplementary Tables 1 and 3. The source data underlying Figs. 2, 4–7, and 9 are provided as Supplementary Data 1.

Code availability

Model code is available on GitHub (lisa439/LCM).

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Author contributions

L.G.C. contributed to the conception, design, analysis, and interpretation of data and writing of the paper. B.J.B. and R.W.Z. contributed to design and interpretation of the work and manuscript revisions; B.E.C. contributed to the analysis, developing new methods for the marine survival stage, and writing. D.L.W. led data acquisition from PTAGIS, design, and analysis of the juvenile migration stage.

Competing interests

The authors declare no competing interests.

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PERSISTENT ORGANIC POLLUTANTS IN CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*): IMPLICATIONS FOR RESIDENT KILLER WHALES OF BRITISH COLUMBIA AND ADJACENT WATERS

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Abstract—We measured persistent organic pollutant (POP) concentrations in chinook salmon (*Oncorhynchus tshawytscha*) in order to characterize dietary exposure in the highly contaminated, salmon-eating northeastern Pacific resident killer whales. We estimate that 97 to 99% of polychlorinated biphenyls (PCBs), polychlorinated dibenzo-*p*-dioxins (PCDDs), polychlorinated dibenzofurans (PCDFs), dichlorodiphenyltrichloroethane (DDT), and hexachlorocyclohexane (HCH) in returning adult chinook were acquired during their time at sea. Highest POP concentrations (including PCBs, PCDDs, PCDFs, and DDT) and lowest lipids were observed in the more southerly chinook sampled. While feeding by salmon as they enter some more POP-contaminated near-shore environments inevitably contribute to their contamination, relationships observed between POP patterns and both lipid content and $\delta^{13}C$ also suggest a migration-related metabolism and loss of the less-chlorinated PCB congeners. This has implications for killer whales, with the more PCB-contaminated salmon stocks in the south partly explaining the 4.0 to 6.6 times higher estimated daily intake for ΣPCBs in southern resident killer whales compared to northern residents. We hypothesize that the lower lipid content of southerly chinook stocks may cause southern resident killer whales to increase their salmon consumption by as much as 50%, which would further increase their exposure to POPs.

Keywords—Persistent organic pollutants Polychlorinated biphenyls Chinook salmon Killer whale Dietary exposure

INTRODUCTION

Two populations of resident killer whales (*Orcinus orca*) frequent the coastal waters of British Columbia, Canada, and Washington, USA. The Canadian Species at Risk Act has designated northern resident killer whales as threatened, while the Species at Risk Act and the U.S. Endangered Species Act have designated southern residents as endangered. Although both are fish-eating, polychlorinated biphenyl (PCB) concentrations in the southern residents (males: 146 mg/kg lipid wt) are almost four times that of northern residents (males: 37 mg/kg lipid wt), placing them among the most PCB-contaminated marine mammals in the world [1]. Both populations elicit a strong preference for chinook salmon (*Oncorhynchus tshawytscha*), which comprises 70% of their estimated diet [2], underscoring the need to characterize persistent organic pollutant (POP) concentrations in this salmonid.

Anadromous chinook, the largest of the Pacific salmon, spend the majority of their life in the pelagic marine environment, where they undergo the majority of their growth before returning to freshwater natal streams for spawning [3]. Fish accumulate POPs through gill uptake (bioconcentration) and dietary uptake (biomagnification) [4]. Exposure to POPs in freshwater, estuarine, and coastal environments may explain the relative contamination of some salmon stocks [5], especially in the relatively PCB-contaminated Puget Sound [6,7]. However, it is apparent that global sources acquired by salmonids during their time in the North Pacific Ocean also contribute substantially to their contamination [8,9]. This has implications for wildlife, because POPs are delivered by salmon to coastal, freshwater, and terrestrial ecosystems [8,10,11]. Salmon partly explain the POPs found in British Columbia wildlife, including resident killer whales [1] and grizzly bears [12], though questions linger about their importance relative to other prey items.

As adult salmon enter near-shore marine waters en route toward their natal streams, they undergo dramatic changes in body weight, and lipid, protein, and water content [13]. Chinook salmon can lose more than 80% of their lipid during their return migration [13], which has profound ramifications for lipid-soluble contaminant concentrations.

The extent to which chinook salmon deliver POPs to resident killer whales is unclear [1], as are the sources of POPs to salmon. In the present study we measured POPs including flame-retardants, industrial by-products, and organochlorine (OC) pesticides in ocean-migrating smolts and in returning adults from four stocks of chinook salmon from British Columbia (Canada) and Washington (USA). Our objectives were to characterize in chinook salmon the POPs acquired locally as juveniles (i.e., prior to ocean migration) and the POPs acquired during time at sea, and to estimate the contribution of chinook to POP exposure in resident killer whales.

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MATERIALS AND METHODS

Chinook salmon collections

Chinook salmon smolts (n = 18) and adults (n = 24) were collected in southern British Columbia and Washington (Fig. 1). British Columbia adult chinook salmon were collected from Johnstone Strait and near the mouth of the Fraser River in October 2000. Chinook smolts were collected from central Strait of Georgia in August 2000. Washington adult chinook salmon were collected near the mouth of the Duwamish River and from the Tumwater Falls Hatchery on the Deschutes River in September 2001. Puget Sound chinook smolts were collected from the Green/Duwamish River and the Deschutes River during the period May through June 2001. Samples were individually wrapped in aluminium foil, bagged, and frozen at −20°C for transport and subsequent analysis.

Morphometrics and stock identification

Body weight and fork length were recorded for all chinook salmon, while sex was recorded for adult chinook only (Table 1). Dorsal muscle samples (1 cm^2) were collected for the adult chinook collected in Johnstone Strait and the Lower Fraser River and smolts from the Strait of Georgia and placed in 95% ethanol for DNA analyses. Stock identification was carried out by the Molecular Genetics Lab at the Pacific Biological Station (Fisheries and Oceans Canada, Nanaimo, BC). Thirteen microsatellite loci were amplified and DNA fragments were sized and sequenced on an automated ABI 377 DNA sequencer (Applied Biosystems, Foster City, CA, USA). Data analyses and classification procedures for species and stock identification are described elsewhere [14]. Fish scales from the left side posterior of the dorsal fin above the lateral line were removed for age determination, described in detail elsewhere [15]. Age determination was carried out by the Aging Lab at the Pacific Biological Station in accordance with their procedures and criteria, also described in detail elsewhere [16].

Sample preparation

Johnstone Strait and Lower Fraser River chinook fillet (muscle) tissue homogenates were prepared for analyses for both this study and a human health hazard assessment, whereas for Duwamish River, Deschutes River, and all chinook smolts whole fish tissue homogenates were prepared. Strait of Georgia chinook smolts were prepared as individual samples. However, Puget Sound smolts were pooled due to their small body size. Additionally, pooled fillet homogenates were prepared for Lower Fraser River and Duwamish River adult chinook. For Johnstone Strait and Lower Fraser chinook, rest of fish homogenates, which included all fish tissues except for fillet, were constructed for lipid determination in order to calculate POP body burdens, described in detail later. Fillet, rest of fish, and whole fish tissues were homogenized according to procedures described in detail elsewhere [17].

Stable isotope analysis

Whole salmon homogenates (20 g) were freeze-dried for 48 to 72 h and then ground to a fine powder using a mortar and pestle. Bulk stable carbon and nitrogen isotope ratio (^{15}N:^{14}N and ^{13}C:^{12}C) measurements were carried out at the Biogeochemistry Laboratory at the University of Victoria (Victoria, BC, Canada), equipment and standards described elsewhere [17]. Isotopic composition is expressed in δ notation as the proportional deviation in parts per thousand (‰) of the isotope ratio in a sample from that of a standard as in the following equation:

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1{,}000 \quad (1)$$

where X is ^{13}C or ^{15}N, and R_{sample} and $R_{standard}$ are the ratios of ^{13}C:^{12}C or ^{15}N:^{14}N for the sample and standard [18].

Contaminant analysis and lipid determination

Whole body (n = 12) and fillet (n = 12) adult chinook, whole body chinook smolts (n = 6), and one chinook smolt pool of 12 individuals (10 g) were analyzed for congener-specific polychlorinated biphenyls (PCBs), polychlorinated dibenzo-*p*-dioxins (PCDDs), polychlorinated dibenzofurans (PCDFs), and two pooled fillet samples for polybrominated diphenyl ethers (PBDEs), polychlorinated diphenyl ethers (PCDEs), and polybrominated biphenyls (PBBs) (reported as either individual or co-eluting congeners) using high-resolution gas chromatography–high-resolution mass spectrometry (HRGC-HRMS). For Duwamish River adults and all chinook smolts, organochlorine pesticides, including the dichlorodiphenyltrichloroethane (DDT) group [*o,p'*-DDT, dichlorodiphenyldichloroethane (DDD), dichlorodiphenyldichloroethylene (DDE), and *p,p'*-DDT, DDD, DDE], hexachlorobenzene (HCB), hexachlorocyclohexane (HCH) [α-HCH, β-HCH, γ-HCH], heptachlor, aldrin, chlordane [oxy-, γ-, α-], nonachlor [*trans-*, *cis-*], and mirex were measured using low-resolution gas chromatography–mass spectrometry (LRGC-MS) and gas chromatography with electron capture detection (GC-ECD).

Extraction and clean-up procedures, instrumental analysis and conditions, lipid determination, and quality assurance/quality control criteria used for PCBs, PCDDs, and PCDFs by the Regional Contaminant Laboratory (Fisheries and Oceans Canada) are described elsewhere [1,19]. Polybrominated diphenylethers, PCDEs, PBBs, and OC pesticides were analyzed by AXYS Analytical Services (Sidney, BC, Canada) according to their laboratory procedures and criteria and are described in detail elsewhere [17]; the PCDE method publication is in process. Lipid values were also determined by AXYS for samples analyzed for PBDEs, PCDEs, PBBs, and OC pesticides. Where whole fish lipid percentage data were compared, Regional Contaminant Laboratory values were reported.

Organochlorine pesticide analyses and lipid determinations for Johnstone Strait and Lower Fraser River fillet tissues were carried out by the Western Regional Laboratory, Health Canada (Burnaby, BC) using an in-house validated analytical method. The sample batch for OC pesticides included 10 samples, a reagent blank, and a replicate. Samples were spiked with ^{13}C-labeled surrogate standards and extracted with acetone:hexane (2:1 v/v) using a Polytron homogenizer (Luzern, Switzerland). The extract was centrifuged and the organic layer was further re-extracted with hexane and saturated sodium chloride. An aliquot of the organic layer was taken to dryness under vacuum with a rotary evaporator for lipid determination. The sample residue was redissolved in dichloromethane and the lipids removed by preparative gel permeation chromatography using a Waters high-pressure liquid chromatograph (Milford, MA, USA). The solvent of the gel permeation chromatography eluate was exchanged to hexane and the sample purified by eluting through a Florisil® (U.S. Silica, Berkeley Springs, WV, USA) column (2% deactivated) with dichloromethane:hexane (60:40 v/v). The purified eluate as concentrated to near dryness, dissolved quantitatively into iso-octane

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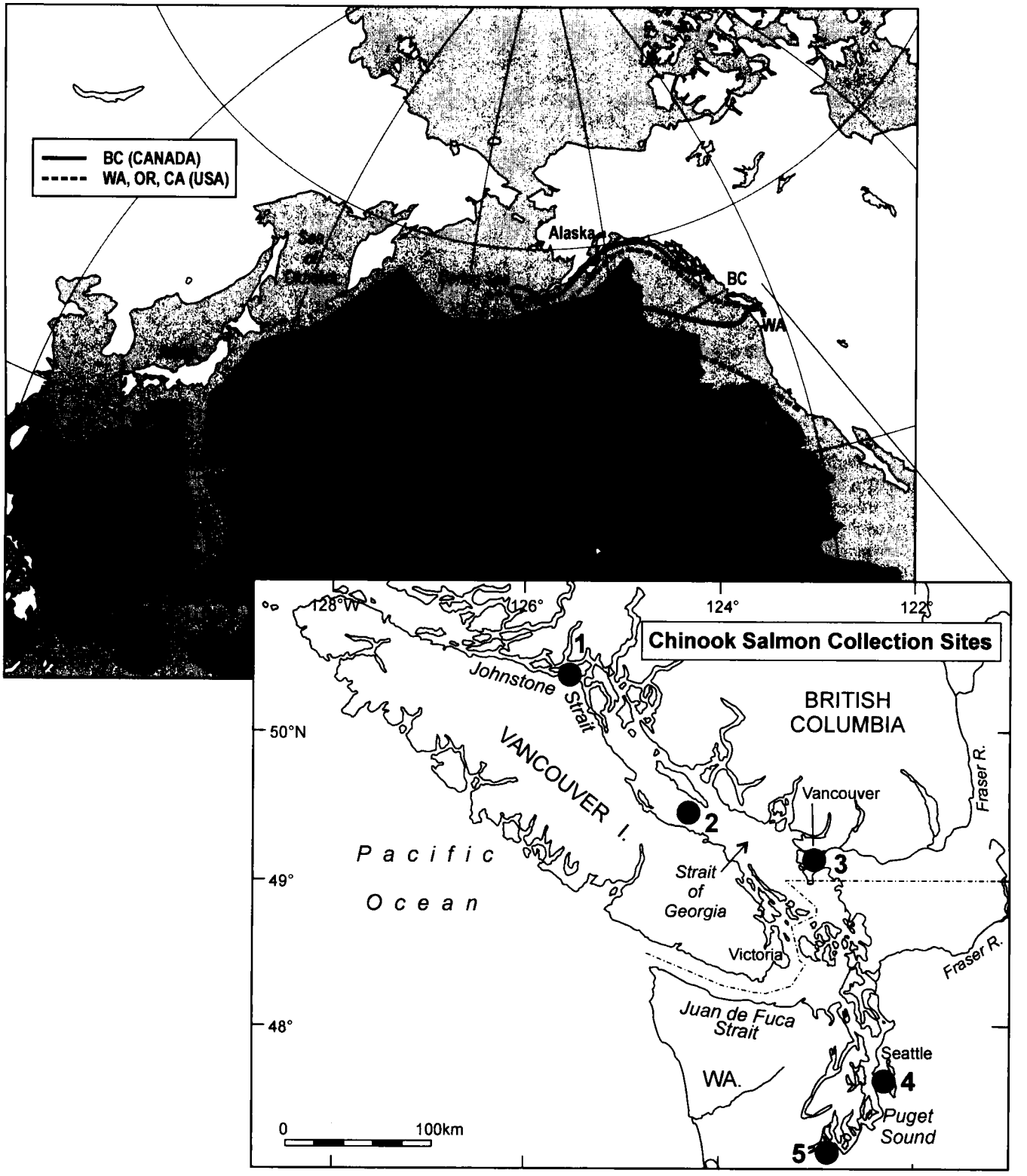


Fig. 1. Migratory routes [adapted from Fisheries and Oceans Canada, 2006 (www.pac.dfo-mpo.gc.ca/species/salmon/salmon_facts/chinook_e.htm)] and collection sites (inset map) for British Columbia (Canada) and Washington (USA) adult chinook salmon (*Oncorhynchus tshawytscha*) (n = 24). Johnstone Strait adult chinook were collected from site 1, Strait of Georgia chinook smolts were collected from site 2, Lower Fraser River adults from site 3, Duwamish River adults from site 4, and Deschutes River adults from site 5, Puget Sound smolts were collected upstream from both sites 4 and 5. Although ocean distribution for BC and Washington chinook encompasses the North Pacific Ocean and Bering Sea, greatest abundance has been observed along the North American coastal shelf waters [3]. BC = British Columbia; WA = Washington; OR = Oregon; CA = California.

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Table 1. Morphometric and related data for chinook salmon (*Oncorhynchus tshawytscha*) collected from Johnstone Strait and Lower Fraser River (British Columbia, Canada), Duwamish River, and Deschutes River (Washington, USA) and chinook smolts from the Strait of Georgia (British Columbia, Canada) and Puget Sound (Washington, USA). Values represent mean ± standard error of the mean. One-way analysis of variance (ANOVA) tests were used to assess significant differences ($\alpha = 0.05$) between the four adult salmon groups ($\nu = 23$) and Tukey post hoc tests to assess which groups differed (results in italics). Student's *t* test was used to assess significant differences between fillet and rest of fish lipid percentages

Group:	Strait of Georgia smolts	Johnstone Strait adults 1	Lower Fraser River adults 2	Puget Sound smolts	Duwamish River adults 3	Deschutes River adults 4	ANOVA test *(Tukey test)*
No. of fish (n =)	6	6	6	12	6	6	NS[a]
Fork length (cm)	17.98 ± 1.08	88.70 ± 2.47	73.88 ± 3.13	6.90 ± 0.19	77.28 ± 2.39	78.23 ± 2.28	0.004 *(1–2; 1–3; 1–4)*
Body wt (kg)	0.08 ± 0.02	10.86 ± 1.07	6.08 ± 0.57	0.003 ± 0.0001	6.32 ± 0.57	5.95 ± 0.44	0.001 *(1–2; 1–3; 1–4)*
Age (years)	NA[b]	3.50 ± 0.22	2.50 ± 0.34	NA	2.33 ± 0.21	2.33 ± 0.21	0.010 *(1–2; 1–3; 1–4)*
Sex (male:female)	3:3	3:3	5:1	NA	3:3	3:3	0.607
Whole fish lipid (%)	0.87 ± 0.26	14.06 ± 1.37[c]	9.48 ± 0.62[c]	1.35[d]	6.38 ± 0.61	4.29 ± 0.82	0.000 *(1–2; 1–3; 1–4; 2–4)*
Fillet lipid (%)	NA	10.03 ± 1.42	5.37 ± 0.92	NA	NA	NA	0.016
Rest of fish lipid (%)		19.45 ± 1.44	12.84 ± 0.77		NA		0.002
Moisture (%)	74.93 ± 0.85	62.55 ± 1.31	66.54 ± 0.17	79.41	69.70 ± 0.65	71.66 ± 1.62	0.000 *(1–3; 1–4; 2–4)*
$\delta^{15}N$	13.68 ± 0.17	14.97 ± 0.23	15.51 ± 0.05	10.26 ± 0.42[d]	15.59 ± 0.24	15.54 ± 0.37	0.282
$\delta^{13}C$	−18.23 ± 0.24	−20.51 ± 0.35	−18.59 ± 0.27	−22.84 ± 0.26[d]	−18.94 ± 0.36	−18.11 ± 0.50	0.001 *(1–2; 1–3; 1–4)*

[a] NS = no significant difference.
[b] NA = not analyzed.
[c] Whole fish lipid percentage calculated using fillet lipid percentage and rest of fish lipid percentage.
[d] Data generated from a pooled sample of 12 individuals.

and spiked with a ^{13}C-labeled internal standard for instrumental analysis.

Instrumental analysis by HRGC-MS was carried out using a VG Autospec-Q magnetic sector mass spectrometer (Manchester, UK) coupled with a Hewlett-Packard 5890 Series II gas chromatograph (Palo Alto, CA, USA), a CTC A200S autosampler (Canboro, NC, USA), and Micromass OPUS data system. Chromatographic separation was achieved through an Agilent (Santa Clara, CA, USA) J&W DB-5 capillary chromatography column (60 m × 0.25 mm internal diameter × 0.25 μm film thickness). The mass spectrometer was operated at a resolution of 5,000 in selected ion monitoring mode using two intense ions for each analyte.

Number of congeners detected either as individual or coeluting congeners out of a theoretical possible number in 31 salmon samples were 135 out of 209 for PCBs, 3 out of 75 for PCDDs, 2 out of 135 for PCDFs, and in two muscle pools, 26 and 28 out of 44 for PBDEs, 34 and 34 out of 44 for PCDEs, and 12 and 12 out of 21 for PBBs. Detection limit substitutions were made for PCB, PCDD, PCDF, and OC pesticide analytes that were not detected when at least 70% of samples had detectable concentrations. Where more than 70% of samples did not have detectable concentrations of analytes, concentrations were not reported. For the two pooled samples analyzed for PBDE, PCDE, and PBB analytes, detection limit substitutions were made when one sample had a detectable concentration. Toxic equivalent quotients (TEQs) were calculated for PCBs, PCDDs, and PCDFs using World Health Organization International toxic equivalent factors for humans and wildlife [20].

Statistical analyses

For comparisons among adult chinook salmon groups single factor analysis of variance (ANOVA) was done. The degrees of freedom (ν) for ANOVA test were 23 (including numerator and denominator) for all analyses except for OC pesticides where ν was 17. Data met the assumptions of normality and homogeneity of variance, or were log-normalized. If significant differences ($\alpha = 0.05$) existed among the adult chinook groups, Tukey post hoc tests were done to determine which groups were significantly different from each other. For comparison between fillet and rest of fish lipid percentages student's *t* tests were used (equal variances). Since chinook smolt groups consisted of one group of six samples and one pooled sample a statistical comparison was not possible.

Body burden calculations

Estimates of POP body burdens for chinook salmon adults and smolts were determined from either concentrations from whole fish homogenates, or, in the case of Johnstone Strait and Lower Fraser River salmon, from fillet concentrations. We assumed that lipid-normalized POP concentrations would be equally partitioned between whole fish and fillet, as previously documented in salmon [21]. Lipid content was determined for Johnstone Strait and Lower Fraser River salmon using a weighted combination of fillet lipid values and rest of fish (ROF) lipid values as follows:

$$\text{mass lipid (whole fish)} = \left(\frac{\text{mass fillet}}{\text{mass whole fish}}\right)\cdot\%\text{lipid (fillet)} + \left(\frac{\text{mass ROF}}{\text{mass whole fish}}\right)\cdot\%\text{lipid (ROF)} \quad (2)$$

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Body burden estimates were subsequently calculated using whole fish lipid percentages as follows:

$$\text{body burden (POPs)} = [\text{POP}]_{\text{lipid wt}} \cdot \text{mass lipid} \quad (3)$$

Principal components analysis

Principal components analysis (PCA) was used to characterize POP patterns among salmon and generate insight into the factors affecting them. Each PCB, dibenzo-*p*-dioxin, and dibenzofuran congener was evaluated for potential interferences, closeness to the limit of detection, and the percentage of undetectable (random value estimated) values. Borderline variables were tested in preliminary PCA models before inclusion in the final PCA data set, which included two dioxins (1,2,3,6,7,8-HxCDD and OCDD), two furans (2,3,7,8-TCDF and 2,3,4,7,8-PnCDF), and 130 PCBs (Appendix). Undetectable values (42 instances, or 1.31% of the data set; maximum of six undetectable values for 2,3,4,7,8-PnCDF and PCB188) were replaced by a random number between zero and the limit of detection, while the stated concentration was used for two values reported by the laboratory as not detected due to incorrect isotope ratio or NDR (peak detected but confirming-ion ratios outside of the specified range).

Samples were normalized to the concentration total to remove artifacts related to concentration differences between samples. The centered log-ratio transformation (division by the geometric mean of the concentration-normalized sample followed by log transformation) was then applied to this compositional data to produce a data set that was unaffected by negative bias or closure [7,22]. Data were then autoscaled (congeners were scaled by subtracting the variable mean and dividing by the variable standard deviation) to give every variable equal weight. Finally, a Varimax rotation was applied to the first three principal components (PCs) to simplify the physical interpretation of the PCA projections [7,23]. This rotation maximized or minimized the loading of each variable on each PC while preserving trends.

With $n = 24$ adult chinook and $p = 134$ contaminants, the PCA model provided a case where $n < p$ and the PCA model would be limited to $n - 1 = 23$ statistically valid eigenvectors [24]. The first few eigenvectors are little affected when the PCA data matrix is not of full rank and having $n < p$ does not lead to incorrect interpretations.

Linear relationships involving the PCA results were quantified using geometric mean (GM) linear regression [25,26]. The GM slope was calculated by dividing the y on x slope by the correlation coefficient for the regression, r [25]; the mean values for the x and y variables were then used to calculate the intercept for the GM regression equation. To estimate the relative shift in contaminant distribution for each sample we used the linear distance along the GM linear regression line for the fish samples, with the intersection point between the regression line and a perpendicular between the line and the sample position calculated using standard trigonometry mensuration formulae [23].

Dietary exposure calculations

As a means of characterizing health risks associated with dietary exposure we calculated estimated daily intakes (EDIs) of POPs by resident killer whales. Based on food consumption studies of captive killer whales, estimated intake as a function of body weight was calculated where food intake = $0.277\ \text{mass}^{0.663}$ [27]. We used this relationship to estimate food intake by a 2,500-kg adult killer whale and calculated EDIs for POPs with an assumption of 71.5% chinook consumption of a 96% salmonid diet [2]. Given the limited information on nonsalmon prey items in the diet of resident killer whales, we restrict our exercise here to their dominant prey item (chinook).

$$\text{Daily food intake for a 2,500 kg killer whale} = 0.277\ \text{mass}^{0.663} \quad (4)$$

$$\text{Salmonid portion of diet} = 96\% \cdot 50\ \text{kg/d} \quad (5)$$

$$\text{Chinook portion of diet} = 71.5\% \cdot 48\ \text{kg/d} \quad (6)$$

$$\text{EDI}\ (\mu\text{g/d}) = [\text{POP}]_{\text{wet wt}} \cdot 34\ \text{kg/d} \quad (7)$$

RESULTS AND DISCUSSION

As their primary prey item, chinook salmon provide both a source of nutrition and contaminants to northern and southern resident killer whales. The highly contaminated southern resident killer whales frequent the near-urban waters of the Strait of Georgia and Puget Sound, while northern resident killer whales ply the more remote waters of central and northern British Columbia. While logistical and ethical challenges preclude an accurate evaluation of dietary exposure to POPs by killer whales, we can estimate dietary POP exposure in these killer whales using data from chinook salmon.

Life history and feeding ecology of chinook

Since chinook salmon is the primary prey of killer whales, an understanding of their life history and feeding ecology is important to exploring issues related to exposure and bioaccumulation in the killer whale food web. Stock identification assigned at least 67% of the adults collected from Johnstone Strait to the Thompson River region and 83% of the adults collected from the mouth of the Fraser River to the Lower Fraser River region (with Harrison River being the most probable population). Harrison River stock is known to be predominantly coastal in its marine distribution, being found on the west coast of Vancouver Island, the Strait of Georgia and Washington waters, whereas Johnstone Strait (Thompson River stock) are known to migrate into the northern waters of British Columbia and the Gulf of Alaska [28] (www-comm.pac.dfo-mpo.gc.ca/publications/speciesbook/Salmon/chinook.fraser.html). All six chinook smolts sampled in the Strait of Georgia originated from eastern Vancouver Island, with five from Big Qualicum River and one from Little Qualicum River. Stock identification, $\delta^{13}C$, $\delta^{15}N$, morphometric, and meristic data provide an overview of the biology and ecology of sampled chinook salmon (Table 1).

Scale data from our chinook samples indicated that all adults migrated to marine waters during their first year of life with the exception of three British Columbia adults (two Johnstone Strait and one Lower Fraser River) that spent one year in freshwater before going to sea. Although scale data indicated that Duwamish and Deschutes river stocks migrated to marine waters during their first year of life, some fish from these populations are known to be resident stock that remain in Puget Sound waters year-round without migrating into open ocean [9].

A significant difference in $\delta^{13}C$ ratios was observed among adult stocks (one-way ANOVA, $\nu = 23$, $p = 0.001$) and lipid-normalizing the $\delta^{13}C$ ratios [29] did not statistically affect $\delta^{13}C$ ratios among adults ($r^2 = 0.24$, $\nu = 23$, $p = 0.0123$). However, no significant difference was apparent in $\delta^{15}N$ ratios among adults, suggesting similarities in trophic level (Table 1). Our

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Table 2. Wet weight-based concentrations of persistent organic pollutants and toxic equivalents (TEQs) to 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD) for polychlorinated biphenyls (PCBs), polychlorinated dibenzo-*p*-dioxins (PCDDs), and polychlorinated dibenzofurans (PCDFs) in returning adult chinook salmon (*Oncorhynchus tshawytscha*) from Johnstone Strait (n = 6) and Lower Fraser River (n = 6) (British Columbia, Canada); Duwamish River (n = 6) and Deschutes River (n = 6) (Washington, USA); and chinook smolts (n = 6) from the Strait of Georgia (British Columbia, Canada) and Puget Sound (n = 1 pool of 12) (Washington, USA). Values represent mean ± standard error of the mean. One-way analysis of variance (ANOVA) tests were used to assess significant differences (α = 0.05) between the four adult salmon groups (ν = 23) and Tukey post hoc tests to assess which groups differed (results in italics)

	μg/kg wet weight (except for ΣPCDD and ΣPCDF)[b]						
Sum congeners/ isomers[a] Group:	SG Smolts	Johnstone Strait 1	Lower Fraser River 2	PS Smolts	Duwamish River 3	Deschutes River 4	ANOVA test *(Tukey test)*
Lipid (%)[c]	0.87 ± 0.26	10.03 ± 1.42	5.37 ± 0.92	1.35	6.38 ± 0.61	4.29 ± 0.82	*(refer to Table 1)*
ΣPCB[d]	12.03 ± 1.46	9.07 ± 1.49	46.97 ± 8.06	9.63	34.61 ± 8.09	56.09 ± 17.97	0.001 *(1-2; 1-3; 1-4)*
ΣPCB TEQ	0.30 ± 0.04	0.17 ± 0.03	0.74 ± 0.11	0.28	0.55 ± 0.12	1.09 ± 0.35	0.007 *(1-2; 1-4)*
ΣPCDD[d] (ng/kg)	1.39 ± 0.32	0.58 ± 0.05	0.81 ± 0.14	1.57	0.83 ± 0.15	1.74 ± 0.63	0.011 *(1-4)*
ΣPCDD TEQ	0.35 ± 0.10	0.03 ± 0.02	0.27 ± 0.08	0.00	0.12 ± 0.04	0.31 ± 0.05	0.00 *(1-2; 1-3; 1-4)*
ΣPCDF[d] (ng/kg)	2.03 ± 0.48	0.50 ± 0.12	1.90 ± 0.38	0.26	1.30 ± 0.24	1.92 ± 0.31	0.000 *(1-2; 1-3; 1-4)*
ΣPCDF TEQ	0.24 ± 0.06	0.06 ± 0.02	0.28 ± 0.05	0.00	0.11 ± 0.04	0.25 ± 0.06	0.007 *(1-2; 1-4)*
ΣPBDE[e]	NA[f]	NA	17.71	NA	6.43	NA	ND[g]
ΣPCDE[e]	NA	NA	0.53	NA	0.24	NA	ND
ΣPBB[e]	NA	NA	0.10	NA	0.04	NA	ND
ΣTEQs	0.89 ± 0.20	0.26 ± 0.06	1.30 ± 0.19	0.28	0.78 ± 0.18	1.65 ± 0.44	0.006 *(1-2; 1-4)*

[a] PCB = polychlorinated biphenyl; PBDE = polybrominated diphenyl ether; PCDE = polychlorinated diphenyl ether; PBB = polybrominated biphenyl; PCDD = polychlorinated dibenzo-*p*-dioxin; PCDF = polychlorinated dibenzofuran.
[b] SG = Strait of Georgia; PS = Puget Sound.
[c] Whole fish percentage lipid for SG smolts, PS smolts, Duwamish and Deschutes river adults; fillet percentage lipid for Johnstone Strait and Lower Fraser River adults.
[d] Whole fish analyzed for SG smolts, PS smolts, Duwamish and Deschutes river adults; fillet analyzed for Johnstone Strait and Lower Fraser River adults.
[e] Pooled fillet (n = 1 pool of 6 fish) analyzed.
[f] NA = not analyzed.
[g] ND = statistical comparison not possible.

chinook $\delta^{15}N$ ratios and $\delta^{13}C$ ratios decreased with lipid % in whole fish (r^2 = 0.18, ν = 23, p = 0.0404 and r^2 = 0.59, ν = 23, $p < 0.0001$, respectively) (data not shown). Previous studies have demonstrated that $\delta^{13}C$ and $\delta^{15}N$ ratios can be affected by the nutritional status of organisms [30–32] and that a range of at least 4 to 6‰ should be expected in both $\delta^{13}C$ and $\delta^{15}N$ values during the migration of salmon that is due to changes in lipid and protein concentrations [30]. Therefore, enrichment in $\delta^{13}C$ and $\delta^{15}N$ ratios with decreasing lipid content in our chinook salmon likely reflects the migration-associated influence of declining lipid stores on $\delta^{13}C$ and $\delta^{15}N$ values, rather than trophic level or feeding ecology. This is consistent with changes in physiological condition in chinook salmon as they near their natal streams.

Contaminant concentrations in chinook salmon

Significant differences in PCB, PCDD, and PCDF concentrations, on a wet weight basis, were observed among adult salmon (ν = 23, p = 0.001, p = 0.011, p = 0.000, respectively), with Johnstone Strait salmon having the lowest concentrations and Deschutes River salmon having the highest concentrations (Table 2). Polychlorinated biphenyls were the dominant POP detected in all salmon sampled, including smolts. Two of the six adult chinook sampled from each of the Lower Fraser, Duwamish, and Deschutes rivers exceeded mean PCB concentrations found in a previous study where Puget Sound returning chinook, collected from either near-shore estuaries or river locations had a detected mean value of 49.1 μg/kg wet weight [9].

Significant differences in OC pesticides were observed among the adult salmon stocks (Table 3). Duwamish River salmon had the highest concentrations of all OC pesticides with the exception of HCH compounds. Total DDT dominated the OC pesticide rankings among both British Columbia and Washington smolts and three out of the four returning adult groups (Table 3), while total HCH dominated the OCs in Johnstone Strait adults. Although DDT and HCH appear to be the dominant OC pesticides detected in both British Columbia and Washington salmon, their isomeric compositions may reflect differences in distance from source or use regions. The contribution of the DDT degradation products (ΣDDE and ΣDDD) in all chinook samples was 88 to 97% of the ΣDDT, suggesting fresh input to be minimal. The high concentrations of the predominant parent α-HCH isomer, the most bioaccumulative isomer β-HCH, and lower concentrations of the insecticide γ-HCH are apparent as one moves away from source/use regions, reflecting partitioning properties which favor colder, more northerly waters [33]. The volatility of HCH ensures its ready atmospheric transport from Asia to the northeastern Pacific Ocean via prevailing winds [34].

Of the two adult chinook pools analyzed for PBDEs, the most predominant congeners detected were BDE-47 and BDE-99, respectively. The PBDE profile for Lower Fraser River chinook was 47 > 99 > 100 > 49 > 209, and for Duwamish River chinook was 47 > 99 > 100 > 49 > 120. Similar congener profiles have been observed in chinook from Oregon (BDE-47 > 99 > 100 > 49 > 154) [35] and in Lake Michigan salmonids (BDE-47 > 99 > 100 > 154 > 153) [36]. The ratio of PBDE to PCB concentrations were 0.4:1 for the Lower Fraser River adults and 0.2:1 for the Duwamish River adults, highlighting the emergence of PBDEs as a significant environmental contaminant.

Significant differences in ΣPCB TEQs, ΣPCDD TEQs, ΣPCDF TEQs, and ΣTEQs were observed among the four adult

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Table 3. Wet weight-based concentrations of organochlorine pesticides in returning adult chinook salmon (*Oncorhynchus tshawytscha*) from Johnstone Strait (n = 6) and Lower Fraser River (n = 6) (British Columbia, Canada); Duwamish River (n = 6) and chinook smolts (n = 6) from the Strait of Georgia (British Columbia, Canada) and Puget Sound (n = 1 pool of 12) (Washington, USA). Values represent mean ± standard error of the mean. One-way analysis of variance (ANOVA) tests were used to assess significant differences (α = 0.05) between the three adult salmon groups (ν = 17) and Tukey post hoc tests to assess which groups differed (results in italics)

	μg/kg wet weight[a]						
Sum congeners/ isomers[b] Group:	SG Smolts[c]	Johnstone Strait[d] 1	Lower Fraser River[d] 2	PS Smolts[c]	Duwamish River[c] 3	Deschutes River[c]	ANOVA test *(Tukey test)*
Lipid (%)	0.87 ± 0.26	10.03 ± 1.42	5.37 ± 0.92	1.35	6.38 ± 0.61	4.29 ± 0.82	*(refer to Table 1)*
ΣDDT	4.38 ± 0.55	1.46 ± 0.27	4.29 ± 0.50	2.68	18.31 ± 3.94	NA[e]	(0.000) *(1-2; 1-3; 2-3)*
o,p'-DDT	*0.05 ± 0.01*	*0.07 ± 0.02*	*0.04 ± 0.00*	*0.02*	*0.12 ± 0.01*	NA	(0.014) *(2-3)*
p,p'-DDT	*0.27 ± 0.04*	*0.10 ± 0.02*	*0.22 ± 0.03*	*0.10*	*0.40 ± 0.08*	NA	(0.000) *(1-2; 1-3)*
o,p'-DDD	*0.06 ± 0.01*	*0.07 ± 0.01*	*0.06 ± 0.01*	*0.01*	*0.21 ± 0.02*	NA	(0.001) *(1-3; 2-3)*
p,p'-DDD	*0.40 ± 0.08*	*0.25 ± 0.03*	*0.60 ± 0.05*	*0.13*	*2.88 ± 0.50*	NA	(0.000) *(1-2; 1-3; 2-3)*
o,p'-DDE	*0.08 ± 0.02*	*0.07 ± 0.01*	*0.04 ± 0.00*	*0.02*	*0.12 ± 0.02*	NA	(0.000) *(1-2; 1-3; 2-3)*
p,p'-DDE	*3.52 ± 0.43*	*0.90 ± 0.21*	*3.34 ± 0.42*	*2.40*	*14.58 ± 3.39*	NA	(0.000) *(1-2; 1-3; 2-3)*
(ΣDDE + ΣDDD) ÷ ΣDDT	0.93 ± 0.00	0.88 ± 0.01	0.94 ± 0.00	0.95	0.97 ± 0.01	NA	(0.002) *(1-2; 1-3)*
HCB	0.36 ± 0.06	1.50 ± 0.16	0.85 ± 0.09	0.29	2.15 ± 0.12	NA	0.000 *(1-2; 1-3; 2-3)*
ΣHCH (α-, β-, γ-)	1.09 ± 0.25	2.28 ± 0.23	0.68 ± 0.14	0.27	1.60 ± 0.20	NA	0.000 *(1-2; 1-3; 2-3)*
alpha (α-)	*0.32 ± 0.08*	*0.98 ± 0.10*	*0.25 ± 0.05*	*0.08*	*0.84 ± 0.10*	NA	0.000 *(1-2; 2-3)*
beta (β-)	*0.34 ± 0.08*	*1.09 ± 0.11*	*0.37 ± 0.08*	*0.10*	*0.63 ± 0.08*	NA	0.000 *(1-2; 1-3)*
gamma (γ-)	*0.43 ± 0.10*	*0.21 ± 0.02*	*0.06 ± 0.01*	*0.08*	*0.12 ± 0.03*	NA	0.005 *(1-2; 1-3)*
Heptachlor	<DL[f]	<DL	<DL	<DL	<DL	NA	ND
Aldrin	<DL	<DL	<DL	<DL	<DL	NA	ND
Chlordane (*oxy*-, γ-, α-)	0.78 ± 0.14	0.68 ± 0.04	0.62 ± 0.06	0.43	1.90 ± 0.14	NA	0.000 *(1-3; 2-3)*
oxy-	*0.44 ± 0.11*	*0.14 ± 0.00*	*0.14 ± 0.01*	*0.31*	*0.49 ± 0.08*	NA	0.018 *(1-3; 2-3)*
gamma (γ-)*trans*	*0.13 ± 0.02*	*0.10 ± 0.01*	*0.07 ± 0.01*	*0.05*	*0.22 ± 0.02*	NA	0.000 *(1-2; 1-3; 2-3)*
alpha (α-)*cis*	*0.21 ± 0.04*	*0.43 ± 0.03*	*0.42 ± 0.04*	*0.07*	*1.18 ± 0.11*	NA	0.003 *(1-3; 2-3)*
ΣChlordanes[g]	1.41 ± 0.20	1.47 ± 0.07	1.6 ± 0.16	0.84	4.75 ± 0.38	NA	0.003 *(1-3; 2-3)*
ΣNonachlor (*trans*-, *cis*-)	0.58 ± 0.10	0.64 ± 0.03	0.87 ± 0.10	0.27	2.53 ± 0.25	NA	0.002 *(1-3; 2-3)*
trans-	*0.41 ± 0.07*	*0.46 ± 0.02*	*0.63 ± 0.07*	*0.22*	*1.87 ± 0.17*	NA	0.002 *(1-3; 2-3)*
cis-	*0.17 ± 0.03*	*0.18 ± 0.01*	*0.25 ± 0.03*	*0.05*	*0.67 ± 0.09*	NA	0.002 *(1-3; 2-3)*
Mirex	0.05 ± 0.01	0.02 ± 0.00	0.02 ± 0.00	0.03	0.06 ± 0.01	NA	0.003 *(1-3; 2-3)*
Heptachlor epoxide	0.05 ± 0.02	0.14 ± 0.01	0.09 ± 0.01	0.02	0.28 ± 0.04	NA	0.000 *(1-2; 1-3; 2-3)*
Endosulphan, *alpha* (α-)	<DL	<DL	<DL	<DL	<DL	NA	ND[h]
Dieldrin	0.16 ± 0.04	0.45 ± 0.02	0.64 ± 0.06	0.03	0.75 ± 0.11	NA	0.012 *(1-3)*
Endrin	0.02 ± 0.01	0.08 ± 0.01	0.06 ± 0.01	0.06	0.38 ± 0.07	NA	0.002 *(1-3; 2-3)*
Methoxychlor	<DL	<DL	<DL	<DL	<DL	NA	ND

[a] SG = Strait of Georgia; PS = Puget Sound.
[b] DDT = dichlorodiphenyltrichloroethane; DDD = dichlorodiphenyldichloroethane; DDE = dichlorodiphenyldichloroethylene; HCB = hexachlorobenzene; HCH = hexachlorocyclohexane.
[c] Whole fish analyzed.
[d] Fillet analyzed.
[e] ΣChlordanes = heptachlor + heptachlor epoxide + oxychlordane + *cis*- and *trans*-chlordane + *cis*- and *trans*-nonachlor.
[f] NA = not analyzed.
[g] <DL = less than detection limit.
[h] ND = statistical comparison not possible.

salmon stocks (Table 2). Although PCBs explained the majority of ΣTEQs in the adult salmon groups, Lower Fraser River adults had a significantly lower Σplanar PCB TEQ contribution to the ΣTEQ compared with the Johnstone Strait and Duwamish River adults (ν = 23; p = 0.007 and p = 0.011, respectively). This in part is due to the higher ΣPCDD contribution to the ΣTEQ in the latter samples. While this may in part reflect differences in dietary exposure for the different stocks, metabolic removal or preferential elimination of the planar PCBs may also explain this observation. Polychlorinated biphenyls made up 100% of the ΣTEQs in the Puget Sound smolts, whereas in the Strait of Georgia the ΣPCDD and ΣPCDF TEQs made up a greater proportion of the ΣTEQs. These results are consistent with those found in our Puget Sound and Strait of Georgia harbor seal food baskets, likely reflecting differences in regional source inputs between pulp mills in the Strait of Georgia and more industries in Puget Sound [17].

POP origin in returning adult salmon

By comparing body burdens of POPs in returning adult chinook to out-migrating smolts and juveniles, we estimate that 97 to 99% of the body burden of PCBs, PCDDs, PCDFs, DDT, and HCH in all stocks originated during their time at sea (Table 4). Field sampling provided us with salmon that could be identified only after genetic analysis. As a result of differences in stock identification between some smolts and adults, stock-specific assignment of the POPs in adults was not directly possible. Our estimation that the majority of POPs in chinook salmon can be ascribed to their growth stage in coastal and marine waters is consistent with other studies. A study of chinook from Washington ascribed 99% of PCBs in returning Duwamish River adults to the waters of Puget Sound and the Pacific Ocean [9]. The concentrations of POPs detected in our smolts are comparable to values previously reported in outmigrating chinook salmon smolts from a number of stocks

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Table 4. Estimated body burdens of persistent organic pollutants in returning adult chinook salmon (*Oncorhynchus tshawytscha*) from Johnstone Strait (n = 6) and Lower Fraser River (n = 6) (British Columbia, Canada); Duwamish River (n = 6) and Deschutes River (n = 6) (Washington, USA); and chinook smolts (n = 6) from the Strait of Georgia (British Columbia, Canada) and Puget Sound (n = 1 pool of 12) (Washington, USA). Body burden estimates calculated using POP lipid weight concentrations and whole fish lipid mass. Values represent mean ± standard error of the mean. One-way analysis of variance (ANOVA) tests were used to assess significant differences (α = 0.05) between the four adult salmon groups (ν = 23) and three adult groups for total dichlorodiphenyltrichloroethane (ΣDDT) and total hexachlorocyclohexane (ΣHCH) (ν = 17). Tukey post hoc tests were used to assess which groups differed (results in italics)

	Body burden (μg) (except for ΣPCDD and ΣPCDF)						
Sum congeners/ isomers[a] Group:	Strait of Georgia smolts	Johnstone Strait adults 1	Lower Fraser River adults 2	Puget Sound smolts	Duwamish River adults 3	Deschutes River adults 4	ANOVA test *(Tukey test)*
ΣPCBs as % returning burden	1.12 ± 0.40	141.54 ± 30.48 99.21%	537.58 ± 99.01 99.79%	0.03	216.32 ± 56.88 99.99%	339.62 ± 108.82 99.99%	0.017 *(1-2)*
ΣPCDDs (ng) as % returning burden	0.13 ± 0.04	8.99 ± 1.44 98.56%	10.14 ± 3.18 98.72%	0.005	5.50 ± 1.34 99.91%	9.76 ± 3.07 99.95%	0.194
ΣPCDFs (ng) as % returning burden	0.21 ± 0.10	8.07 ± 2.30 97.40%	23.94 ± 8.05 99.12%	0.001	8.21 ± 1.87 99.99%	11.48 ± 2.01 99.99%	0.018 *(1-2; 2-3)*
ΣPBDEs	NA[b]	NA	165.75	NA	54.34	NA	ND[c]
ΣDDT[d] as % returning burden	0.15 ± 0.08	24.11 ± 6.30 99.38%	44.46 ± 8.00 99.66%	0.01	107.96 ± 28.08 99.99%	NA	0.003 *(1-3)*
ΣHCH[e] as % returning burden	0.04 ± 0.02	35.01 ± 3.74 99.88%	6.68 ± 1.21 99.40%	0.001	9.32 ± 1.55 99.99%	NA	0.000 *(1-2; 1-3)*

[a] PCB = polychlorinated biphenyl; PCDD = polychlorinated dibenzo-*p*-dioxin; PCDF = polychlorinated dibenzofuran; PBDE = polybrominated diphenyl ether; DDT = dichlorodiphenyltrichloroethane; DDD = dichlorodiphenyldichloroethane; DDE = dichlorodiphenyldichloroethylene; HCH = hexachlorocyclohexane.
[b] NA = not analyzed.
[c] ND = statistical comparison not possible.
[d] ΣDDT includes DDT (*o,p'*-DDT, *p,p'*-DDT), DDD (*o,p'*-DDD, *p,p'*-DDD), and DDE (*o,p'*-DDE, *p,p'*-DDE).
[e] ΣHCH includes (α-, β-, γ-) HCH.

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in Washington and Oregon [37], further underscoring the limited contribution of locally acquired contaminants during the juvenile stage. It is increasingly clear that salmon acquire the majority POPs during their growth period at sea and that more research is needed on the extent of Pacific Ocean food web contamination.

Lipid-normalized ΣPCB and ΣDDT concentrations increased with $\delta^{15}N$ ratios among adult chinook ($r^2 = 0.31$, $v = 23$, $p = 0.0046$ and $r^2 = 0.46$, $v = 17$, $p = 0.0020$, respectively), as did ΣPCB and ΣDDT body burdens ($r^2 = 0.25$, $v = 23$, $p = 0.0306$ and $r^2 = 0.34$, $v = 17$, $p = 0.155$, respectively) (results not shown). While our observed relationship between these POPs and $\delta^{15}N$ could be interpreted as reflecting an influence of trophic level, it may also signal an effect of migration-associated lipid changes. Changes in tissue concentrations of lipid and protein in migrating salmon complicate this interpretation of stable isotope-defined trophic level assignment [30].

Contaminant patterns in adult chinook

In the present study the primary purpose of PCA modeling is to quantitatively compare the contaminant distributions between different adult chinook populations. Because the PCA algorithm uses the variable magnitudes when decomposing the data set into a series of orthonormal rank 1 matrices or PCs, the substantial concentration differences between populations (Table 2) have to be removed by normalizing each sample before PCA. The difficulty is that this normalization step introduces closure (spurious negative correlations in the highest variables and negative correlations in the smallest). Centered log ratio transformation removes this closure and produces a data set where the average concentration and concentration total are identical for every sample [22,23]. In the PCA model the first two PCs account for the largest percentage of total variance in the data set and, particularly when data are normalized, reflect the most discriminating compositional features. The contaminants with variable loadings near axis center have essentially no contribution to a PC, while the contribution to a PC increases as the absolute magnitude of the variable loading.

Principal component analyses differentiated adult chinook on the basis of variation in PCB, PCDD, and PCDF congener proportions (Fig. 2a). In the Varimax rotated PCA model, chinook salmon samples project along a line from the upper left to the lower right of the samples plot (Fig. 2a). Because both variables (the PCs) in this relationship between chinook samples are affected by natural variability, rather than just measurement error, the appropriate regression line to use quantify the relationship is GM linear regression [23,25,26].

Geometric mean linear regression for the sample projections of chinook samples indicates that this linear relationship in Figure 2a is highly significant ($r^2 = 0.840$, $v = 22$, $p = 3.1 \times 10^{-10}$). In the corresponding variables plot, most PCDD, PCDF, and lower chlorine number PCB congeners project in the upper left quadrant while the higher chlorine number PCB congeners project in the lower right quadrant (Fig. 2b). Geometric mean regression for the variables also indicates that this linear relationship is highly significant ($r^2 = 0.377$, $v = 132$, $p = 3.1 \times 10^{-15}$), despite the greater amount of scatter in the variables plot. Comparison of samples and variables indicates that salmon samples projecting towards the upper left of the samples plot have higher proportions of the PCDD, PCDF, and lower chlorine number and non- and mono-*ortho* PCB congeners while samples projecting on the lower right have higher proportions of the higher chlorine number, di-*ortho* PCB congeners.

The differences in contaminant composition are not obviously related to either sex or sampling location (urban vs remote, or BC vs Puget Sound) for the salmon samples (Fig. 2a). The shifts in contaminant composition along the GM regression line for the samples (Fig. 2c) correlated with lipid content ($r^2 = 0.328$, $p = 0.0034$), $\delta^{13}C$ composition ($r^2 = 0.605$, $p = 7.7 \times 10^{-6}$), and body weight ($r^2 = 0.214$, $p = 0.0227$), but are not significantly related to $\delta^{15}N$ ($r^2 = 0.152$, $p = 0.0596$, $v = 22$ in all cases). Accordingly, the change in contaminant composition for the salmon appears to reflect metabolism or solubilization of the PCDD and PCDF and lower chlorine number and non- and mono-*ortho*-PCB congeners as the salmon lose lipid during migration. This suggests that the migrating salmon PCB burdens will be increasingly dominated by the more heavily chlorinated congeners. Similar observations in sockeye salmon were thought to reflect a greater metabolic capacity by salmonids for PCDDs and PCDFs as compared to PCBs [11]. While our results support the notion of compositional loss associated with depleting lipid reserves during migrating salmon, a contribution of local POP sources from more contaminated areas, such as Puget Sound, cannot be ruled out [5,6]. Indeed, feeding in such an area during outward- and inward-bound migrations likely does lead to increased POP concentrations in certain salmon individuals and stocks.

While our results suggest that salmon accumulate the majority of POPs during their growth period at sea, lipid depletion and metabolism in salmon associated with migration may have profound consequences for dietary exposure to POPs in resident killer whales. While both northern and southern resident killer whales preferentially consume chinook salmon, southern residents likely intercept more chinook in relatively contaminated, near-urban areas and at points closer to their natal streams. Southern residents may therefore be consuming chinook salmon that is both more contaminated and less lipid-rich.

Health risks for killer whales

Dietary POP concentrations and patterns have profound implications for killer whale POP accumulation and consequent related health risks. High trophic level marine mammals have shown susceptibility to adverse health effects such as immunotoxicity, endocrine disruption, reproductive impairment, and developmental abnormalities with elevated exposure to POPs [1]. To characterize health risks in killer whales associated with dietary exposure to POPs, chinook ΣPCB, ΣPCDD/PCDF TEQ, and ΣDDT concentrations were compared with Canadian Council of Ministers of the Environment (CCME) tissue residue guidelines for the protection of mammalian wildlife consumers of aquatic biota [38] (www.ccme.ca/assets/pdf/trg_summary_table.pdf). The Deschutes River salmon exceeded, and the Lower Fraser River salmon were approaching (Table 2), the CCME PCB tissue residue guidelines (0.79 ng TEQ/kg diet wet wt) [38]. The Duwamish River salmon (Table 2) exceeded the ΣDDT tissue residue guidelines (14.0 μg/kg diet wet wt) [38].

The ΣPCB and ΣDDT concentrations in all salmon groups were below the less conservative U.S. guidelines (New York State Department of Environmental Conservation) for protection of fish-eating wildlife [39]. All of the chinook analyzed

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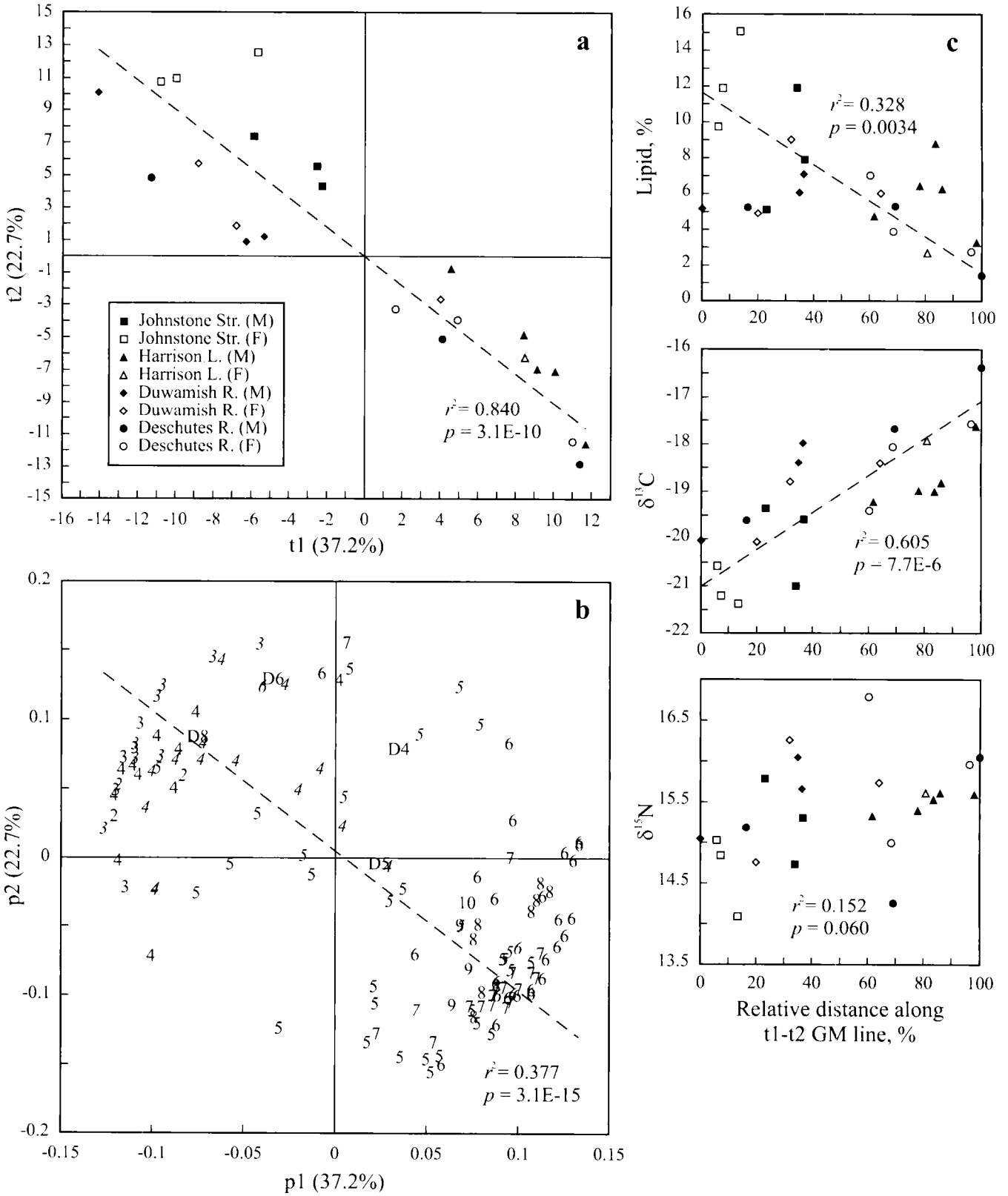


Fig. 2. Contaminant patterns in chinook salmon are relevant to assessing the influence of feeding ecology in chinook and dietary exposure of persistent organic pollutants in resident killer whales. Varimax rotated projections of the first two principal components (PCs) for a principal components analysis model based on normalized concentrations (see text) showing (**a**) chinook salmon scores (t1 and t2) by sampling location and sex (M = male; F = female), and (**b**) dibenzo-*p*-dioxin (PCDD), dibenzofuran (PCDF), and polychlorinated biphenyl (PCB) congener variable loadings (p1 and p2) by chlorine number. In (**b**) PCDDs and PCDFs have a "D" preceding the number, the dioxin-like non-*ortho* and mono-*ortho*-PCBs are in italics and di-*ortho*-PCBs use a regular font. In (**c**) the lipid, $\delta^{13}C$ and $\delta^{15}N$ content is plotted by sampling location and sex against the relative distance along the GM linear regression line in the first PC for the salmon samples (**a**).

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Table 5. Estimated daily intake (EDI) of persistent organic pollutants (POPs) by northern and southern resident killer whales. Johnstone Strait (British Columbia, Canada) chinook POP concentrations have been used to calculate EDIs for northern residents and all four chinook stocks for southern residents. We have further calculated the EDI for southern residents if they were to consume chinook of equivalent lipid content to that of northern residents, i.e., if northern residents were to consume 34 kg chinook per day (8.5% lipid); southern residents may consume up to 85 kg chinook per day (3.4% lipid)

	Estimated daily intake μg/d (except for ΣPCDD, ΣPCDF, and ΣTEQ ng/d)		
Sum congeners/isomers[a]	Northern residents	Southern residents	Southern residents (lipid-equivalent)
ΣPCB	308.49	1,248.00	2,051.38
ΣPBDE	No data	410.62	674.95
ΣPCDD	19.75	33.67	55.34
ΣPCDF	17.17	47.82	78.60
ΣDDT (DDT, DDD, DDE)	49.72	272.88	448.55
HCH (α-, β-, γ-)	77.76	51.74	85.05
ΣTEQ (PCB, PCDD, PCDF)	9.00	36.85	60.58

[a] PCB = polychlorinated biphenyl; PBDE = polybrominated diphenyl ether; PCDE = polychlorinated biphenyl ether; PBB = polybrominated biphenyl; PCDD = polychlorinated dibenzo-*p*-dioxin; PCDF = polychlorinated dibenzofuran; TEQ = toxic equivalents; DDT = dichlorodiphenyltrichloroethane; DDD = dichlorodiphenyldichloroethane; DDE = dichlorodiphenyldichloroethylene; HCB = hexachlorobenzene; HCH = hexachlorocyclohexane.

in the present study exceeded the 8 μg/kg dietary PCBs that was estimated to protect 95% of a killer whale population, based on a 17 mg/kg PCBs adverse effects threshold for marine mammals [40].

Another means of characterizing health risks associated with dietary exposure is through the calculation of EDI. Based on food intake estimates derived from studies of captive killer whales [27], we have estimated the food intake of a 2,500-kg resident killer whale to be approximately 50 kg per day. We have further estimated the chinook portion, 71.5% of a 96% salmonid diet [2], to be 34 kg/d. Taking into account observed ranges for resident killer whales [41], POP concentrations (wet wt) for Johnstone Strait chinook were used to calculate EDIs for northern residents and all four chinook stocks for southern residents (Table 5).

Our EDIs suggest that southern residents may be consuming, on a body weight basis, 4.0 times more PCBs than their northern counterparts, consistent with the differences in PCB concentrations measured in biopsies collected from free-ranging northern and southern resident killer whales [1]. However, since studies of marine mammal energetics suggest that calorimetric content is an integral component of food needs [27,42], we have also adjusted consumption to reflect equivalent lipid content. Because of the lower lipid content of our more southerly chinook salmon, there may be a compensatory increase in consumption by southern resident killer whales. This nutritionally adjusted scenario would predict that southern residents would consume 6.6 times more PCBs than northern residents. Similarly, we previously speculated that Puget Sound harbor seals consume nearly twice as much prey as Strait of Georgia seals in order to compensate for the lower lipid content in their prey, with results explaining a near-doubling of their contaminant burden [17]. Additional studies on killer whale feeding ecology and on the behavior of POPs in salmon during different life history stages will shed more insight into the sources and fate of contaminants in killer whale food webs.

The present study underscores the global nature of contaminant dispersion with chinook salmon acquiring the majority of their POPs during their time at sea. As the two resident killer whale populations in British Columbia intercept these returning salmon, they are exposed to different dietary POP concentrations. We conclude that the endangered southern resident killer whales are exposed to much higher concentrations of POPs than their northern counterparts through the consumption of more POP-contaminated chinook salmon, and may increase their consumption of salmon in order to compensate for the reduced lipid content observed in southerly chinook. In this regard, increasing climate-related stresses on salmon abundance and lipid content raise the specter of increased contaminant exposures for resident killer whales in the future.

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APPENDIX 1. Principal components analysis variable

Variable[a]	PCB substitution	Chlorine No.	No. <	Variable	PCB substitution	Chlorine No.	No. <
Dibenzo-*p*-dioxins and dibenzofurans				PCB94	22′356′	5	1
1,2,3,6,7,8-		6	—	PCB102/93	22′456′/22′356	5	—
OCDD		8	—	PCB95	22′35′6	5	—
2,3,7,8-TCDF		4	—	PCB88	22′346	5	—
2,3,4,7,8-PnCDF		5	6	PCB91	22′34′6	5	—
Non-*ortho* PCBs				PCB92/84	22′355′/22′33′6	5	—
PCB11	33′	2	—	PCB89	22′346′	5	—
PCB15	44′	2	—	PCB101/90	22′455′/22′34′5	5	—
PCB35	33′4	3	2	PCB99	22′44′5	5	—
PCB37	344′	3	—	PCB119	23′44′6	5	—
PCB80	33′55′	4	—	PCB109/83	233′46/22′33′5	5	—
PCB79	33′45′	4	—	PCB97/86	22′3′45/22′345	5	—
PCB81	344′5	4	—	PCB115/87	2344′6/22′345′	5	—
PCB77	33′44′	4	—	PCB85	22′344′	5	—
PCB126	33′44′5	5	—	PCB110	233′4′6	5	—
PCB169	33′44′55′	6	—	PCB82	22′33′4	5	—
Mono-*ortho* PCBs				PCB155	22′44′66′	6	2
PCB26	23′5	3	—	PCB150	22′34′66′	6	4
PCB25	23′4	3	—	PCB148	22′34′56′	6	2
PCB31	24′5	3	—	PCB136	22′33′66′	6	—
PCB28	244′	3	—	PCB154	22′44′56	6	—
PCB33/20	2′34/233′	3	—	PCB151	22′355′6	6	—
PCB22	234′	3	—	PCB135/144	22′33′56′/22′345′6	6	—
PCB72	23′55′	4	—	PCB147	22′34′56	6	—
PCB68	23′45′	4	—	PCB149	22′34′5′6	6	—
PCB57	233′5	4	1	PCB139/140	22′344′6/22′344′6′	6	—
PCB67	23′45	4	—	PCB143/134	22′3456′/22′33′56	6	—
PCB58	233′5′	4	2	PCB142/131	22′3456/22′33′46	6	—
PCB63	234′5	4	—	PCB146/161	22′34′55′/233′45′6	6	—
PCB61/74	2345/244′5	4	—	PCB132/153	22′33′46′/22′44′55′	6	—
PCB70/76	23′4′5/2′345	4	—	PCB168	23′44′5′6	6	—
PCB66	23′44′	4	—	PCB141	22′3455′	6	—
PCB56/60	233′4′/2344′	4	—	PCB137	22′344′5	6	—
PCB111	233′55′	5	2	PCB130	22′33′45′	6	—
PCB120	23′455′	5	—	PCB160/163/164/138	233′456/233′4′56/233′4′5′6/22′344′5′	6	—
PCB124	2′3455′	5	—	PCB158	233′44′6	6	—
PCB108/107	233′45′/233′4′5	5	—	PCB129	22′33′45	6	—
PCB123	2′344′5	5	—	PCB166	2344′56	6	—
PCB118	23′44′5	5	—	PCB128	22′33′44′	6	—
PCB114	2344′5	5	—	PCB188	22′34′566′	7	6
PCB122	2′33′45	5	—	PCB184	22′344′66′	7	—
PCB105	233′44′	5	—	PCB179	22′33′566′	7	—
PCB159	233′455′	5	5	PCB176	22′33′466′	7	—
PCB162	233′4′55′	6	—	PCB178	22′33′55′6	7	—
PCB167	23′44′55′	6	—	PCB175	22′33′45′6	7	—
PCB156	233′44′5	6	—	PCB187/182	22′34′55′6/22′344′56′	7	—
PCB157	233′44′5′	6	—	PCB183	22′344′5′6	7	—
PCB189	233′44′55′	7	—	PCB185	22′3455′6	7	—

[a] PCB = polychlorinated biphenyl; HxCDD = hexachlorodibenzo-*p*-dioxin; OCDD = octachlorodibenzo-*p*-dioxin; TCDF = tetrachlorodibenzofuran; PnCDF = pentachlorodibenzofuran.

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APPENDIX 1. Continued

Variable[a]	PCB substitution	Chlorine No.	No. <	Variable	PCB substitution	Chlorine No.	No. <
Di-*ortho* PCBs				PCB174/181	22′33′456′/22′344′56	7	—
PCB10/4	26/22′	2	—	PCB177	22′33′4′56	7	—
PCB19	22′6	3	—	PCB171	22′33′44′6	7	—
PCB18	22′5	3	—	PCB192/172	233′455′6/22′33′455′	7	—
PCB17	22′4	3	—	PCB180	22′344′55′	7	—
PCB27/24	23′6/236	3	—	PCB193	233′4′55′6	7	—
PCB16/32	22′3/24′6	3	—	PCB191	233′44′5′6	7	1
PCB53	22′56′	4	—	PCB170/190	22′33′44′5/233′44′56	7	—
PCB51	22′46′	4	—	PCB202	22′33′55′66′	8	—
PCB45	22′36	4	—	PCB201	22′33′45′66′	8	—
PCB46	22′36′	4	—	PCB197	22′33′44′66′	8	—
PCB73/52	23′5′6/22′55′	4	—	PCB200	22′33′4566′	8	—
PCB49	22′45′	4	—	PCB198	22′33′455′6	8	3
PCB47/75/48	22′44′/244′6/22′45	4	—	PCB199	22′33′455′6′	8	—
PCB44	22′35′	4	—	PCB203/196	22′344′55′6/22′33′44′5′6	8	—
PCB59/42	233′6/22′34′	4	—	PCB195	22′33′44′56	8	—
PCB71/41/64	23′4′6/22′34/234′6	4	—	PCB194	22′33′44′55′	8	—
PCB40	22′33′	4	—	PCB208	22′33′455′66′	9	—
PCB96	22′366′	5	4	PCB207	22′33′44′566′	9	1
PCB103	22′45′6	5	—	PCB206	22′33′44′55′6	9	—
PCB100	22′44′6	5	—	PCB209	22′33′44′55′66′	10	—

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Recommendations for Improving Recovery Criteria under the US Endangered Species Act

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Recovery criteria, the thresholds mandated by the Endangered Species Act that define when species may be considered for downlisting or removal from the endangered species list, are a key component of conservation planning in the United States. We recommend improvements in the definition and scientific justification of recovery criteria, addressing both data-rich and data-poor situations. We emphasize the distinction between recovery actions and recovery criteria and recommend the use of quantitative population analyses to measure the impacts of threats and to explicitly tie recovery criteria to population status. To this end, we provide a brief tutorial on the legal and practical requirements and constraints of recovery criteria development. We conclude by contrasting our recommendations with other alternatives and by describing ways in which academic scientists can contribute productively to the planning process and to endangered species recovery.

Keywords: conservation, ecology, population biology, extinction, endangered species

Over the past 20 years, ecologists and conservation biologists have conducted multiple reviews of the US Endangered Species Act (ESA) focused on legal, policy, and especially scientific elements of the act's implementation (e.g., Tear et al. 1993, 1995, Foin et al. 1998, Boersma et al. 2001, Gerber and Hatch 2002, Hoekstra et al. 2002, Lawler et al. 2002, Morris et al. 2002, Moyle et al. 2003, Scott et al. 2005, Gibbs and Currie 2012). These reviews have shown numerous shortcomings in the effectiveness and scientific basis of recovery plans and recovery criteria and have suggested just as many remedies. In response to these academic reviews and to court decisions interpreting the ESA, the two government agencies that implement the act (the US Fish and Wildlife Service [USFWS] and the National Marine Fisheries Service [NMFS]; henceforth, *the services*) have continued to update their procedures for recovery planning (NMFS and USFWS 2010).

Despite these efforts, recent reviews of the ESA's implementation have still shown little improvement in key metrics of scientific rigor, including the clear articulation and biological justification of recovery criteria (Neel et al. 2012). This situation prompted us to convene a workshop to find pragmatic ways to improve this central part of ESA recovery planning. To increase the odds that our recommendations would have traction, we sought to understand the viewpoints of representatives from many parts of the conservation community and to focus on one key element of the ESA—recovery criteria and their use—rather than conducting a general critique of the act or its implementation.

We focus on recovery criteria for three reasons. First, they specify the conditions under which a species may be considered for downlisting (i.e., being moved from *endangered* to *threatened* status) or delisting (i.e., being removed from ESA protection), thereby defining what characteristics the services expect a population to exhibit once it reaches a state of recovery. Criteria therefore serve as a structuring element for a recovery plan as a whole and guide the actions of government agencies and other entities. Second, the ESA stipulates that recovery criteria be "measurable and objective" and that delisting decisions be based on "the best scientific and commercial data available" (16 U.S.C. § 1533); both requirements inject a primary role for science, although exactly how recovery standards are to be defined or assessed is left unclear. Finally, a vast amount has been written about assessing extinction risk, establishing targets for healthy populations in the face of harvest and habitat loss, analyzing the consequences of population size and connectivity for inbreeding, and other topics directly relevant to setting recovery thresholds. Therefore, recovery criteria appeared to be a relatively tractable target for improving the scientific implementation of the ESA.

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Box 1. Sociopolitical factors influencing recovery criteria.

Multiple analyses have shown that sociopolitical factors have strong influences on many aspects of Endangered Species Act (ESA) implementation, including recovery criteria (Vucetich et al. 2006, Goble 2009). Two crucial components of recovery criteria that are particularly influenced by social and policy considerations are the following:

The portion of the range to which a species should be restored

The ESA calls for a species to be listed if it is endangered or threatened in all or a significant portion of its range (SPR), and, therefore, delisting should specify the geographic area to which healthy populations must be restored. Despite ongoing debate about the meaning of SPR (Vucetich et al. 2006, Carroll et al. 2010), the issue of where endangered species must or should be restored is clearly influenced by the sociopolitical setting and constraints imposed by feasibility and societal desirability. Within existing recovery plans, the extent of occupied range for recovered populations is typically addressed through viability needs. Similarly, the US Fish and Wildlife Service recently issued guidance on SPR, clarifying that a portion of the range is considered significant if "its contribution to the viability of the species is so important that, without that portion, the species would be in danger of extinction" (76 Fed. Reg. 237 (December 2011), pp. 76987–77006). The viability-based approach to recovery criteria that we advocate neither requires nor precludes broader definitions of SPR arising from the policy arena.

Acceptable risk of extinction

Under the ESA, *recovery* implicitly means that a species is not in danger of extinction (box 2), but any population has some possibility of extinction, and the ESA does not quantitatively define acceptable or unacceptable risk. Several authors have advocated for normative standards for acceptable extinction risk (e.g., Gilpin 1987, Mace and Lande 1991, Gerber and Demaster 1999) and National Marine Fisheries Service documents have proposed some guidelines (Demaster et al. 2004, McElhany et al. 2000, Regan et al. 2009). Similarly, the IUCN has established extinction risk levels for its categories of endangerment (IUCN 2012). Nonetheless, the acceptable risk of extinction for a recovered species has, so far, been determined on a case-by-case basis. We surveyed plans from 2009 to the present and show in figure 1 the combinations of extinction risk and time horizons for species for which both risk and horizon were defined in recovery criteria. We also indicate IUCN viability standards. Across plans, there is high variation but also a negative association between time horizon and extinction risk (Spearman rank correlations –0.59 and –0.83, $p < 0.02$, for delisting and downlisting, respectively), further exacerbating the high variance in acceptable extinction risk across plans. Society is willing to accept a higher extinction risk for some species (upper left) than for others (lower right). One striking trend was how few of these plans (only 6 of 23) employed quasiextinction thresholds, with the majority using complete extinction in defining risk. Although we do not propose or advocate for any universal standards for risk here, viability-based recovery criteria are compatible with the establishment of either universal or taxon-specific standards arising from the policy arena.

Although we see a crucial role for science in setting recovery criteria, defining what *recovery* should mean for a population or species involves more than scientific analysis. In particular, the risk of partial or complete failure (i.e., extinction) that we as a society are willing to accept and the degree to which we try to restore species to former numbers, distributions, and ecological functions blend into matters legal and ethical. These decisions are often made in part by biologists, but we emphasize that they are not objective biological decisions and that they require careful attention (box 1).

We begin with a brief tutorial on recovery planning, emphasizing the development of criteria. Even though all of us have read or reviewed numerous plans, served on recovery teams, or both, we nonetheless did not appreciate the practical constraints that several key legal and administrative rulings impose on how recovery plans must be written. Given our advocacy of increased involvement of academics in recovery planning, this description of *everything you (should have) always wanted to know about recovery planning, but were too ignorant to ask* is especially germane.

Legal and policy context

Recovery plans describe the biology of the species and its threats, develop a strategy for attaining recovery, outline actions needed to carry out the strategy, and detail the criteria by which attainment of recovery (box 2) can be assessed. Although a bevy of requirements and recommendations shape how recovery criteria are developed (NMFS and USFWS 2010), a handful of rules and legal decisions are also of key importance. The only explicit guidelines in the ESA regarding recovery criteria and actions are that recovery plans must "to the maximum extent practicable," contain "objective, measurable criteria, which, when met, would result in a determination, in accordance with the provisions [of the ESA], that the species be removed from the list" and "a description of such site-specific management actions as may be necessary to achieve the plan's goal for the conservation and survival of the species" (16 U.S.C. § 1533(f)(1)(B)). The ESA definition of *endangered* ("in danger of extinction throughout all or a significant portion of its range") highlights the role of extinction risk and spatial distribution in defining recovery but otherwise provides little guidance for recovery criteria and, in fact, injects additional need for policy clarification for undefined terms such as *in danger of* and *significant portion of its range* (Vucetich et al. 2006, Carroll et al. 2010). The services' *Recovery Planning Guidance* (NMFS and USFWS 2010), intended to provide more explicit guidelines for recovery planning and to outline

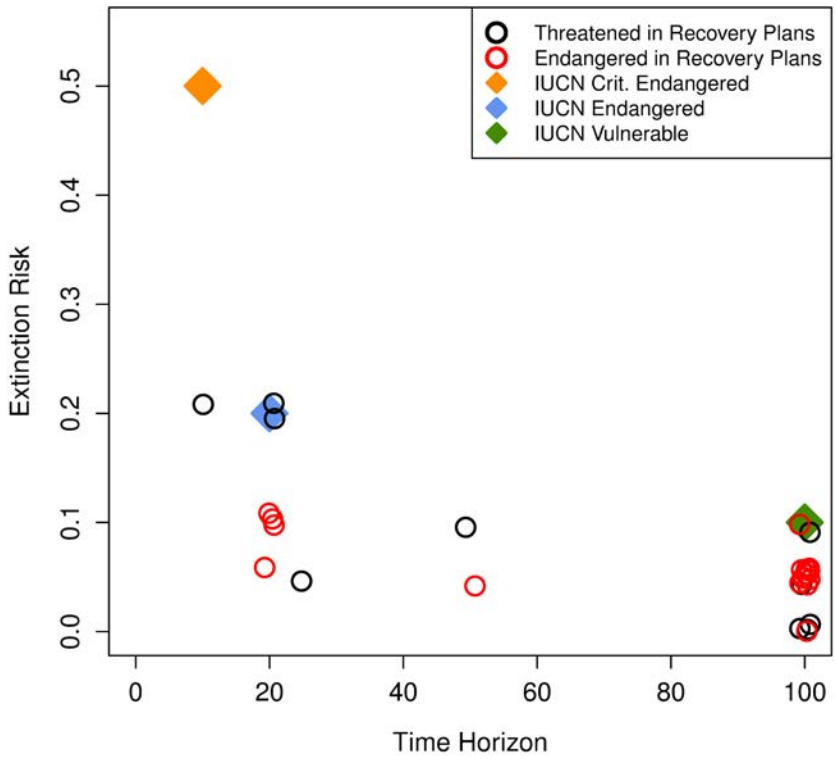


Figure 1. Viability criteria used to assess recovery are highly variable across recovery plans. A common way to assess population viability is the estimated probability (risk) that a population will become extinct or will fall below a specified quasiextinction threshold, over some time horizon. Endangered Species Act (ESA) recovery plans published between 2009 and 2013 used a wide range of acceptable risks of extinction or quasiextinction for delisting or downlisting, and there was a similarly broad set of time horizons employed. Viability standards defined for different International Union for Conservation of Nature (IUCN) categories of risk are also shown; for a given time horizon, the ESA criteria are generally more restrictive (i.e., require a lower risk of extinction) than are those used by the IUCN.

policy directives, indicates that they do not consider the measureable and objective requirement to mean that criteria must be quantitative (section 5.1.8.3). The guidance document defines recovery *actions* to be all activities "necessary to achieve full recovery of the species," as well as "the monitoring actions necessary to track the effectiveness of these actions and the status of the species" (NMFS and USFWS 2010).

One aspect of the services' approach to recovery criteria stems from the ESA requirement that prior to listing, the services must conduct a formal review to assess the extent to which the species is affected by five specific "threat factors": (1) destruction, modification, or curtailment of habitat or range; (2) overuse; (3) disease or predation; (4) inadequacy of existing regulation; and (5) any other natural or manmade factors. A species can only be removed from the list when none of the five factors threatens or endangers it. The courts have ruled that recovery criteria must address all five threat factors and must measure whether they have been ameliorated (*Fund for Animals v. Babbitt*: 903 F. Supp. 96 (D.D.C 1995)). The services interpret this ruling literally and recommend that plan writers formulate separate recovery criteria targeted at each threat factor (GAO 2006, NMFS and USFWS 2010). The services also suggest that demographic criteria (which we use in the sense of any estimates of population status; e.g., population size, trends through time, demographic rates, genetic factors, spatial distribution, or population viability indices) be listed separately from "threat-based" criteria (NMFS and USFWS 2010).

A final aspect of real-world recovery planning worth highlighting is that only about half of recovery plans are written by recovery teams, which include nonagency experts and may include agency staff as well. The rest are written by only one or a few agency personnel or contractors (Debby Crouse, US Fish and Wildlife Service, personal communication, 27 September 2014). This limited authorship demonstrates that resources (expertise, time, and money) for writing recovery plans are even more restricted than is widely recognized.

Current approaches to defining recovery criteria

How do these requirements and constraints affect the formulation of recovery criteria? Even very recent plans differ greatly in the number, range, format, quantity, and degree of specificity of their recovery criteria (see supplemental appendix S1 for examples of criteria from different plans, including many of those referred to in this section). For example, some plans contain only demographic criteria, such as the short-tailed albatross (*Phoebastria albatrus*) plan, whose sole delisting criterion stipulates requirements for population size, growth rate, and spatial distribution of the population.

However, most recent plans also—or primarily—use threat-based criteria that specify control or reduction of threats. The level of threat reduction required can vary in specificity and may or may not be linked explicitly to demography or viability. For example, one delisting criterion for the vermilion darter (*Etheostoma chermocki*) requires the attainment of specific water quality standards for turbidity over 10 consecutive years under a specified sampling regime. In contrast, the sei whale (*Balaenoptera borealis)* threat-based recovery criteria are more general, requiring that each

Box 2. Key definitions under the ESA.

The Endangered Species Act (ESA) protects species listed under the act as *endangered* or *threatened*:

Endangered

"In danger of extinction throughout all or a significant portion of its range" (16 USC § 1532).

Threatened

"Likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range" (16 USC § 1532).

The ESA requires the development of recovery plans whose purpose is "to restore a species to ecological health" (USFWS 2013a). Several closely related concepts form the foundation of a recovery plan:

Recovery or recovery goal

The ESA's "ultimate goal is to 'recover' species so they no longer need protection under the ESA" (USFWS 2013). Therefore, at a minimum, *recovery* means that the species is not in danger of extinction in the foreseeable future. Translating this to the terms of quantitative conservation biology, recovery is the attainment of the conditions by which the species is viable over a long time frame. According to the services, "some recovery planning efforts may attempt to set goals higher than those needed to achieve delisting of the species" (NMFS and USFWS 2010). An example of such a goal might be reaching densities and distributions that allow the species to fulfill key ecological roles.

Recovery objective

The services use recovery objectives to link the recovery goal and criteria, stating "recovery objectives are the parameters of the goal, and criteria are the values for those parameters" (NMFS and USFWS 2010).

Recovery criteria

Recovery criteria are the conditions that signify recovery has been attained. As was stated by the services, "recovery criteria are the values by which it is determined that [a recovery] objective has been reached" (NMFS and USFWS 2010). Therefore, a clearly stated concept of recovery might be a 95% probability of persistence over 100 years.

Recovery actions

Recovery actions are the steps the services or other managers take to manage the species to achieve the goal of recovery. As was stated by the services, recovery actions are the steps "that will alleviate known threats and restore the species to long term sustainability. These actions might include (but are not limited to) habitat protection, limitations on take, outreach, research, control of disease, control of invasive species, controlled (including captive) propagation, reintroduction or augmentation of populations, and monitoring actions" (NMFS and USFWS 2010).

threat identified in the plan, such as reduced prey abundance due to climate change, anthropogenic noise, ship collisions, and gear entanglement, continue "to be investigated and any necessary actions being taken to address the issue are shown to be effective or this is no longer believed to be a threat."

Some threat-based criteria essentially consist of actions, including administrative or monitoring directives, focused on specific threats. For example, the downlisting criteria for the smalltooth sawfish (*Pristis pectinata*) stipulate that public education programs about the species and the prohibitions against harming it be in place. Similarly, delisting criteria for Kemp's ridley sea turtle (*Lepidochelys kempii*) include the establishment of a network of monitoring sites.

Occasionally, threats are accounted for by weighing their impacts on demographic processes. For example, the delisting criteria for the Gila trout (*Oncorhynchus gilae*) are focused on the number of populations and length of occupied streams, that were determined by quantitative analysis to best demonstrate resilience to the effects of catastrophic fires, the primary proximal threat to the species. More generally, the Gulf Coast jaguarundi (*Puma yagouaroundi cacomitli*) plan calls for habitat loss, degradation, and fragmentation to be reduced to the point that the species is no longer in danger of extinction. Similarly, the Wyoming toad (*Anaxyrus baxteri*) plan calls for chytridiomycosis infection rates to be maintained at levels that ensure the long-term sustainability of the population.

Other demographic criteria take the form of "viability criteria" that are either direct measures of a population's risk of extinction or quasiextinction (e.g., 5% risk of extinction within 100 years) or demographic measures (e.g., population size or trend) that have been shown to directly relate to a target recovery threshold—commonly, extinction risk. For example, one delisting criterion for the island fox (*Urocyon littoralis)* is based on extinction risk, calculated from population size and mortality rates. This criterion also details the time period, the quasiextinction threshold, and the number of years of consistently meeting the risk threshold required before recovery is declared. This plan also explicitly states that the analyses of risk can and should be updated as more data become available. Many more variations on

demographic- and threat-based criteria exist among recent plans (appendix S1).

Regardless of their content, the ESA mandates that recovery criteria be measurable, but there is no history of this requirement being interpreted in the narrowest, most literal sense. Rather, a wide variety of measures, most of which are indirect and imprecise in the sense that they require statistical extrapolation from partial information (e.g., population sizes estimated from mark–recapture analyses, indirectly assayed threat abatement standards, estimated genetically effective population sizes, and probabilities of future extinction) have all been included in plans.

Some plans specify that additional evaluation, such as monitoring, population viability analyses (PVA), and threat assessment will be needed to develop or clarify criteria that are not immediately measureable. For example, some criteria (e.g., for the Mariana fruit bat, *Pteropus mariannus mariannus*; Bexar County karst invertebrates; the dwarf lake iris, *Iris lacustris*) state specific viability targets for a PVA that is yet to be developed. Others (e.g., for gentian pinkroot, *Spigelia gentianoides*; the scaleshell mussel, *Leptodea leptodon*; Guthrie's ground plum, *Astragalus bibullatus*; the Puerto Rican parrot, *Amazona vittata*) merely state criteria stipulating that future analyses must show that populations are "viable," without defining *viability*. Many threat-based criteria also call for additional analyses to specify target levels. For example, the criteria may state that habitat adequate in extent, quality, and quantity will be identified and protected (e.g., the plan for the Caribbean manatee, *Trichechus manatus*) or that a threat will continue to be investigated and ameliorated until it no longer limits recovery (e.g., entanglement for sei whales, water flows for the Caribbean manatee).

Common problems with current recovery criteria

We see two problems with the way criteria are often framed and justified. First, many plans fail to link the recovery criteria, either demographic or threat based, to some clearly specified definition of population recovery. In other words, many plans do not articulate how meeting recovery criteria will result in a population that is at reduced risk of extinction or otherwise deemed to be "recovered." This issue has a considerable history in critiques of recovery plans (Schemske et al. 1994, Gerber and Hatch 2002) and continues to be a problem in even the most recent plans (Neel et al. 2012, Himes Boor 2014).

A second but related problem is the conflation of recovery criteria and recovery actions. Although these two aspects of a plan are described as distinct elements in the ESA (box 2), in practice, many plans include what would commonly be considered *actions* (Salafsky et al. 2008) among their recovery "criteria." For example, many plans include criteria requiring the establishment of monitoring programs or other biological studies (appendix S1). We heard from both service personnel and personnel from conservation nongovernmental organizations that recovery plan writers may seek to highlight the importance of actions by listing them as criteria and that funding may be more available for actions that are listed as criteria. Still, we view this mixing of actions and criteria as problematic. Recovery *criteria* should reflect something about the status of the species itself (e.g., population size or distribution, rate of population growth, rate of mortality from some threat) that indicates that it has reached a state of recovery, whereas recovery *actions* are what managers do to achieve and evaluate recovery (box 2).

Recommendations for improved recovery criteria

Regardless of the exact degree of risk that a plan's recovery criteria embrace—part of the societal decisions that underlie any plan—a scientifically defensible plan should include quantitative recovery criteria establishing that the species is safe from extinction or extreme declines for the moderate-term future or that the species is likely to maintain an even higher number or wider geographical distribution deemed necessary for it to play its proper ecological role. Such criteria must account for existing and anticipated or potential future threats (Salafsky et al. 2008), including climate change effects and the shifting regulatory and threat landscapes faced by delisted species (Soulé et al. 2005, Goble et al. 2012). The broad set of analytical methods used to judge whether a population or set of populations meets such a standard is usually called *population viability analysis*, or PVA. Although we use this acronym, we emphasize that we are not advocating solely for matrix population models or similar approaches (e.g., integral projection models). Many simpler and also more sophisticated modeling tools exist in which quantitative approaches are used to synthesize a wide range of information (e.g., demographics, spatial distribution, threats) to do more than simply assess extinction risk (e.g., Bayesian, hierarchical, state-space, or integrated population models; also see supplemental appendix S3). These tools can and should be used to judge the likelihood of sustaining a wide range of desired attributes of a recovered species, including the number and density of individuals, the number and geographic distribution of populations, fulfillment of ecological functioning, and other population traits that are associated with the conservation biology principles of representativeness, redundancy, and resiliency.

Within this broad suggestion, we offer three more specific recommendations:

Recommendation 1: The central recovery criteria should be quantitative, biologically-based, and clearly justified. To the greatest extent possible, criteria should be quantitative; focused on traits of the species, itself, rather than external factors; and based on clear scientific reasoning. To ensure this direct link between criteria and species biology, plans should have a distinct section that outlines the biological justification for each criterion, with evidence of how the quantitative standards are objectively linked to a clearly stated definition of recovery (box 3). Given the ambiguity in the ESA regarding what recovery is, this recommendation serves to facilitate both an unambiguous statement of how recovery is defined

Box 3. Illustrative wording for recovery criteria.

We present the following templates for demographic, threat-based, and combined criteria that follow the recommendations outlined in the text as well as recommendations made in Himes Boor (2014). They are presented as illustrative examples; many other criteria could be formulated that meet the standards set out in our recommendations.

Demographic criterion with adequate data

Estimated intrinsic growth rate for the entire population must meet or exceed _ with _% probability of certainty for more than _ years based on our analyses that such growth will result in a population with less than _% probability of quasiextinction within _ years (see appendix _ for analysis details, including assumptions and definitions).

Demographic criterion with inadequate data

The species as a whole should have less than an _% probability of extinction within _ years and each individual population should maintain a probability of extinction less than _% within _ years. The PVA models must be peer reviewed and must take into account uncertainty in parameter estimates and future scenarios, including potential impacts of climate change and threat factors _ and _. The data to complete such an assessment should meet the standards outlined in section _ of this recovery plan.

Threat-based criterion with adequate data

Threat _ must be reduced to an estimated (based on the upper _% confidence interval) _ units per year across the entire species current range and must remain at or below that level for _ years. We estimate that this reduction will result in a _% increase in vital rate _, therefore allowing a population growth rate consistent with less than an _% probability of extinction within _ years (see appendix _ for the detailed analysis and model assumptions).

Threat-based criterion with inadequate data

Threats _ and _ should be reduced such that their cumulative impact on the species is no longer threatening its viability and the population has greater than _% probability of persistence for more than _ years. The model developed to estimate viability must be peer reviewed and must take into account uncertainty in parameter estimates, future management scenarios, and threat impacts.

Combined demographic and threat-based criterion

Estimates of total population size must meet or exceed _ breeding individuals with _% probability of certainty for more than _ years, based on our analyses demonstrating that a population maintaining that number of breeding individuals has less than _% probability of quasiextinction within _ years and has overcome threats _ and _.

Each criterion for which a model (e.g., PVA or threats analysis) is used should also specify the section of the recovery plan containing the detailed model description, including all model assumptions and justifications. Criteria should also be accompanied by references to the section of the recovery plan describing explicit methodologies for collecting data and estimating parameters, including acceptable levels of uncertainty surrounding estimated parameters. This will ensure the appropriate data are collected for the desired analysis.

for a species and how the specified criteria demonstrate that the species has a high probability of remaining in this "recovered" state. Both the definition and the rationale are essential to ensure that the connections between available information about the species and the plan's recovery criteria are transparent to the public and to plan reviewers. We recognize that many other ancillary criteria will often be included in plans that address less direct aspects of recovery and population management, but without the inclusion of criteria that are directly related to biological recovery, a plan is not scientifically defendable.

Recommendation 2: All plans should include demographic criteria. Plans should include one or more demographic criteria (criteria focused on population number, dynamics, or demography) and should state how analyses have been (or will be) done to tie these criteria to the probability of populations meeting specific quasi-extinction risk thresholds or other indices of population health (box 3). If adequate data are available at the time a plan is written, plan developers should conduct analyses of population viability and identify quantitative population metrics, such as population size, population trends over a specified time period, and geographical distribution, that indicate that the population has an acceptably low risk of falling below recovery thresholds. If the data are not in hand to support such analyses when a plan is written, the criteria can state the thresholds and risks that are deemed acceptable, and recovery actions can specify collection of the data that will be needed to assess when that criterion has been met (figure 2). Both of these approaches are preferable to setting arbitrary demographic thresholds that have no clear link to a species' ecosystem role or its future viability (Schemske et al. 1994, Tear et al. 1995). As was noted above, these approaches have already been taken in some approved plans (e.g., the sei whale, the Mariana fruit bat) and have been advocated by NMFS scientists (Demaster et al. 2004) and others (Himes Boor 2014), so they are not untested nor too uncertain to pass muster under the ESA. In practice, many of the best plans take a combined approach, defining demographic standards that predict a certain safety

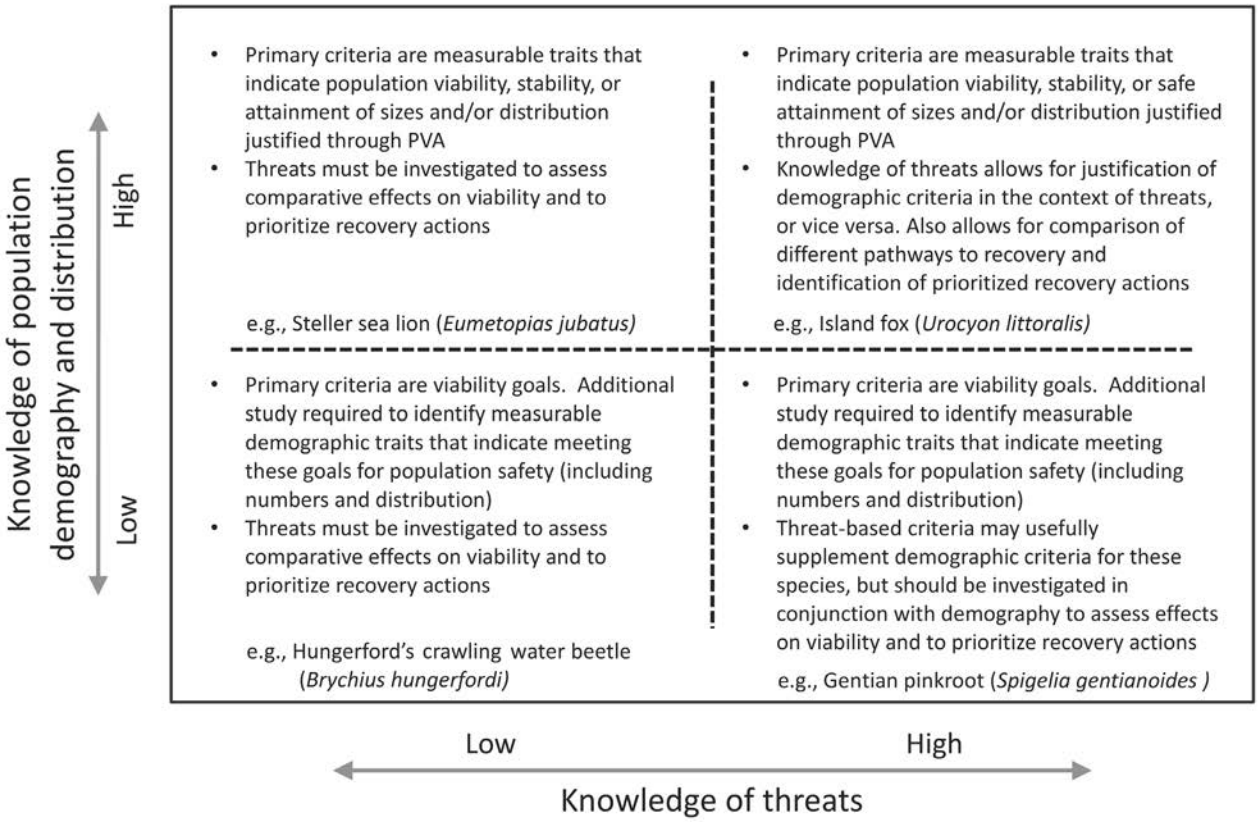


***Figure 2. Formulating the path to recovery for threatened and endangered species is influenced by the degree of knowledge of threats and of population demography and distribution. We present general guidelines for developing demographic and threat-based recovery criteria for listed species based on the initial levels of knowledge about the species and its threats. All completed recovery plans, including those listed here as examples, are available at* www.fws.gov/endangered/species/recovery-plans.html.**

from falling below desired thresholds but also stipulating further data collection to refine the link between numbers and safety, which will, in general, involve use of some type of PVA (appendix S3).

Recommendation 3: Threat-based criteria should derive from the population consequences of threats. A plan that has only threat-based criteria, unlinked to population trends or demographic measurements, is difficult or impossible to defend scientifically. When quantitative estimates of the impacts of threats on demographic processes or population growth rates are available, the level of threat reduction stipulated as a goal for recovery should be based on their population-level effects, in the context of other threats and the species' life history. As the classic case of the loggerhead sea turtle (*Caretta caretta*) shows, such analyses are necessary to correctly prioritize among different threats (Crouse et al. 1987, Crowder et al. 1994) and therefore to gauge the threat reduction needed to achieve self-sustaining populations, in part because threat factors, themselves—let alone specific levels for their abatement—are inherently difficult to precisely and defendably define. We recommend that threat-based recovery criteria—that is, criteria that specify the threat abatement necessary for the removal of a species from ESA protection—be expressed in terms of the level of threat reduction needed for population viability. Specifically, the impacts of current and anticipated future threats (including the loss of ESA protections) should be included in population models so that the interactive effects of multiple threats or threat reductions are folded into an overall assessment of viability (see supplemental appendix S2). An alternative option, already taken in some plans (e.g., for the black-footed ferret, *Mustela nigripes*), is to justify the demographic thresholds in the context of threats and describe how achievement of the criteria would indicate that the threats have been adequately addressed. All criteria should specify that any new information about the demographic impacts of threats and the expected impact of regulatory changes after delisting be incorporated when assessing whether the population is recovered. Although accurately anticipating novel or changing threats is not trivial, our approach incorporates this uncertainty into a framework that is flexible and

that requires any new threats to be controlled to the levels necessary to achieve population safety before delisting can be considered.

If the demographic impacts of a threat cannot be adequately quantified when a plan is written, one alternative is to define criteria addressing this threat in terms of viability (box 3). In these data-poor situations (figure 2), this would involve a two-pronged approach that takes advantage of the requirement for plans to define actions, as well as criteria. First, recovery *criteria* would specify that the threat must be low enough to allow the population to meet a specific viability standard. Second, recovery *actions* would include activities that lower threat levels and also that collect data to quantify the demographic or population-level responses to these threat reductions.

This approach to threat reduction can also effectively address conservation-reliant species. Managers are increasingly aware that many endangered species will require conservation measures in perpetuity (Goble et al. 2012). Well-executed PVA analyses can take into account future threat management scenarios, including the effects of delisting on the regulatory mechanisms needed to ensure that essential management continues. In our view, assessing whether even the seemingly nonbiological threat factor 4 (the inadequacy of existing regulation) has been sufficiently ameliorated requires a population perspective (e.g., will laws limiting future harvest allow the species to sustain numbers above the desired population thresholds?). In some cases, a realistic consideration of a species' biology and future threat scenarios (e.g., climate change, regulatory changes) may preclude recovery criteria that are attainable in the foreseeable future; nevertheless, such a determination would be a successful outcome of quantitative analyses and of the ESA, rather than a failure (Doremus and Pagel 2001).

Implications of these recommendations

Our recommendations contrast with the services' current guidelines on viability-based criteria, which state that such criteria should be ancillary to "traditional population and listing factor-based recovery criteria" because, they state, PVAs rely on estimates of vital rates and on assumptions about threat conditions and their effects on demographic rates (NMFS and USFWS 2010; as has been noted elsewhere, PVAs can be based on many other kinds of data). However, "traditional" criteria not linked to PVA are also based on guesses or assumptions about population processes, including demographic rates, as well as assumptions about threat conditions and their effects on demography, with the important difference that these assumptions and estimates are often unclear, implicit, and indirect. This lack of transparency in the estimates and assumptions linking traditional criteria and population health is their key weakness. In viability-based criteria, assumptions about the effects of threats on recovery are explicitly stated, which allows for updating of criteria (and models) as assumptions are tested and additional data are collected.

We acknowledge that we are setting a high bar for the services, especially in suggesting that threats be tied to population responses and extinction risk, but we believe that it is crucially important to push for these high standards so as to ensure the long-term survival of imperiled species and efficient and effective management. Following our recommendations will make criteria more scientifically and legally defensible, more transparent, and more aligned with the already-developed conservation planning literature (e.g., Salafsky et al. 2002, 2008). In particular, our recommendations are intended to create a scientifically justifiable approach that can accommodate the diverse situations of different listed species (figure 2). For some species, large, long-term data sets are available, the effects of threat factors have been experimentally estimated, and adequate financial resources to support management are in hand. For most species, none of these advantages exist, and a recovery plan can count on only modest monitoring and analysis efforts, which make rigid numerical recovery criteria set at the time the plan is written impractical and indefensible. The approach that we suggest can accommodate both these extremes, without resorting to weak generalizations, guesswork, or untested expert opinion. Furthermore, they are designed to be flexible enough to allow recovery criteria to stay relevant in the face of shifting threat conditions such as climate change, exotic species, and land-use change.

Just as importantly, an emphasis on recovery criteria that are tied to a population's status, rather than to the amelioration of specific threats, can give the services flexibility to change management tactics if new threats arise after the recovery plan is written. Using demographic criteria, the degree of threat abatement needed can be directly tied to the ultimate goal of recovery, and when new information indicates that more or less attention to a given threat is needed, the criteria can accommodate this updated information.

Finally, having to show that recovery criteria actually mean that a population is relatively safe from extinction or from dropping to a low level that impedes its functional role in an ecosystem may mean that some species are not removed from the list as quickly. We underscore, however, that this is not a valid objection to these recommendations. If we are slower to remove species from ESA protections because we cannot say with an acceptable degree of certainty that they are indeed recovered, that is the scientifically justifiable, legally required, and precautionary outcome. That said, making clearer statements of how recovery is defined and justified should also mean faster delisting of some species, as well as making recovery actions more targeted and delisting decisions less contentious.

In considering our first and most fundamental recommendation, it is important to address several aspects of PVA and related population analysis tools. First, this is not a recommendation to adopt hopelessly complex approaches to viability assessment. Population analyses can be quite simple, even when applied to spatially complex situations (see appendix S3 for examples); this recommendation does

not require mountains of data or cutting-edge analysis, nor is it designed to be a job creation program for population modelers. What it does require is a clear statement of what risk of population deterioration is deemed acceptable and why the recovery criteria proposed would indicate that a species has likely met this goal. The need to define such clear standards is the most fundamental advantage of taking this approach to recovery criteria development.

Second, implementing these recommendations does not require that PVA and other population analysis methods be flawless. The strengths and weaknesses of predicting population fates have been thoroughly dissected in the conservation literature (Beissinger and Westphal 1998, Ludwig 1999, Coulson et al. 2001, Ellner et al. 2002). However, the core shortcomings of PVA as a predictive tool are shared with all other predictive methods. Some may argue that, because they are based on analyses more complex than simple statistics, viability-based criteria may be less palatable to policymakers and managers. But this objection applies to many types of scientific evidence already used in legal and social contexts, such as genetic analyses used in criminal cases or the formulation of ecotoxicological standards in pollution control and, in this case, can be addressed by clear explanation of the details of the data and assumptions used to estimate population viability and its uncertainty.

Finally, with regard to the use of population analysis methods to assess recovery, the limitations of PVAs must be judged against the shortcomings of alternative methods for determining recovery. We do not see a good argument for the use of criteria justified mostly or solely by expert opinion, as opposed to standards based on actual analysis of population status and dynamics. Another potential option would be to adopt the International Union for Conservation of Nature's (IUCN) listing criteria (IUCN 2012). However, we believe that this would be a poor way to improve recovery planning. Although their adoption would standardize recovery criteria, IUCN benchmarks were designed as a one-size-fits-all system for global priority setting across all taxa and multiple conservation situations and, as such, do not take into account species-specific biology and threat conditions, which we believe is a crucial component of effective management and precautionary delisting. With that said, our recommendations are not incompatible with the IUCN approach, because one of the requirements for moving a species to a lower IUCN threat level is the completion of a quantitative analysis to evaluate its risk of extinction.

Implementing the recommendations

Criticism of ESA implementation is easy, but practical improvements likely to be adopted given the services' legal, political, and budgetary constraints are hard. Based on our conversations with service personnel, we offer these suggestions for how to implement our recommendations.

First, we suggest that the recovery planning guidelines be revised to provide clear guidance to recovery plan authors on why and how to set quantitative, scientifically defensible criteria. We have tried to describe as lucidly as possible how such criteria could be formulated (box 3; appendix S3).

Second, we suggest that the services develop mechanisms to encourage both natural and social scientists from outside the agencies to contribute their expertise and time to the process of developing recovery criteria. Writing a well-articulated, objective, and defensible plan would seem nearly impossible without input from individuals with multiple perspectives and expertise, including those with an understanding of the legal and regulatory sideboards of recovery planning; knowledge of the species and its ecosystem, as well as the threats the species faces and their biological impacts; knowledge of the political, social, and land-use settings where the species occurs; and expertise in analytical and modeling methods necessary to assess a species' recovery status in a scientifically defensible way. For high-profile species, it is easier for the services to assemble recovery teams that include members with each of these types of expertise. But the many species for which plans are written by individuals or small teams will often not have the benefit of this complete set of knowledge and skills. This is not a trivial obstacle to improving recovery planning.

One possibility to redress this limitation is for university biologists to incorporate recovering planning into their teaching. For example, graduate students in a population ecology course could construct, parameterize, and use population models to craft demography-based threat reduction actions and recovery criteria. If adequate data are not available, students and faculty members could work with plan writers to design effective recovery actions to collect the data needed to assess recovery. Close coordination with the services in such efforts is essential so that the contributions of academic partners are useful to the planning process. A different approach to achieve the same end would be to find funding for postdoctoral researchers or other individuals outside the services to contribute expertise that could allow the services to more rapidly produce defensible plans. An added benefit of either scenario is that a cohort of young scientists will gain real-world experience at the intersection of conservation science, practice, and policy, and thereby foster their careers in conservation. Experts on planning, policy, social science, and environmental law could likewise be tapped to work on other elements of recovery planning.

Finally, the services are required to review the status of each listed species every five years, including the evaluation of new information and threats that can trigger a revision of an outdated recovery plan (NMFS and USFWS 2010). We encourage nonagency scientists with species-specific expertise to communicate their work to the services, and we urge the services to create openings for nonagency experts to participate in these reviews, including updating population assessments in light of new data. This phase of the recovery process presents another opportunity for early-career scientists to make substantive contributions to conservation practice.

Conclusions

We believe that we have presented practical and important ways to enhance the scientific integrity of the recovery planning process. Similarly, we think that creating ways to better tap the expertise, time, and enthusiasm of scientists outside of the services can be a means to implement these recommendations and overcome the very real constraints faced by the services in writing strong recovery plans. For that external involvement to be efficient and effective, however, the services must be open to working with outsiders, and scientists must understand the needs and constraints inherent in ESA implementation.

Although we have focused here on recovery planning under the US ESA, many other nations have similar legislation with provisions for endangered species recovery. Although there are parallel sets of proposed approaches to endangered species assessment and recovery planning in other jurisdictions, these proposals and critiques are similar to those of the US ESA; there are many suggestions but little evidence of on-the-ground improvement (Salafsky et al. 2008, Mooers et al. 2010, but see Salafsky and Margoluis 1999). The general approaches that we suggest here can help improve the management of threatened species elsewhere and may also be applicable to other aspects of ESA planning, such as critical habitat designation and section 7 consultation. With our emphasis on defining clear standards by which to judge recovery and requiring that recovery criteria and threat reductions be explicitly linked to these measures of population safety, our recommended approach will help ensure that recovery plans more effectively and efficiently guide recovery of imperiled species.

Acknowledgments

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Supplemental material

The supplemental material is available online at *http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biu215/-/DC1*.

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COASTAL AND MARINE ECOLOGY

Survival of the fattest: linking body condition to prey availability and survivorship of killer whales

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Abstract. Recovering small, endangered populations is challenging, especially if the drivers of declines are not well understood. While infrequent births and deaths may be important to the outlook of endangered populations, small sample sizes confound studies seeking the mechanisms underlying demographic fluctuations. Individual metrics of health, such as nutritive condition, can provide a rich data source on population status and may translate into population trends. We examined interannual changes in body condition metrics of endangered Southern Resident killer whales (SRKW) collected using helicopters and remotely operated drones. We imaged and measured the condition of the majority of all three social pods (J, K, and L) in each of seven years between 2008 and 2019. We used Bayesian multi-state transition models to identify relationships between body condition changes and both tributary-specific and area-based indices of Chinook salmon abundance, and *K*-fold cross-validation to compare the predictive power of candidate salmon covariates. We found that Fraser River (tributary-specific) and Salish Sea (area-based) Chinook salmon abundances had the greatest predictive power for J Pod body condition changes, as well as the strongest relationships between any salmon covariates and SRKW condition across pods. Puget Sound (tributary-specific) Chinook salmon abundance had the greatest predictive power for L Pod body condition changes, but a weaker relationship than Fraser River or Salish Sea abundance had with J Pod body condition. The best-fit model for K Pod included no Chinook covariates. In addition, we found elevated mortality probabilities in SRKW exhibiting poor body condition (reflecting depleted fat reserves), 2–3 times higher than whales in more robust condition. Collectively, these findings demonstrate that (1) fluctuations in SRKW body condition can in some cases be linked to Chinook salmon abundance; (2) the three SRKW pods appear to have distinct patterns of body condition fluctuations, suggesting different foraging patterns; and (3) aerial photogrammetry is a useful early-warning system that can identify SRKW at higher risk of mortality in the near future.

Key words: adaptive management; body condition; drones; foraging ecology; multi-state modeling; *Orcinus orca*; photogrammetry; resident killer whale.

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Introduction

Endangered species with small population sizes approaching extinction or local extirpation present a diversity of management challenges (Soulé 1987, Dennis 1989). When the causes of population declines are not well established, it is difficult to identify management strategies that will prevent declines and promote recovery. Studies of small populations by definition suffer from sample size limitations (Walsh 2000, Brosi and Biber 2009), complicating efforts to identify stressors that may be influencing population trends (Schönbrodt and Perugini 2013). For example, infrequent births or deaths may have dramatic impacts on population trends, but may be too sparse to identify mechanisms. In these cases, non-invasive metrics of individual health can help identify drivers of population trends and allow for management strategies that preempt demographic casualties that impact population viability, such as the loss of reproductive females.

Nutritive condition in long-lived vertebrates can provide a sensitive signal of short-term individual or population health. Changes in condition may reflect changes in the environment or foraging success, and persistent variation may translate into population trends (Berger 2012, Boulanger et al. 2013, Vindenes et al. 2014). Aerial imaging technology has provided one example of such non-invasive individual health metrics (Perryman and Lynn 2002). Photogrammetry with remotely controlled drones has been used increasingly over the past 5–10 yr as drones have become cheaper, safer, and more efficient compared with traditional photogrammetry using crewed aircraft (Durban et al. 2015). These methods have been widely applied to both terrestrial and marine species (Goebel et al. 2015, Hu et al. 2020). Working with marine or other aquatic organisms is particularly challenging, as individuals are highly mobile and may spend little time near the surface where they can be imaged. Nevertheless, aerial photogrammetry has been used to collect individual measurements of marine mammal species including investigations of life-history characteristics (Christiansen et al. 2016, Groskreutz et al. 2019) and nutritive condition (Christiansen et al. 2018, Fearnbach et al. 2018, 2020). A strength of aerial photogrammetry is that it can non-invasively provide quantitative metrics of body condition at the individual level (Durban et al. 2015, Fearnbach et al. 2018), which can be used to evaluate the health or status of a large portion of a population in near real time. These high-resolution measures of condition and fitness may in turn contribute to an understanding of the mechanisms underlying demographic variability, for example, by linking condition to reproductive success (Christiansen et al. 2016) or mortality (Christiansen et al. 2020).

Collecting individual health data from wild populations may be challenging, particularly if individuals cannot be identified or the population is not censused. Killer whales (*Orcinus orca*) represent an ideal case for relating individual health metrics to the environment, as population sizes are typically small, and individuals are readily identifiable. One of the smallest populations of killer whales, the Southern Resident killer whale (SRKW) population, is censused annually and demographic characteristics (age, sex) have been recorded for the entire population since the mid-1970s (Center for Whale Research 2020). This small ($n = 73$) population of fish-eating killer whales is found in the eastern north Pacific (Ford et al. 1998) with a range including coastal waters from central California to Southeastern Alaska, and core summer habitat in the Salish Sea between Puget Sound and Southern Vancouver Island (National Marine Fisheries Service 2019). Because of its small size and a decline in abundance of approximately 25% since 1995, the SRKW population is listed as endangered under the Endangered Species Act (ESA) in the United States and the Species-at-Risk Act (SARA)

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in Canada. The diet of SRKWs comprises primarily Chinook salmon (*Oncorhynchus tshawytscha*), although other species such as Coho salmon (*Oncorhynchus kisutch*), chum salmon (*Oncorhynchus keta*), halibut (*Hippoglossus stenolepis*), and groundfish have also been identified in their diets (Hanson et al. 2010, Ford et al. 2016). Three main stressors are thought to be responsible for SRKW population declines: (1) elevated levels of environmental pollutants in their core habitat range that could impact survivorship and reproductive success (Krahn et al. 2009); (2) increasing vessel noise and disturbance in the Salish Sea which could interfere with communication and foraging efficiency (Lusseau et al. 2009); and (3) declining Chinook salmon populations and therefore prey scarcity (Ford et al. 2010), which in addition to direct effects could compound the other stressors (e.g., Lundin et al. 2016).

Several studies have supported the hypothesis that prey limitation is a primary threat to the SRKW population, linking aggregates of Chinook salmon abundance to both fecundity and mortality (Ward et al. 2009, Ford et al. 2010, Vélez-Espino et al. 2014, Wasser et al. 2017) as well as to declines in adult body size (Fearnbach et al. 2011, Groskreutz et al. 2019). However, the range of both SRKWs and their salmon prey is enormous, encompassing over 3000 km of coastline, and identifying the prey populations that are most important for SRKWs is challenging. Chinook salmon face a complex suite of stressors including habitat modification and degradation (Greene and Beechie 2004), restricted access to spawning tributaries (Sheer and Steel 2006), fisheries pressure (Ruckelshaus et al. 2002), increased natural mortality due to recovering marine mammal populations (Chasco et al. 2017), variable at-sea survival (Losee et al. 2019, Welch et al. 2021), and climate impacts (Crozier et al. 2008). Chinook populations from four tributaries within the SRKW range are themselves listed as endangered in the United States or Canada, with several others listed as threatened. To date, no studies have been able to identify relationships between specific salmon populations and SRKW survivorship or population health (Pacific Fishery Management Council 2020).

Aerial photogrammetry can provide a precise measure of individual killer whales' nutritive condition by quantifying the relative amount of adipose fat stored behind the cranium; as individuals decline in nutritive condition, they metabolize adipose fat in addition to blubber stores (Fearnbach et al. 2020). As such, photogrammetry datasets potentially provide more power to evaluate relationships between prey abundance and population status compared with efforts to link prey to infrequent births and deaths. In this study, we used aerial photogrammetry images of individually recognizable SRKWs collected in 7 September field efforts across 12 yr (2008–2019) to evaluate how changes in body condition might be related to the abundance of different Chinook salmon populations. The SRKW population is composed of three distinct collections of matrilineal family units (hereafter referred to as J, K, and L pods; Parsons et al. 2009), and we considered each pod separately in our analyses based on previously described differences in range and movement patterns (National Marine Fisheries Service 2019, Riera et al. 2019).

Methods

Data collection

Aerial images of Southern Resident killer whales were collected in the Salish Sea near the San Juan Islands, WA (Fearnbach et al. 2011, Groskreutz et al. 2019) in the month of September in each of seven years. Images were collected from a manned helicopter in 2008 and 2013 (Fearnbach et al. 2011, 2018) and using a drone in 2015–2019 (Durban et al. 2015, Fearnbach et al. 2020). Briefly, vertical images were collected using a digital camera at altitudes of 230–460 m by helicopter and 25–45 m by drone. Despite changes in aircraft platforms, all images were obtained with a Normal lens to ensure a flat image with no wide-angle distortion, with the specific camera and lens chosen based on aircraft altitude to achieve a water-level pixel resolution of 1–2 cm (Durban et al. 2015). Research activities were permitted by the National Marine Fisheries service in the U.S. and the Department of Fisheries and Oceans in Canada, and aerial photogrammetry was approved as an observational (non-invasive) method by the Institution Animal Care and Use Committee of the NOAA Southwest Fisheries Science Center Marine Mammal and Turtle

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Division. Individual whales can be identified by unique markings that are visible from aerial images, allowing measurements to be linked to individual whales of known age and sex (Fearnbach et al. 2011, 2020, Durban et al. 2015). As a quantitative metric of body condition, we used the eye patch ratio (EPR), which is the ratio of the pixel distance between the inside of the white eye patch pigmentation at their anterior end relative to their distance at 75% of the eye patch length, described in Fearnbach et al. (2020; Fig. 1). The eye patch ratio is a sensitive metric of nutritive condition as it measures the relative amount of adipose fat stored behind the cranium. As killer whales become nutritionally stressed, they lose this adipose tissue along with blubber fat reserves, resulting in lower EPRs, and as such, this is a more sensitive metric of nutritive condition in killer whales compared to other commonly used metrics such as head width to body length ratios (Fearnbach et al. 2020). Multiple measurement-quality images were available of a single whale on a given day and within years, and we used the mean EPR for each whale in each year because EPR calculations had very low variability (e.g., typical coefficients of variation of 0.003–0.008 for within-year variability of a given whale; Fearnbach et al. 2020).

Accounting for age and sex

To prepare the raw eye patch ratio data for analysis, we first fit a generalized additive model to the EPRs using the mgcv package (Wood 2006) in R (R Core Team 2016) to account for expected variability in nutritive condition and EPRs by age and sex. Age and sex data were available from long-term demographic modeling efforts (Center for Whale Research 2020). We fit separate smooth terms to male and female EPRs from whales aged 0–60 (Fig. 1). We used the raw residuals (observed EPR minus mean EPR estimated by the spline fit) as the basis for defining body condition classes. Ages of a few mature Southern Resident killer whale females that were reproductive when monitoring began in the 1970s are not known precisely, so we calculated residuals for those whales by subtracting observed EPRs from the mean EPR of whales age 60+. We aggregated the residuals of all EPR measurements from all pods across all years and split that distribution into five equal quantiles, representing the age- and sex-normalized body condition classes to be used in the multi-state model, with body condition class 1 (BC1) being the lowest 20% quantile and BC5 being the highest 20% quantile. Finally, we created a matrix of individuals' body condition classes by year, including unsampled years 2009–2012 and 2014. In unsampled years, and in years where a whale was not photographed despite survey effort, individual condition was logged as NA. Known deaths from the annual census (Center for Whale Research 2020) were also included in the matrix to facilitate estimation of both age/sex- and body condition-specific mortality probabilities. Because photogrammetry data were collected in September of each year, we considered deaths that occurred between October and the following September to belong to the following survey year. For example, if a whale was measured in September 2016 and died in November 2016, we logged that death in the following time step of the condition matrix, 2017, to allow the model to account for the transition from the condition measured in September 2016 to death. Two known anthropogenic-related deaths were not included in the model: whale J34 died of blunt force trauma in 2016 (Raverty et al. 2020) and was measured in body condition class 5 the same year; L95 died in 2016 of a fungal infection that may have been associated with a satellite tag attachment (Huggins et al. 2020) and was measured in body condition class 1 the previous year. The condition matrix for those whales was left as unknown (NA) after their last measurements, to prevent them from influencing mortality probabilities for their respective body condition classes prior to death.

Statistical model

We developed a Bayesian multi-state modeling framework to evaluate changes in body condition between years and the probability of mortality of different condition classes, after accounting for differences in mortality by age and sex. All modeling was performed in JAGS via R (Plummer 2003) and built upon previous multi-state modeling approaches (Kery and Schaub 2012). The model estimated annual transition probabilities between body condition classes, as well as transitions from each body condition class to death, which are the condition-specific mortality

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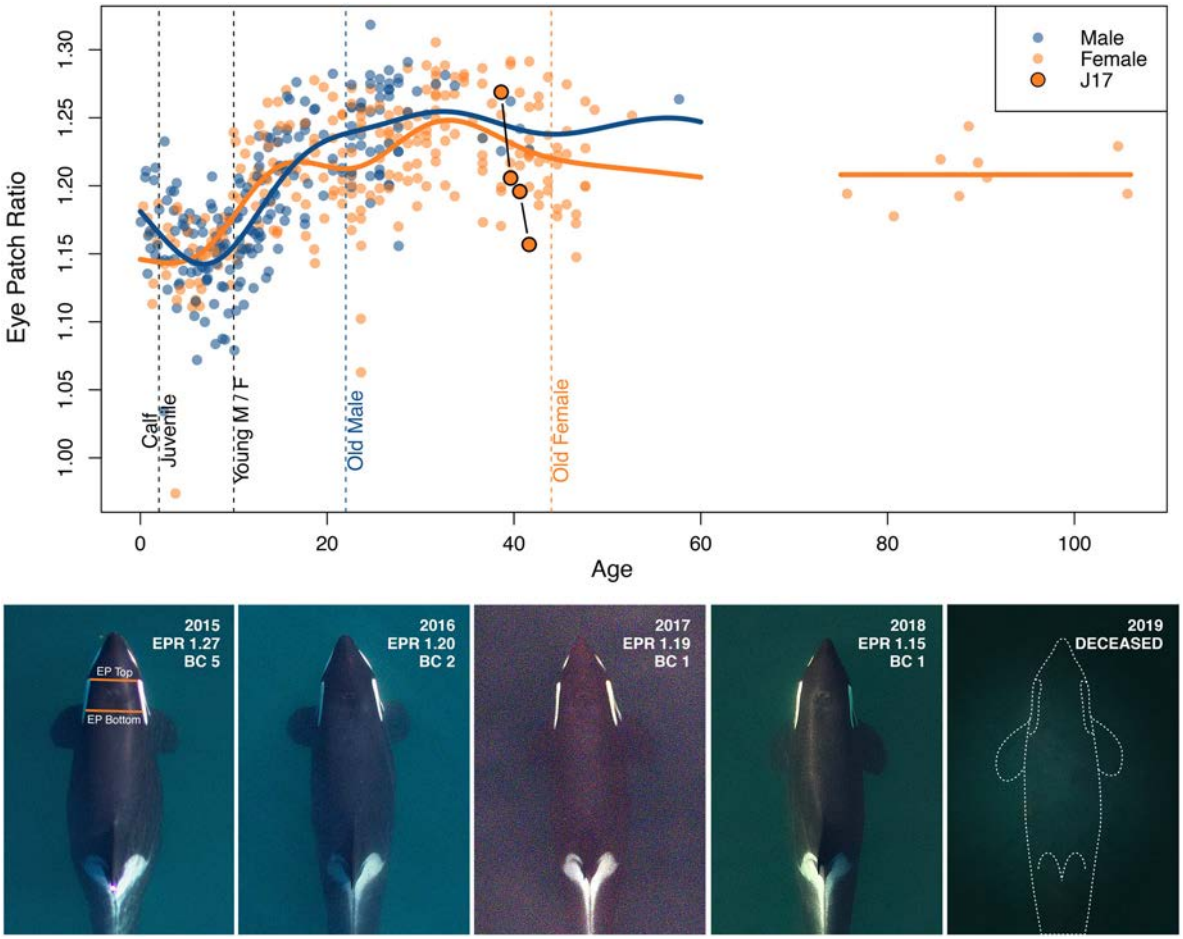


Fig. 1. Eye patch ratios by age and sex for Southern Resident killer whale individuals from all three pods during the study period. The top panel shows the measured eye patch ratio by age for males (blue) and females (orange). The spline fits for males (blue) and females (orange) were used to define body condition classes based on residuals, while a mean eye patch ratio was used to calculate residuals for females aged 60+ that did not have reliable age estimates (see Methods). Vertical dashed lines delineate the age and sex classes used to estimate age- and sex-specific mortality probabilities. The series of images tracks the eye patch ratio (EPR) and body condition class (BC) of adult female J17 from 2015 to 2018, demonstrating the observed decline in condition preceding her death in summer 2019. The progression of J17's eye patch ratios is highlighted in the top panel in larger, dark orange circles connected by lines. The orange horizontal lines in the far-left image show how the eye patch ratio is calculated (EP bottom divided by EP top), providing a metric of adipose fat behind the cranium as a proxy for nutritive condition.

probabilities. An increase of one condition class (e.g., BC 1–BC 2; BC 3–BC 4) was considered growth (G). Increases of two or more condition classes were considered multiple single Growth steps, and their probabilities were therefore exponentiated (e.g., BC 1–BC 3 = G^2; BC 1–BC 4 = G^3). Remaining in the same condition class in two sequential years was considered stable (S). A decrease of one condition class was considered decline (D), and decreases of two of more condition classes were exponentiated as with growth transitions. The advantages of using power functions for the G and D elements are that the number of parameters is reduced relative to an unconstrained matrix, and transitioning across multiple steps is constrained to be less likely than

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transitioning a single step. In order to make population-level inferences from individual changes in condition, all animals transitioning in the same direction and magnitude contributed to the same transition probabilities, regardless of their starting condition class:

	BC1	BC2	BC3	BC4	BC5	Dead
BC1	S_t	G_t	G_t^2	G_t^3	G_t^4	$M_{1_{i,t}}$
BC2	D_t	S_t	G_t	G_t^2	G_t^3	$M_{2_{i,t}}$
BC3	D_t^2	D_t	S_t	G_t	G_t^2	$M_{3_{i,t}}$
BC4	D_t^3	D_t^2	D_t	S_t	G_t	$M_{4_{i,t}}$
BC5	D_t^4	D_t^3	$\mathrm{D_t^2}$	D_t	S_t	$M_{5_{i,t}}$
Dead	0	0	0	0	0	1

where rows are the condition class in year $t - 1$, columns are the condition class in year t, and the matrix is populated by transition probabilities for year t. To make the sum of each row equal to 1, we normalized each row by dividing each element by its row sum (e.g., Cobb and Chen 2003, Liu et al. 2008). Mortality probabilities M were dependent on an individual whale's age, sex, and body condition. As a result, differences in mortality probability based on age, sex, and body condition slightly affected transition probabilities during row normalization. This can be interpreted as making transition probabilities between condition classes conditional upon a whale surviving.

Mortality probability was estimated in two steps: first based on the age and sex of a whale and then based on the condition class of that whale. We assigned an age class to each whale at each time step in the model, following previous classifications used for SRKW demographic modeling (Ward et al. 2013). Both males and females age 0–2 were defined as calves and 2–10 as juveniles. Females age 10–44 were defined as young females and 45+ as old females. Males age 10–22 were defined as young males and 23+ as old males (Fig. 1). The baseline mortality probability for whales in each age class was defined as:

$$M_{\mathrm{Base}_a} \sim N[\mathrm{logit}(\widehat{M}_{\mathrm{Base}}), \sigma]$$

$$\widehat{M}_{\mathrm{Base}} \sim U[0, 1]$$

where M_{Base} is the baseline mortality probability for a whale in age class a (of the 6 age/sex classes defined above), which is normally distributed around the overall mean mortality probability, $\widehat{M}_{\mathrm{Base}}$, with variance σ in logit space. We then added a random effect of body condition such that the mortality probability of a whale at a given time step was calculated as:

$$M_{i,t} = \mathrm{inv.logit}(M_{\mathrm{Base}_{i,t}} + M_{\mathrm{bc}_{i,t}})$$

$$M_{\mathrm{bc}} \sim N[0, \sigma]$$

where M is the mortality probability (in proportional space) for whale i at time t, M_{Base} is the age-specific baseline mortality probability (in logit space) for whale i given its age and sex class at time t, and M_{bc} is the condition-specific effect (in logit space) on baseline mortality for whale i given its body condition class bc at time t. M_{bc} for body condition class bc (1–5) is normally distributed around zero with variance σ in logit space. After applying the random effect of body condition to the whale's baseline mortality probability, that sum is converted to proportional space using the inverse logit transformation.

To incorporate salmon abundance covariates into the model, we used a cumulative logit transformation to allow covariates to have independent relationships to growth and decline transition probabilities while remaining bounded by [0, 1] in proportional space. For growth and decline transitions, we used the following equation:

$$\mathrm{Transition}_{c,t} = e^{\mathrm{intercept}_c + \mathrm{slope}_c \times \mathrm{covariate}_t + \varepsilon_{c,t}}$$

where Transition is the uncorrected transition probability in cumulative logit space of transition type c (i.e., G or D) at time t, intercept and slope are the linear relationship terms for each transition type c, covariate is the salmon index at time t, and ε is the residual error around the linear fit for transition type c at time t, with

$$\varepsilon_{c,t} \sim N[0, \sigma]$$

where the ε terms for each transition type c are normally distributed around zero with variance σ. In the cumulative logit transformation, one parameter must be fixed at 1 for identifiability, which we applied to the probability of stable condition (S):

$$\mathrm{Transition}_{S,t} = 1$$

The uncorrected transition probabilities are then transformed to proportional space so that they are bounded by [0, 1]:

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$$\text{Prob}_{c,t} = \frac{\text{Transition}_{c,t}}{\sum_i \text{Transition}_t}$$

where Prob is the corrected probability for each transition type c (G, D, and S) at time t.

Missing values of condition classes (included as NA in the condition matrix) were estimated by the model as part of the joint posterior distribution and were treated as an unknown model parameter or latent state. As the number of consecutive missing values for an individual whale increases, the uncertainty in the posterior estimates of those condition classes is also expected to increase, as there will be more plausible condition sequences to link the observed conditions on either side of the missing values. Because the model requires condition classes in two consecutive years in order to estimate a transition probability, this approach allowed us to include data from whales with incomplete measurement histories (and span the field sampling gap from 2009 to 2012) by using the model to probabilistically assign missing condition classes based on estimated covariate relationships and condition data before and after missing values.

Salmon covariates

We evaluated seven different Chinook salmon abundance indices to identify potential relationships between SRKW body condition and prey availability. We only considered Chinook salmon given the reported importance of Chinook to SRKW life history and reproductive success (Ward et al. 2009, Ford et al. 2010). We used estimates of Chinook salmon abundance from a model used to manage salmon harvest (Fishery Regulation Assessment Model; FRAM; Pacific Fishery Management Council 2008). The FRAM model estimates the abundance of multiple west coast salmon populations (or stocks) available to fisheries, and its outputs were recently synthesized with Chinook spatiotemporal distribution models to generate indices of Chinook available to killer whales by area, year, and season (Pacific Fishery Management Council 2020).

We used three tributary-specific and four area-specific Chinook indices (Pacific Fishery Management Council 2020). In this framework, estimates of Chinook are generated by season, corresponding to the seasons in the FRAM model (October–April, May–June, July–September). For all analyses, we used estimated starting abundances on July 1st of each year, representing abundance at the beginning of the summer season. SRKW are imaged in September each year, so this summer index of abundance provides the closest match to the true prey availability experienced by whales prior to condition measurements. Furthermore, condition at the time of measurement is unlikely to represent the availability of prey more than a few months prior, as SRKW condition is known to fluctuate seasonally, presumably in response to foraging opportunities (Fearnbach et al. 2020). We focused on three of the larger tributary-specific indices (Fraser River, Columbia River, and Puget Sound) and included all modeled stock abundances originating from those tributaries (Appendix S1: Table S1). We note that there is no spatial component to the tributary-specific indices. The four area-specific indices we used were North of Cape Falcon (NOF), Oregon (OR), the Salish Sea (Salish), and Southwest Vancouver Island (SWVI) (Pacific Fishery Management Council 2020). These area-specific indices summed the model estimated abundances of all Chinook salmon from all index stocks that were estimated to be present.

Transition probabilities within the model were related to the salmon index of the year that the whales were transitioning into. For example, the probability of growth (G) from condition class in September 2014 to condition class in September 2015 was linked to estimated Chinook abundance in the summer season (starting July 1st) of 2015. Given the observed differences in body condition trends between SRKW pods, we ran J, K, and L pods through the model separately, each with the same seven candidate covariates to identify potential relationships between each pod and various salmon indices. To determine whether there was support for the inclusion of covariates on transition probabilities, we also considered a null model (condition transition probabilities fixed across all years) and a time-only model (condition transition probabilities estimated independently each year with no covariate). Given the relatively small number of deaths that occurred during the study period, and previous studies that have assumed shared mortality probabilities across pods (Ward et al. 2013), we also ran null and time-only models for all pods combined to estimate population-wide

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mortality probabilities with body condition effects. For each model, we ran three chains of 100,000 iterations each, with a burn-in of 50,000 iterations and thinning of 50 for a total of 3000 samples from the posterior distribution. We used non-informative uniform priors for all parameters (Mitchell and Beauchamp 1988) and confirmed model convergence using potential scale reduction factors (Gelman and Rubin 1992; all parameters PSRF < 1.05) and visual inspection of chain convergence.

Model selection

To identify which (if any) Chinook salmon covariates best predicted SRKW body condition transitions, we used a *K*-fold cross-validation approach (Vehtari et al. 2017). There are many different ways to split training and test data sets for cross-validation, depending on the goals of inference. Because our focus is on the temporal aspect, and in developing tools for making short-term future predictions of body condition, we treated data from each year iteratively as a fold. For each pod and covariate combination, we ran the multi-state condition transition model once with each year of observed condition data held out ($n = 7$ yr), using the remaining years of observed condition data to fit the estimated condition transition probabilities and covariate relationships. We then calculated the expected log pointwise predictive density (ELPD) across all held out years of observed body conditions based on the conditions in the previous year and the model-estimated transition probabilities, following (Vehtari et al. 2017). We performed *K*-fold cross-validation for each of the pod and covariate combinations, as well as for each pod with the null and time-only models described above. In addition to the computing the ELPD for each model (models with the highest ELPD receive the highest data support), we calculated the standard error, which is useful in quantifying the uncertainty associated with model selection (Vehtari et al. 2017).

Results

In the seven sampled years between 2008 and 2019, a total of 473 measurements of body condition were collected from 99 whales, which were used in our analyses. We recorded a median of 5 yr of body condition measurements for each whale (range 1–7). A total of 47 deaths and 33 births were documented in SRKWs between 2008 and 2019, while a total of 29 deaths and 15 births were documented in SRKWs during the same 7 yr as the aerial photogrammetry sampling (Center for Whale Research 2020).

In general, *K*-fold cross-validation from our Bayesian models suggested that killer whale body condition is better predicted when salmon covariates are included, relative to models without salmon (J and L pods, Appendix S1: Table S2). For models with salmon included, the standard errors of the ELPD values exceeded the difference in ELPD values among candidate models, which makes it challenging to confidently select one best-fit model. The high standard errors are likely due to having only seven years of condition data with which to calculate ELPDs, given that we considered an entire year of condition data to be a fold. Consequently, we also report the second best-fit model for each pod (Appendix S1: Figs. S1–S3). Due to the complexities of our model and the number of parameters, we present both the raw estimated transition probabilities and aggregated Stable and Growth transition probabilities. This grouping represents a positive transition group that may be more useful for managers targeted at preventing condition declines and maintaining stable or increasing condition.

Fraser River Chinook was the best predictor of J pod condition transitions (Fig. 2, Appendix S1: Table S1), although the ELPD value of the Salish Sea area-based Chinook abundance model fit (which includes a large proportion of the Fraser River stock) was almost identical. J Pod had a significant negative relationship between Fraser River Chinook abundance and the probability of declining condition (Decline), with 95.3% of posterior draws for the slope term in the cumulative logit regression < 0. There was no clear relationship between Fraser River Chinook abundance and the probability of increasing condition (growth; 38.5% of posterior draws > 0), and while the probability of stable condition appears to have a positive relationship with Fraser River Chinook, a slope term for S is not explicitly calculated in the cumulative logit regression. However, as the sum of the probabilities of growth and stable condition is equal to 1 minus the

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probability of decline, we can infer that there is a positive relationship between Fraser River Chinook and positive condition transitions (growth or stable condition; Fig. 2). When Fraser River Chinook salmon abundance was above 750,000 fish, J pod whales had a >0.86 median probability of stable or increasing condition. That probability decreased at lower Fraser River Chinook abundance, to a minimum 0.37 median probability of increasing or stable condition when Fraser River Chinook abundance fell to 347,000 fish.

The best-fit model for L pod included Chinook Salmon from Puget Sound, and nearly all models with salmon included outperformed the null models (Appendix S1: Table S1). There was moderate support for a negative relationship between Puget Sound Chinook abundance and the probability of declining condition, with 88% of posterior draws for the slope < 0. Similar to the results for J pod, there was no clear relationship between this index of salmon abundance and the probability of increasing condition (56.9% of posterior draws > 0). Nevertheless, when Puget Sound Chinook abundance was above 399,000 fish during the study period, L pod whales had a 0.82–0.89 median probability of stable or increasing condition. At the second-lowest Puget Sound Chinook abundance during the study period, 235,000 fish in 2015, L pod whales had a 0.32 median probability of stable or increasing condition. The major deviation from the positive linear relationship between Puget Sound Chinook abundance and condition transitions occurred in 2014, when Puget Sound Chinook was at its lowest point during the study period (208,000 fish), but L pod whales had a 0.60 median probability of stable or increasing condition. Apart from Puget Sound Chinook, all other models for L pod that included salmon covariates (both tributary-specific and area-based abundance) produced potentially spurious results, where higher salmon abundance was associated with declining condition (e.g., Appendix S1: Fig. S3).

Unlike J and L pods, the best-fit model for K pod did not include salmon as a covariate, and transition probabilities were held constant across years. In this null model, the median fixed probability of increasing condition (growth) was 0.40 (95% highest posterior density intervals [HPDIs]: 0.33–0.47). The median probability of decline was 0.31 (0.25–0.37), and the median probability of stable condition was 0.29 (0.21–0.38). The second best-fit model for K pod included Puget Sound Chinook abundance, although we note that this covariate relationship produced relatively constant condition transitions across years (Appendix S1: Fig. S2). Nevertheless, there was a significant positive relationship between Puget Sound Chinook abundance and the probability of increasing condition, with 94.93% of posterior draws for the slope > 0. There was no clear relationship between Puget Sound Chinook abundance and the probability of declining condition (22.6% of draws <0), and the probability of stable condition decreased with increasing Chinook abundance (Appendix S1: Fig. S2). When Puget Sound Chinook abundance was above 399,000 fish, K pod whales had a median 0.43–0.50 probability of increasing condition. In contrast, when Puget Sound Chinook abundance was at a low of 208,000, K pod whales had a median 0.14 probability of increasing condition. However, the probability of the management-relevant combined growth and stable condition remained relatively constant across the study period (median 0.68–0.78 probability; Appendix S1: Fig. S2).

While observations of body condition provided a relatively large sample size for estimating transition probabilities, deaths were relatively uncommon during the 12-year study period. Consequently, we estimated the effects of age, sex, and body condition on mortality probabilities by pooling all pods together and running models without covariates (null and time-only). There were 25 total deaths of whales that also had measurements of body condition in at least one year during the study period (12 in J pod, 3 in K pod, and 10 in L pod). 15 of those deaths occurred in the time step immediately following a body condition measurement. With data from all pods combined, the null model had a higher ELPD score than the time only model (Appendix S1: Table S1) and was therefore used for estimates of mortality probability. The median expected mortality probabilities for whales in each age/sex and body condition class are reported in Table 1. The estimated mortality probability of whales in body condition class 1 was 2–3 times higher than other body condition classes (Fig. 3, Table 1). Mortality probability decreased in condition class 2, was lowest in condition classes 3 and 4, and increased slightly in

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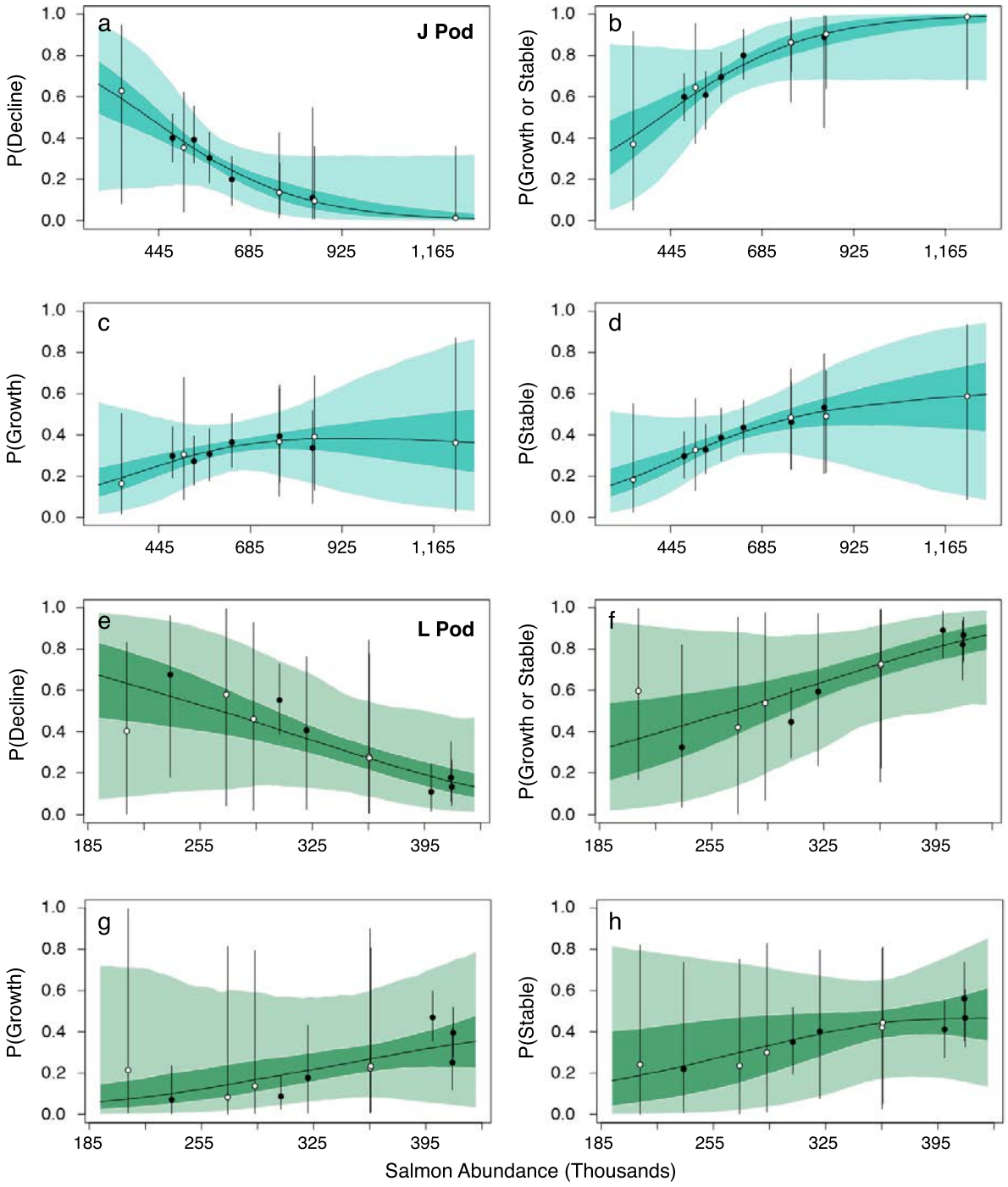


Fig. 2. Body condition transition probabilities for Southern Resident killer whale J (a–d) and L (e–h) pods with best-fit Chinook salmon covariates (Fraser River a–d and Puget Sound e–h). The best-fit model for K pod did not include a covariate (see Results). Panels show the model-estimated relationships between Chinook salmon abundance and the probability of a Decline in body condition (a, e), and the combined probability of Growth or Stable body condition (b, f). The probability of Growth or Stable condition shown in b and f is the sum of the posterior distributions for the probability of Growth (c, g) and the probability of Stable condition (d, h). Put simply,

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(Fig. 2. *Continued*)

b = c + d and f = g + h. Points and vertical bars represent the median estimated transition probability with 95% Highest Posterior Density Intervals. White circles indicate years with no photogrammetry measurements when condition classes were estimated by the model. The light and dark shading represent the 95% and 50% HPDIs, respectively, of the model-estimated relationship between salmon covariates and transition probabilities, along with the median estimate of this fit (black line).

Table 1. Model-estimated mortality probabilities by body condition (BC) and age/sex class for Southern Resident killer whales.

Age/sex class	BC 1	BC 2	BC 3	BC 4	BC 5
Calf	0.04 (0.004–0.177)	0.02 (0.001–0.085)	0.01 (0.001–0.066)	0.01 (0.001–0.069)	0.02 (0.002–0.105)
Juvenile	0.02 (0.003–0.060)	0.01 (0.001–0.030)	0.01 (0.000–0.025)	0.01 (0.000–0.025)	0.01 (0.002–0.037)
Young female	0.03 (0.009–0.081)	0.01 (0.003–0.043)	0.01 (0.001–0.033)	0.01 (0.001–0.033)	0.02 (0.005–0.048)
Old female	0.23 (0.069–0.595)	0.12 (0.026–0.348)	0.08 (0.010–0.261)	0.09 (0.011–0.274)	0.14 (0.042–0.406)
Young male	0.03 (0.006–0.105)	0.01 (0.002–0.052)	0.01 (0.001–0.039)	0.01 (0.001–0.041)	0.02 (0.003–0.062)
Old male	0.16 (0.047–0.432)	0.08 (0.018–0.231)	0.05 (0.006–0.171)	0.06 (0.007–0.173)	0.09 (0.026–0.267)

Note: Reported values are median estimates of the probability of mortality in a one-year time step, with 95% highest posterior density intervals in parentheses.

condition class 5 to levels similar to condition class 2. For example, based on the model estimates, a Young Female whale has expected mortality probabilities of: BC1 0.03 (0.009–0.081); BC2 0.014 (0.003–0.043); BC3 0.009 (0.001–0.033); BC4 0.01 (0.001–0.033); BC5 0.017 (0.005–0.048). Of the whales that died during the study period, condition class 1 whales died soonest after their final condition measurement (mean 169 days), while the time between measurement and estimated death roughly increased with condition class: mean 456, 790, 572, and 905 days for classes 2–5, respectively (Fig. 4).

Discussion

The Southern Resident killer whale population offers a unique study opportunity for individual-based body condition monitoring, providing a robust framework that can be extended to other marine and terrestrial populations. Due to the small population size, intensive demographic monitoring, and known fates of virtually every individual, paired with annual photogrammetry measurements of most of the population, we were able to make direct estimates of the relationship between individual salmon stocks and SRKW condition, and relate condition to survival probability. While small demographic fluctuations limit statistical power for identifying the influence of covariates such as prey abundance, aerial photogrammetry allows for more individuals to be sampled in each year and repeatedly sampled across years, increasing power to evaluate changes in body condition against possible drivers. In this case, we obtained more than ten times as many observations of body condition as observations of births and deaths in the seven years of data collection. While our time series of condition measurements was relatively short, we posit that with continued annual monitoring this method will provide sufficient statistical power for even finer scale investigations of prey availability and population status (e.g., at the individual stock level rather than tributary-level aggregates). Evaluating changes in body condition over time likely provides more insights into drivers of population health than simply comparing single measures of condition (e.g., annual population mean and variance) to potential

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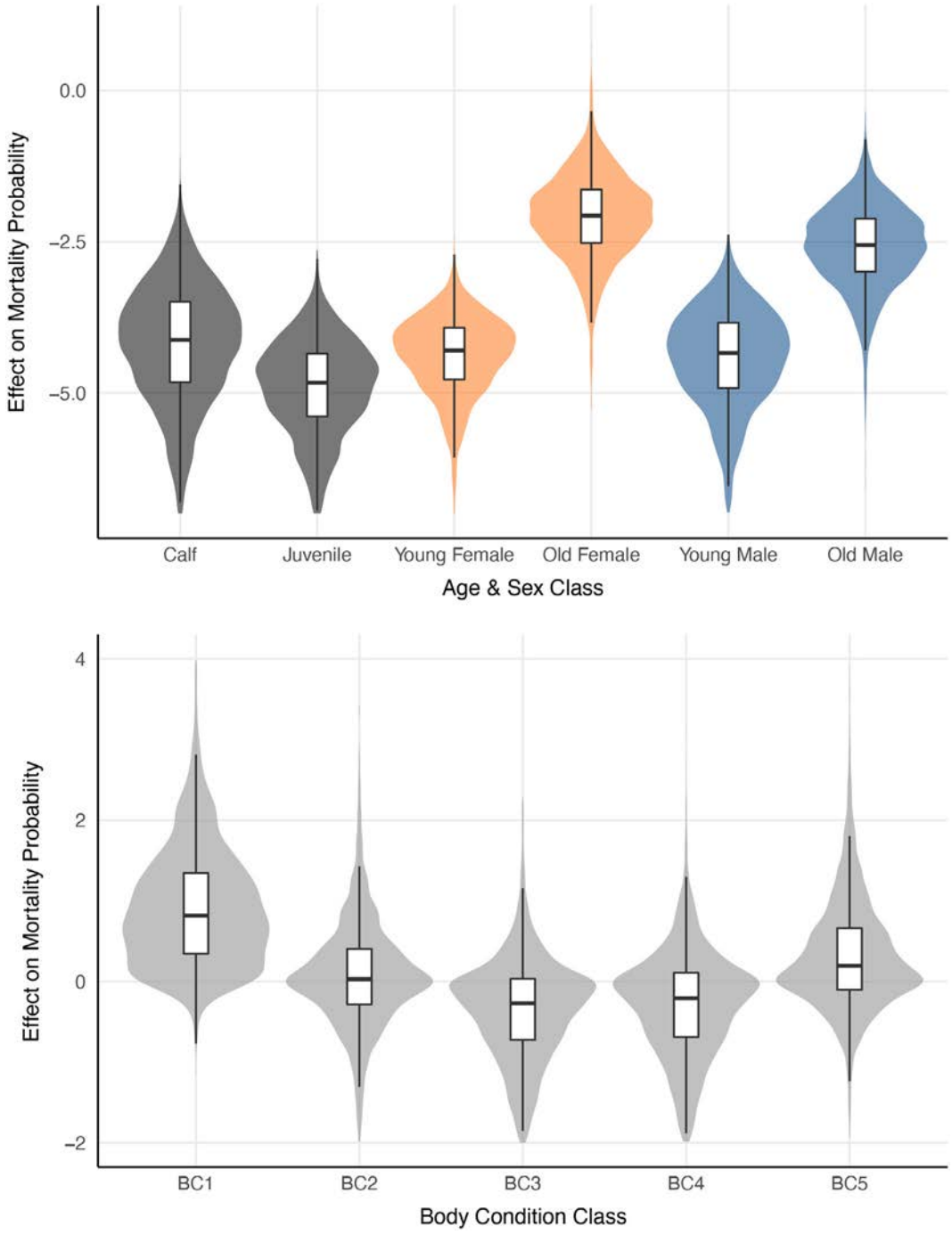


Fig. 3. Age/sex class- and condition-specific mortality probabilities for Southern Resident killer whales (all pods combined). Calf and Juvenile age classes include both sexes. Violin plots represent the posterior distributions of the baseline age- and sex-specific mortality probabilities (top) and the effects of body condition class on mortality probability (bottom). Inset boxplots represent the median (black horizontal bar), 50% HPDI (white box), and 95% HPDI (vertical black lines). Note that the effects are estimated (and represented here) in logit space before transformation to proportional space. See Table 2 for estimated mortality probabilities of each age/sex and body condition class combination.

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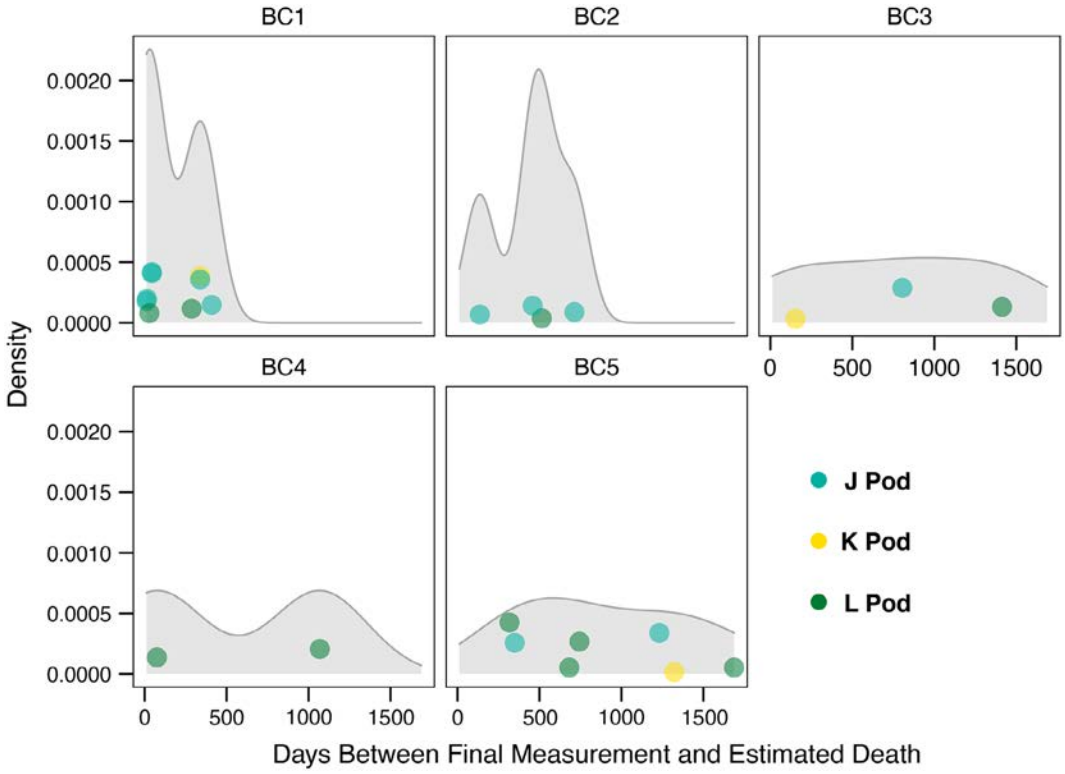


Fig. 4. Time between final condition measurement and estimated death for Southern Resident killer whales that died during the 2008–2019 study period. Each density plot represents the estimated number of days between when a whale was last measured and when it died, broken out by the condition class (BC1–5) that whales were last recorded as before death. Points represent the time between final measurement and death for individual whales, color coded by pod and jittered randomly on the *y*-axis.

covariates, given the ability of long-lived animals such as killer whales to live through bottlenecks in resource availability. In addition, there may be inherent differences in baseline condition between individuals, so evaluating individual changes between years rather than raw condition further accounts for individual variability.

Our cross-validation analyses suggest that, in the case of J and L pods, models including salmon covariates better predicted held-out years of body condition data than models without salmon covariates. Given that salmon managers use the FRAM model to generate pre-season estimates of Chinook abundance by stock, the modeling framework we present here could be used to generate predictions of fall SRKW body condition based on those salmon abundance estimates, quantify short-term risks to the population, and identify potential management interventions. Our model results suggest the strongest correlation between killer whale body condition and prey is between the SRKW J pod and Chinook salmon returning to the Fraser River. The Salish Sea area-based Chinook index was essentially tied for the best-fit J pod model, which is unsurprising considering the Salish Sea index is typically made up of 40–50% Fraser-origin Chinook. Over the last decade, when Fraser River Chinook abundance was above 750,000 (estimated FRAM Chinook model abundance on July 1st), J pod whales had a low chance (<14%) of declining body condition. Such a target could be used in a management setting to define thresholds supporting the stability and recovery of this population segment. For example, management actions focused on habitat restoration that ensures effective anadromous migration and productivity of Fraser River Chinook stocks could lead to gains

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in the nutritive condition of J pod whales. In the long-term, increasing urbanization of watersheds (Greene and Beechie 2004), increasing abundance of competing predators (Chasco et al. 2017), interspecific competition with other salmon stocks (Losee et al. 2019, Kendall et al. 2020), and climate change (Crozier et al. 2008) all present substantial threats to Fraser River Chinook abundance.

The only positive, ecologically plausible relationship we found for L pod body condition was with the Puget Sound tributary-specific abundance index. This is surprising, given that L pod is rarely in Puget Sound in the summer and spends less time in adjacent inland waters during the summer months than J or K pods (Riera et al. 2019), and Puget Sound origin Chinook are generally smaller and less numerically dominant than other stocks (O'Neill et al. 2014, Pacific Fishery Management Council 2020). However, L pod spends more time during the summer months in the western strait of Juan de Fuca than J or K pods (Riera et al. 2019) and may be targeting Puget Sound Chinook as they migrate from their open ocean phase toward spawning tributaries. The somewhat unique oceanic distribution of Puget Sound Chinook along the west coast of Vancouver Island (Weitkamp 2010, Shelton et al. 2019) may provide a reliable prey base in areas or times when more dominant stocks (Columbia and Fraser rivers) are less abundant. The relationship between L pod body condition transitions and Puget Sound Chinook abundance was weaker than the relationship between J pod and Fraser River Chinook. It is possible that L pod targets Chinook from a variety of stocks as they enter the strait of Juan de Fuca, which could obscure the signal of the Puget Sound Chinook's influence on L pod body condition. However, L pod body condition was negatively correlated with all other tributary-specific and area-based indices, including all Chinook salmon present in the Southwest Vancouver Island region, which presumably would be a better representation of Chinook availability at the mouth of the strait of Juan de Fuca. Previous analyses examining the influence of specific Chinook stocks on SRKW demographic rates found a significant relationship between SRKW fecundity and both Puget Sound and Fraser River Chinook abundance (Vélez-Espino et al. 2014, Wasser et al. 2017), which further indicates the potential importance of these stocks to the SRKW population.

We focused our modeling efforts on Chinook salmon given their majority representation in SRKW diets during the summer months prior to our September condition measurements, but we note that other salmon species such as Coho may also be important to SRKW condition at other times of the year (Hanson et al. 2010, Ford et al. 2016). As photogrammetry measurements become available over a longer time period and throughout the year, it may be possible to extend this approach to evaluate the importance of other prey species and stocks on SRKW condition, including seasonal fluctuations in condition between late summer and spring (Fearnbach et al. 2020). Pink salmon have also been proposed as a possible driver of a reported biennial pattern of births and mortality in the SRKW population (Ruggerone et al. 2019). While pink salmon are not a known prey species for SRKW, the authors hypothesized that high densities of pink salmon returning in odd years could interfere with the ability of SRKW to target lower density Chinook, potentially explaining reduced fecundity and increased mortality in even years. There is some evidence of declines in SRKW condition in odd years, particularly in L pod (Appendix S1: Fig. S6), which may lend support to the foraging interference hypothesis and should be further explored as more data become available.

The best-fit model for K pod had fixed body condition transition probabilities across time and included no salmon covariate. While the abundance of K pod is lower than J or L pods, the proportion of K pod with condition measurements each year was high (Table 2), and we therefore do not consider small sample size to be a likely explanation for the absence of covariates in the best-fit model. K pod may forage on a diverse assemblage of prey that is not easily captured in either tributary-specific or area-based indices of Chinook abundance. However, the second best-fit model for K pod included Puget Sound Chinook and suggested a positive relationship between Chinook abundance and the probability of increasing body condition. Additional studies of the fine scale distribution of Puget Sound Chinook along Vancouver Island and the Washington coast, and their representation in the diets of L and K pod whales during summer months

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Table 2. Number of Southern Resident killer whales measured using aerial photogrammetry in September of each study year, and the percentage of each pod imaged in parentheses.

Year	J pod	K pod	L pod
2008	23 (92.0)	18 (94.7)	19 (46.3)
2013	25 (96.2)	18 (94.7)	25 (67.6)
2015	27 (100)	19 (100)	26 (74.3)
2016	28 (96.6)	19 (100)	35 (100)
2017	22 (91.7)	9 (50.0)	30 (85.7)
2018	23 (100)	18 (100)	29 (85.3)
2019	22 (100)	17 (100)	21 (61.8)

could improve our understanding of the importance of this stock to SRKW population health. The major caveat to our findings is that body condition is known to fluctuate over a period of several months (Fearnbach et al. 2020). The three SRKW pods forage on other salmon stocks in winter and spring months (Hanson et al. 2010), but the September body condition metrics, and therefore the results of our analyses, most likely reflect the effects of the summer foraging period in the Salish Sea. Given the previously recorded increase in body condition from May to September and decline from September to May (Fearnbach et al. 2020), we posit that SRKW may have limited foraging opportunities over the winter and spring months, and that summer foraging in the Salish Sea may be the greatest driver of interannual body condition changes. However, SRKW may experience acute nutritional stress during winter and early spring when prey availability is restricted. Extending photogrammetry data collection throughout the year will help identify seasonal patterns in body condition fluctuations and may allow for comparative studies on the importance of winter/spring versus summer prey availability to SRKW health, survivorship, and reproductive success.

In addition to demonstrating the link between salmon abundance and body condition of killer whales, our model results show that whales in poor condition are more likely to die. Our estimated baseline mortality rates of whales in different age and sex classes are generally in line with previous findings (Ward et al. 2013), with old males and females experiencing the highest mortality probabilities, and calves experiencing slightly elevated mortality probabilities compared to juveniles and young whales. Our model estimated somewhat higher mortality probabilities for old females, and lower for old males, calves, and juveniles than previous analyses (Ward et al. 2013). These small differences are most likely due to the shorter time series of deaths included in our study (2008–2019 vs. 1979–2010) and the exclusion of whales that did not have body condition measurements, although we cannot rule out changes in mortality probability by age and sex class in recent years. Whales in condition class 1 had a mortality probability roughly 2–3 times higher than whales in condition classes 2–5. Interestingly, condition class 5 whales had a slightly elevated mortality probability similar to condition class 2 whales. The two whales that were observed in condition class 5 at the time step immediately prior to death died 317 (L53) and 349 (J14) days after being imaged and may have experienced a substantial, unrecorded decline in condition during that almost year-long period. Furthermore, while we did account for age and sex effects on mortality probability, there are other factors aside from age, sex, and nutritive condition that may contribute to mortality probabilities, such as the presence or condition of other whales in a matriline (Foster et al. 2012, Nattrass et al. 2019). The majority of whales that died shortly after being imaged were in condition class 1 (very poor condition), while deaths of higher condition class whales typically occurred longer after their last measurement (Fig. 4). During the study period, six whales in our photogrammetry dataset (J17, J28, J50, J52, J54, and L67) were also recorded from boat-based observations with a peanut head appearance, exhibiting severely depleted post-cranial fat stores (Fearnbach et al. 2018). All six of these whales were categorized as condition class 1 based on aerial photogrammetry measurements, and all of them died within one year of measurement (most within two months). This suggests agreement between these two indicators of terminal condition in killer whales. However, three additional condition class 1 whales died within a year after measurement and were not recorded as peanut heads (K25, J8, and L92). Aerial photogrammetry provides a quantitative—rather than subjective—and potentially more sensitive metric that can detect declines in condition and identify at-risk whales prior to the

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terminal peanut head phase that is detectable from boat-based observations.

Interestingly, changes in condition for animals from J and L pod were best explained by Chinook indices that are asynchronous (Fraser River and Puget Sound; Appendix S1: Fig. S4), while K pod condition was best explained by constant transition probabilities (or possibly Puget Sound Chinook, similar to L pod). Our findings suggest that the three pods behave differently in terms of body condition fluctuations, which may be driven by independent foraging strategies. Recent analyses of SRKW demographic data attempted to relate births and deaths to a wide range of Chinook salmon area-based indices (including several of the area-based indices used in this study), but found no significant relationships (Pacific Fishery Management Council 2020). Our results indicate that it may be advantageous for similar future analyses of demographic fluctuations to consider the three SRKW pods separately. Furthermore, given the differences in important prey indices reported here, it may be more effective for management strategies to treat the population of SRKWs as multiple management units, as the most effective management actions may be different for each pod based on our findings.

In addition to identifying target prey abundance levels to support SRKW recovery, aerial photogrammetry can provide an early-warning system that has the potential to serve as the basis for dynamic and adaptive management strategies. In an endangered population that had only 73 remaining individuals as of 2019, demographic casualties such as the death of a reproductive female or a year with no successful births can potentially have catastrophic consequences for population viability. Management actions that respond to these demographic casualties, as opposed to preventing them, may be insufficient to support population recovery. Our findings show that aerial photogrammetry can be used to identify at-risk individual whales, as well as to collect an overall metric of population health prior to mortality events that could be used to inform management actions. For example, if a large portion of the population is recorded in body condition class 1 during September (e.g., more than 20% of the population, or some threshold decided upon by managers), then fishery actions could be considered to increase prey availability for SRKW pods over the next year. Assessments of condition could be done in near-real time with a lag of <3 months, rapidly informing upcoming management strategies or allowing for interventions at the individual level. Short-term actions that may result in an increase in Fraser Chinook abundance and accessibility include spatiotemporal closures in areas of high Fraser Chinook encounter rates or mark-selective regulations, as a high proportion of the Fraser stock aggregate is unmarked; and regulations such as vessel noise caps and revised vessel traffic regulations to reduce underwater noise and improve SRKW foraging success (Joy et al. 2019). Longer term proactive strategies to increase Chinook abundance could include habitat restoration and increased hatchery production (Greene and Beechie 2004, Crozier et al. 2008).

In addition to influencing survivorship, body condition is likely also tied to fecundity in killer whales (Ward et al. 2009, Wasser et al. 2017). Future work should examine the relationship between reproductive success in the SRKW population and observed body condition, which would allow for a full evaluation of the influence of individual condition on overall population viability and support further modeling and projection efforts to weigh the efficacy of candidate management strategies. In addition, monitoring body condition in other seasons could provide insights into prey populations that may be important to the SRKW population in winter and spring months. As the time series of condition measurements grows, it may be possible to evaluate the relationship between SRKW condition and finer scale Chinook stock groupings and other prey species.

It may not be possible to apply the approach used in this study to larger, more widely ranging populations of marine mammals where repeated measurements of individuals and samples from a large portion of the population are not feasible. Instead, the average body condition of a random sample of the population may be achievable and, based on our findings, can likely serve as a proxy for short-term, relative population health. In addition, we posit that rapid changes in average body condition within a population can be used as an early-warning indicator of upcoming

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demographic fluctuations, given our findings that individuals in poor condition have higher mortality probabilities. The use of body condition as an indicator of population health shows promise for use in cetacean populations that have long-term photogrammetry datasets and experience substantial population fluctuations, such as eastern north Pacific gray whales (Perryman and Lynn 2002, Christiansen et al. 2020), which may help validate its use as a preceding signal of demographic impacts and support the development of adaptive management strategies.

Acknowledgments

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Data Availability

Data and code to run multi-state models can be found at: https://github.com/stewart6/SRKW-MultiState

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3660/full

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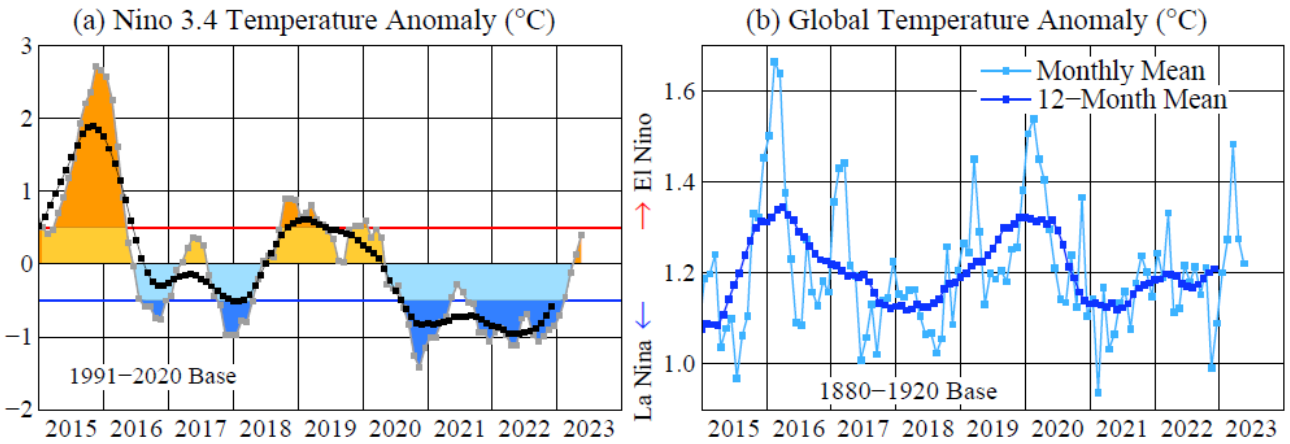


Fig. 1. (a) Nino3.4 and (b) global temperatures relative to indicated base periods.

El Nino and Global Warming Acceleration

14 June 2023

James Hansen, Makiko Sato and Reto Ruedy

The birthing El Nino will be a measuring stick. Is the rate of global warming accelerating? The little futz of an El Nino in 2019 (Fig. 1a) barely qualified[1] as an El Nino, yet it produced (dark blue curve in Fig. 1b) a global temperature matching that of the 2016 super El Nino. Jeremy Grantham noted that the 2016 El Nino produced greater warming than the prior super El Nino (in 1997); he was concerned that it indicated an acceleration of global warming.[2] We have argued[3] that the principal mechanism that may cause acceleration of global warming is a decrease of human-caused aerosols (particulate air pollution), which reflect sunlight and thus have a cooling effect that partially offsets warming by greenhouse gases (GHGs). That cooling has been termed a Faustian bargain,[4] and we have suggested that a significant payment in accelerated global warming is now coming due.[3,5]

Short-term global temperature change is correlated (59%) with the Nino3.4 temperature index[6] (Fig. 2). The Pinatubo volcanic eruption in 1991, and to a lesser extent solar irradiance variation, reduce the correlation. The greatest anomaly in global warming occurs since 2015 (Fig. 2), which we attribute to reduced aerosol cooling, including the effect of increasingly strict limits on the sulfur content of ship fuel imposed by the International Maritime Organization in 2015 and 2020.[3]

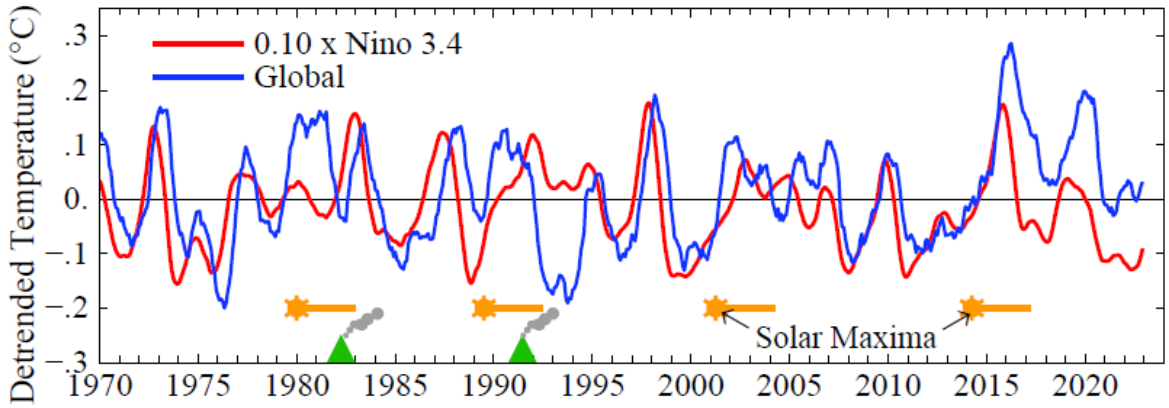


Fig. 2. Detrended global and Nino3.4 12-month running-mean temperatures; the trend subtracted from the temperature records is based on the period 1970-2010.

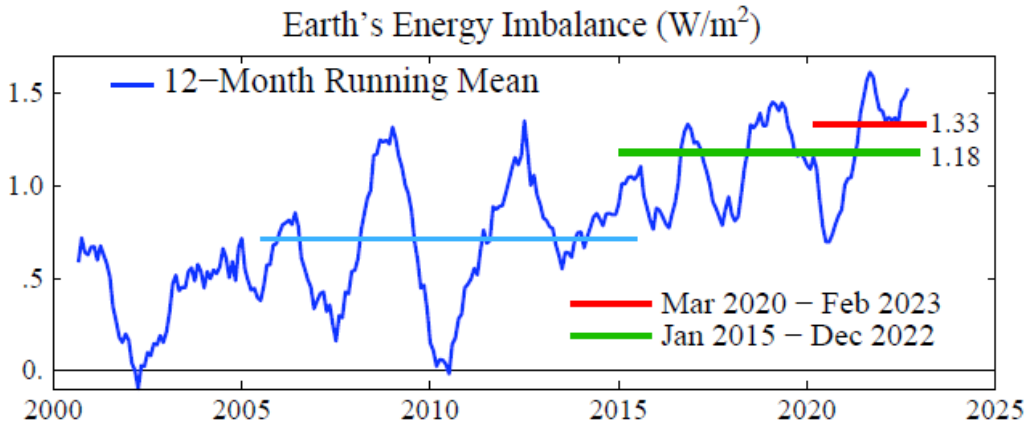


Fig. 3. 12-month running-mean of Earth's energy imbalance, based on CERES satellite data[7] for EEI change normalized to 0.71 W/m² mean for July 2005 – June 2015 from in situ data.

Consistent with this interpretation, there has been a staggering increase in Earth's energy imbalance (Fig. 3). The light blue bar in Fig. 3, the 10 years from July 2005 through June 2015, is the period used for calibration of the satellite-measured[7] Earth's energy imbalance (EEI), the calibration being provided by changes of the heat content of Earth's heat reservoirs.[8] About 90% of the change of EEI is change of the heat content of the ocean, which is sampled by a fleet of about 4000 deep-diving Argo floats. Earth's energy imbalance was 0.71 W/m² during the 10-year calibration period, but EEI has subsequently increased to well over 1 W/m² (Fig. 3). EEI provides the direct driving force for global warming and all of the consequences thereof.[3] It is this increased EEI that leads us to project a 50-100% increase in the rate of global warming during the few decades following 2010. If our projection is correct, we expect observed global temperature to rise into the yellow region in Fig. 4 in 2023 and above the yellow region in 2024. This is a projection that we hope is wrong, but the main factors that might cause it to be wrong are not very comforting: the El Nino strength affects short time scales and aerosol trends affect long time scales.

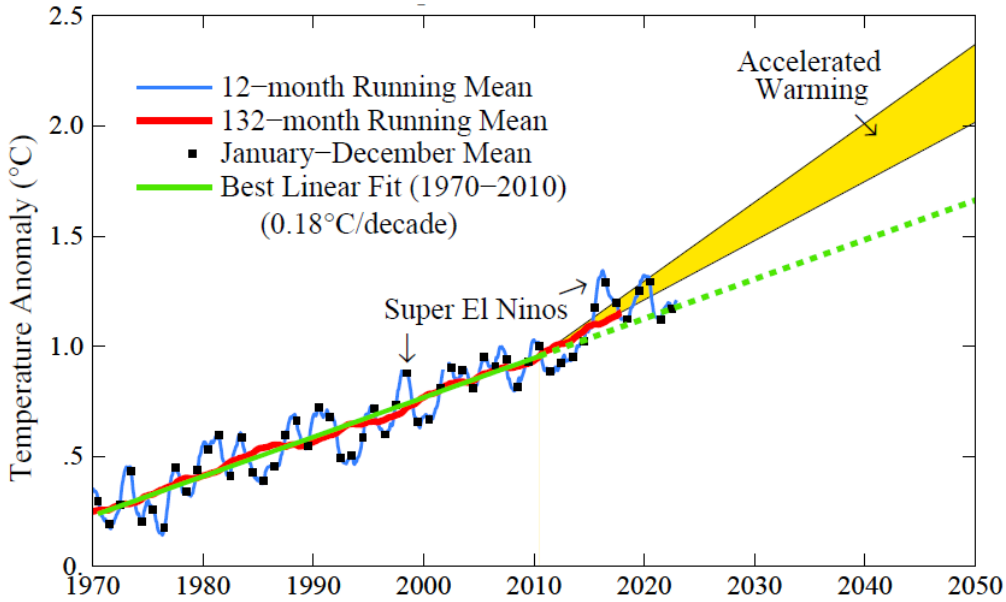


Fig. 4. Global surface temperature relative to 1880-1920 average. The 12-month running-mean extends through May 2023.

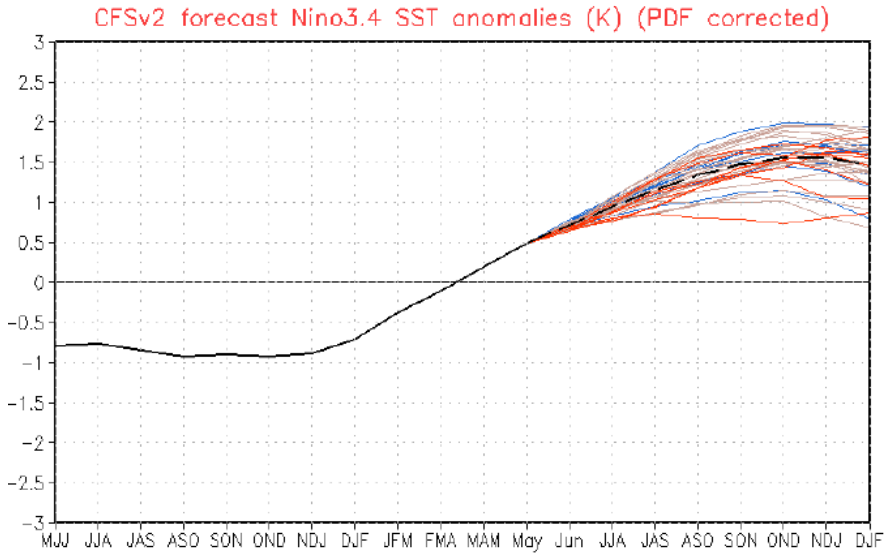


Fig. 5. NCEP forecasts[9] of Nino3.4 in June 2023. El Nino is indicated by a value > +0.5°C.

The current NCEP forecast (Fig. 5) has a Nino3.4 peak at only about 1.5°C, which would not be a super El Nino, but some other models predict a strong El Nino, comparable to those in 1997 and 2016, which are described as super El Ninos. The expectation that aerosols will decline moderately during the next few decades is based on the assumption that the world will trend toward clean energy sources that emit fewer aerosols than fossil fuels. Aerosol sources are complex, however, and include fires that may increase with global warming. It is unfortunate that we are not monitoring the global aerosol climate forcing; that is difficult because it requires precise global measurements of aerosol and cloud microphysics; we knew how to do that in 1990,[10] but chose not to initiate such a monitoring system.

Finally, we note that these topics are discussed in plain language in a prior communication.[11] The distinction between equilibrium warming (which is approximately 10°C for present atmospheric composition) and committed warming (which is a more complex matter that depends on ocean and ice sheet response times and on the rate of future greenhouse gas emissions) is discussed in that communication, where we also explain that we prefer to work on advancing the science, rather than engage in Twitter wars about the difference between equilibrium warming and committed warming. The difference between equilibrium and committed warmings is also discussed in a recent communication.[12]

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[1] NOAA requires NINO3.4 to exceed 0.5°C for 5 consecutive overlapping 3-month periods to qualify as an El Nino.
[2] Global warming acceleration plus miscellaneous, 15 October 2018 communication.
[3] Draft paper submitted to Oxford Open Climate Change. The paper is undergoing revisions. Comments and criticisms are solicited, but we do not intend to release subsequent versions of the paper until it is published.
[4] Hansen, J., 2009: *Storms of My Grandchildren*, Bloomsbury, New York, 320 pages.
[5] Global temperature in 2022, 12 January 2023 communication.
[6] Temperature anomaly in an equatorial Pacific region relative to the mean for 1990-2020.
[7] Loeb, N. G., Johnson, G. C., Thorsen, T. J., Lyman, J. M., Rose, F. G., & Kato, S., Satellite and ocean data reveal marked increase in Earth's heating rate, *Geophys. Res. Lett.* **48**, e2021GL093047, 2021.
[8] von Schuckmann K, Cheng L, Palmer MD *et al.* Heat stored in the Earth system: where does the energy go?, *Earth System Science Data* 2020;**12**:2013-41

[9] NOAA National Center for Environmental Prediction forecasts are available and updated weekly. A new ensemble of climate model runs is made each week. Chart 24 in their Weekly ENSO Evolution, Status and Prediction shows the average of other global atmosphere-ocean models as "DYN AVG."
[10] Hansen, J., W. Rossow and I. Fung, Long-Term Monitoring of Global Climate Forcings and Feedbacks, NASA CP-3234, 91 pages, 1993
[11] Hansen, J., M. Sato, N. Loeb, L. Simons and K. von Schuckmann, Earth's energy imbalance and climate response time, 22 December 2022
[12] Equilibrium warming = committed warming? 25 May 2023 communication.

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ORIGINAL ARTICLE

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"Two-Eyed Seeing": An Indigenous framework to transform fisheries research and management

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Abstract

Increasingly, fisheries researchers and managers seek or are compelled to "bridge" Indigenous knowledge systems with Western scientific approaches to understanding and governing fisheries. Here, we move beyond the all-too-common narrative about integrating or incorporating (too often used as euphemisms for assimilating) other knowledge systems into Western science, instead of building an ethic of knowledge coexistence and complementarity in knowledge generation using Two-Eyed Seeing as a guiding framework. Two-Eyed Seeing (*Etuaptmumk* in Mi'kmaw) embraces "learning to see from one eye with the strengths of Indigenous knowledges and ways of knowing, and from the other eye with the strengths of mainstream knowledges and ways of knowing, and to use both these eyes together, for the benefit of all," as envisaged by Elder Dr. Albert Marshall. In this paper, we examine the notion of knowledge dichotomies and imperatives for knowledge coexistence and draw parallels between Two-Eyed Seeing and other analogous Indigenous frameworks from around the world. It is set apart from other Indigenous frameworks in its explicit action imperative—central to Two-Eyed Seeing is the notion that knowledge transforms the holder and that the holder bears a responsibility to act on that knowledge. We explore its operationalization through three Canadian aquatic and fisheries case-studies that co-develop questions, document and mobilize knowledge, and co-produce insights and decisions. We argue that Two-Eyed Seeing provides a pathway to a plural coexistence, where time-tested Indigenous knowledge systems can be paired with, not subsumed by, Western scientific insights for an equitable and sustainable future.

KEYWORDS

co-production, *Etuaptmumk*, indigenous knowledge, knowledge coexistence, pluralism, Western science

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1 | INTRODUCTION

1.1 | Positionality statement

It is with *t'ooyaks* (Nisga'a for 'thanks') to senior author and Mi'kmaw Elder Dr. Albert Marshall that we (the author team) have come to learn and embrace the concept of *Etuaptmumk* (Mi'kmaw for 'Two-Eyed Seeing') and it is through his guidance that we have envisioned a new path for fisheries research and management. The knowledge Albert has imparted through his work over the decades, he is adamant, is not his own to claim, for he is but a conduit for the knowledge of generations. It is thus to those generations of Mi'kmaq Knowledge Keepers, past, present, and future, Albert included, that we express *t'ooyaks*. Andrea Reid is a Nisga'a fisheries scientist who led this effort from Algonquin Anishinaabeg traditional territory. Andrea carries a responsibility to hold place for Indigenous voices in the academe, especially within the natural sciences, where often no space is held, and she is supported and upheld in this work by settler scholar colleagues, allies, and mentors Lauren Eckert, John-Francis Lane, Dr. Nathan Young, Dr. Scott Hinch, Dr. Chris Darimont, Dr. Steven Cooke, and Dr. Natalie Ban. Together, the author team welcomes the reader to this space created expressly for Indigenous and mainstream fisheries knowledges and ways of knowing to come together, to coexist for the benefit of all – fish, people, and place – today and in the future.

1.2 | Background and purpose

All research, scientific or otherwise, is shaped by philosophical foundations and assumptions. Research paradigms or worldviews are defined and distinguished according to their ontologies (the nature of reality), epistemologies (the theory of knowledge and its validity), axiologies (the nature of values) and methodologies (the purpose and process of research; Godfrey-Smith, 2009; Wilson, 2008). Collectively, these core philosophical underpinnings reflect researchers' perspectives or views of reality, determine what they count as knowledge and accept as ways of knowing, and guide their priorities, choices and actions in research (Held, 2019). It follows that multiple research paradigms exist as there is a plurality of ways in which the world around us is read or interpreted (Guba & Lincoln, 1994). However, it is their long-term coexistence that comes into question as colonial forces and linked power imbalances promote certain knowledge types and ways of generating knowledge (e.g. Western science) over others (e.g. Indigenous; Cajete, 2000).

The science and management of conventional fisheries is based on a Western or Eurocentric paradigm. It was originally developed in the service of single-stock, large-scale and commodity-oriented fisheries in North temperate parts of the world (this is evident in early texts such as Beverton & Holt, 1957; King, 1995; Lackey & Nielsen, 1980; Royce, 1975). In stark contrast to most small-scale, subsistence-oriented fisheries worldwide, the former relies on a positivistic epistemology (i.e. that there is one "knowable" truth; Berkes, 2003; Denny & Fanning, 2016) and adheres to an "illusion of certainty" in which nature is predictable and controllable (Charles, 2001). The dominant worldview has been both hierarchical and paternalistic (Davis & Jentoft, 2001), ascribing to "command and control" resource management (Holling & Meffe, 1996). The net result is a global system that is largely failing both ecologically and socially (Brashares et al., 2014; Loring, 2013; Pauly et al., 2002), although some managed stocks are rebuilding (Hilborn et al., 2020; Hilborn & Ovando, 2014; Krueger et al., 2019). There have been clarion calls for "reinventing fisheries management" (Pitcher et al., 1998; Stephenson & Lane, 1995) and a push for fisheries science to adopt an ecosystem-based approach (Holling, 2001; Jackson et al., 2001). However, these have yet to surmount the substantial inertia of current practices and prevailing paradigms (Caddy & Cochrane, 2001; Tudela & Short, 2005).

Fisheries are tightly coupled and highly complex social–ecological systems—complicating both their management and their study (van Poorten et al., 2011). In a fishery, "resource units" (e.g. fish), "users" (e.g. large- and small-scale fishers) and "governance structures" (e.g. rules, governing bodies) exist and are separable, but all interact to produce outcomes on a system level (Ostrom, 2009). They are considered "complex" in that they involve two-way feedbacks and are characterized by nonlinearity, uncertainty, multiple scales, self-organization and adaptation (Berkes, 2003). Given these features, there is no single comprehensive or "correct" perspective in a complex fisheries system, but it is instead perhaps best understood through a plurality of ways (Olsson et al., 2004). Particularly at this time of stagnating or declining fisheries catches (Watson et al., 2013), intensifying fishing effort and poor management (Pitcher & Cheung, 2013), and having a lack of complete data for many of the world's fisheries (Costello et al., 2012), there is an

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urgency to improving this understanding and our actions towards complex fisheries problems, as well as significant potential costs (i.e. ecological, economic, socio-political, e.g. Pomeroy et al., 2007) in not doing so.

Not only would it behove fisheries scientists to use all and the best tools and knowledge available at this time of crisis, irrespective of their origin and the perceived objectivity and superiority of Western scientific approaches (TallBear, 2014), but this would importantly serve decolonial and reconciliatory efforts that help rectify uneven power relations, knowledge inequalities, and other racially linked and unjust dynamics in fisheries (Held, 2019; Latulippe, 2015).

Addressing this complexity and confronting existing problems, *Etuaptmumk* (Mi'kmaw for "Two-Eyed Seeing") provides a conceptual framework for equitably embracing multiple perspectives within a system. Mi'kmaw Elder Albert Marshall defines Two-Eyed Seeing as "learning to see from one eye with the strengths of Indigenous knowledges and ways of knowing, and from the other eye with the strengths of mainstream knowledges and ways of knowing, and to use both these eyes together, for the benefit of all" (Bartlett et al., 2012). Two-Eyed Seeing has been used to promote the coexistence of disparate paradigms across a variety of fields—for instance, in education (Hatcher et al., 2009; McKeon, 2012), medicine (Hall et al., 2015; Martin, 2012) and wildlife health (Kutz & Tomaselli, 2019)—and while a growing number of studies point to its promise for fisheries research and management (e.g. Abu et al., 2019; Giles et al., 2016; Mantyka-Pringle et al., 2017), there has yet to be equivalent comprehensive consideration of Two-Eyed Seeing applications in this domain.

Here, we move beyond the all-too-common dialogue of integrating, combining or incorporating (commonly used as euphemisms for assimilating) other knowledges and ways of knowing *into* Western science, and instead build an ethic of knowledge coexistence and complementarity in knowledge generation using Two-Eyed Seeing as a guiding framework. We first examine the notion of knowledge dichotomies and imperatives for knowledge coexistence (Section 2) and then draw parallels between Two-Eyed Seeing and other analogous Indigenous frameworks (Section 3). Next, we examine aquatic and fisheries case-studies that embrace Two-Eyed Seeing as they co-develop questions, document and mobilize knowledge, and co-produce insights and decisions (Section 4). Lastly, guided by these works, we detail ontological, epistemological, axiological and methodological changes required to transform fisheries research and management for an equitable and sustainable future (Section 5).

2 | BEYOND DICHOTOMOUS DISCOURSE

Defining Indigenous knowledge is shifting away from a focus of "utility" (what it can do for Western science) and reductionism (how it provides "data" to Western scientific analyses). However, delineating what Indigenous knowledge is and how it operates has remained largely the purview of external organizations, governments, institutions and researchers rather than by Indigenous peoples them/ourselves (Battiste & Henderson, 2000; Eckert et al., 2020; McGregor, 2004a). The associated terminology has been evolving—away from "tradition" or "folk" terms (e.g. traditional ecological knowledge or TEK) that once dominated the conservation literature (Gómez-Baggethun et al., 2013)—towards language that connotes the contemporary and diverse realities of these knowledge systems (Battiste, 2005). Indigenous knowledge (our term of choice—but see Cruikshank (1998) for an alternate view) is now widely accepted as "a cumulative body of knowledge, practice and belief evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment" (Berkes, 2018). A critical addition to this definition is that this "situated knowledge" is neither separable from the knowledge holders or keepers, nor is it divisible from the environment in which it is embedded (McGregor, 2004; see glossary: Table 1). We define this term here for the purpose of the present dialogue while also recognizing problematic aspects of doing so given that Indigenous knowledge is not uniform across all Indigenous peoples (hence, why this term is often referred to in the plural form: Indigenous knowledges), and for many, it is not a definable object, but instead a way of being and living in the world (Battiste & Henderson, 2000).

Society under colonial influence has long perceived Indigenous knowledge as "the other" and in binary opposition to Western scientific knowledge (Battiste, 2005). Where the latter is thought to be quantitative, factual, analytical, reductionist and literate, the former is assumed qualitative, anecdotal, intuitive, holistic and oral (Berkes, 2018; Mistry & Berardi, 2016; Nadasdy, 1999). According to Castleden et al. (2017), who argue that "we need to challenge the dichotomy discourse," this dualistic and simplified view leads directly to notions of knowledge inequality and an othering process that favours continued division over coexistence. There are certainly distinctions in attributes that lead to both having individual strengths in specific contexts, but there is no righteous hierarchy of knowledge systems where one is systematically better or consistently outperforms another (Berkes, 2018). Both centre on improving our understanding of the world around us (Cajete, 2000)—an end that surely becomes more achievable through a plural coexistence (Howitt & Suchet-Pearson, 2006; see glossary: Table 1) where time-tested Indigenous knowledge systems can be paired with revelatory Western scientific insights (Benessia et al., 2012; Mistry & Berardi, 2016; Pierotti & Wildcat, 2000).

The prevailing solution to confronting this plurality has been "knowledge integration" (Nadasdy, 1999), a process fraught with risks and limitations. The process aims to bridge multiple knowledges, bringing new information into an existing body of knowledge (generally that which wields greater power; Hart, 2010), and to identify key similarities and differences so the latter can be minimized and knowledge consolidation simplified (Bohensky & Maru, 2011). But, as noted above, Indigenous knowledges and ways of knowing are far more than simply "information" to be subsumed into the mainstream of Western science (Agrawal, 1995)—which in essence serves only to strengthen Western science for its own ends and "to concentrate power in administrative centers, rather than in [Indigenous] communities" (Nadasdy, 1999). For these reasons, some scholars have abandoned potentially problematic

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TABLE 1 Glossary of key terminology

English term (abbreviation)	Indigenous term (language; area)	Definition (source)
Double-Canoe	*Waka-Taurua* (Māori; Aotearoa/New Zealand)	A conceptual framework formalized in 2018 for unifying knowledges and ways of knowing, especially Western and Māori. It is described as "two canoes… lashed together… each canoe represents the worldview and values of the people who are coming together to achieve a common purpose… each group is inherently different, and the knowledge, values and actions of each, are not made to fit into the other" (from Maxwell et al., 2019).
Indigenous Knowledge (IK) *or* Traditional Ecological Knowledge (TEK)	[a]	A cumulative body of knowledge, practice and belief evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment (from Berkes, 2018). It is not separable from the knowledge holders/keepers or the environment in which it is embedded (McGregor, 2004a).
Māori Guardianship	*Kaitiakitanga* (Māori; Aotearoa / New Zealand)	"Reciprocal care between Indigenous-Māori people and their territorial environment"—"Kaitiaki" means guardian, and "tanga" is a common suffix akin to "ship" (as in "kinship" or "relationship"; from Maxwell et al., 2019; Roberts et al., 1995).
Mi'kmaq Sustainability	*Netukulimk* (Mi'kmaw; Eastern Canada)	"Achieving adequate standards of community nutrition and well-being today without jeopardizing the integrity, diversity, or productivity of the environment for the future"—for seven generations to come (from McMillan & Prosper, 2016; Prosper et al., 2011).
Plural Coexistence	[a]	"A model of cross-cultural relations that acknowledges and respects Indigenous ontologies, or ways of being, and at the same time is attentive to the historical and current dominance of Eurocentric thinking within natural resource management" (from Howitt & Suchet-Pearson, 2006; Zanotti & Palomino-Schalscha, 2016).
Two-Eyed Seeing	*Etuaptmumk* (Mi'kmaw; Eastern Canada)	The gift of multiple perspectives; a conceptual framework coined by Mi'kmaw Elder Albert Marshall in 2004 for unifying knowledge systems. It is described as "learning to see from one eye with the strengths of Indigenous knowledges and ways of knowing, and from the other eye with the strengths of Western knowledges and ways of knowing, and to use both these eyes together, for the benefit of all" (from Bartlett et al., 2012).
Two Row Wampum	*Kaswentha* (Haudenosaunee; Central Canada)	A 17th-century treaty belt to record an agreement between the Haudenosaunee Confederacy and Dutch settlers. "It consists of two rows of purple beads separated by rows of white beads. The purple rows represent the different vessels of the Dutch (a ship) and the Haudenosaunee (a canoe) travelling side-by-side down the "river" of existence (the white beads). While the two vessels remain separate (i.e. the cultures remain distinct), the people from each vessel are meant to interact and assist each other as need be." (from McGregor, 2004b).
Two Ways	*Ganma* (Yolngu; Northern Territory, Australia)	A metaphorical concept of how to mix knowledges equitably and achieve meaningful two-way collaborations. "It relates to the separateness of fresh water and salt water knowledge even at the point where they meet and mix. It is like what some [non-Indigenous people] call a "dialectical" relationship, in which two opposed patterns of ideas complement, interact and relate to one another, but never lose their distinctiveness as separate and opposed parts of one whole." (from Muller, 2012)

[a]Terms for these concepts are found across many Indigenous languages worldwide and vary by language/language group.

terms such as integration or bridging, while others advocate that we can update their meaning and usage as Berkes (2003) has done with respect to "resource" and "management." Both options are viable ones so long as there is concomitant recognition that language choices reflect biases, and can even perpetuate colonial inequalities, so users of these terms (or their alternatives) must be explicit and transparent about their intentions with their usage. Here, we use terms such as "pairing," or better yet "adopting a Two-Eyed Seeing approach," to speak to circumstances where Indigenous and Western scientific knowledge systems contribute in parallel to produce an enriched picture and mutual understanding—while recognizing that ultimately it is the actions taken that matter most, rather that the words used to describe them.

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TABLE 2 Legal and practical imperatives for involving Indigenous knowledge systems in mainstream research across various scales—on the levels of institutions, Indigenous nations, nation states and internationally

Imperative	Scale	Source	Policy / Call to Action[a]
Legal: specific instruments stipulating respect for and/or inclusion of Indigenous knowledge in research, teaching and more generally	Global (148 UN member states)	United Nations Declaration on the Rights of Indigenous Peoples (UNDRIP; UN General Assembly, 2007)	• Respect that Indigenous knowledge contributes to sustainable and equitable development, and proper environmental management [Guiding Principle] • Indigenous peoples have the right to maintain, control, protect and develop their knowledge, sciences and intellectual property over such [Article 31]
	National (Canada)	Truth and Reconciliation Commission (TRC; Government of Canada, 2015)	• Provide necessary funding to post-secondary institutions and Aboriginal schools to bring Indigenous knowledge and teaching methods into classrooms [Actions 62.2 and 62.3]
	Indigenous Nation (Heiltsuk Nation)	Heiltsuk Integrated Resource Management Department (Heiltsuk Nation, 2015)	• All research questions and activities in Heiltsuk territory will be framed to involve Heiltsuk knowledge [Guiding Principle] • All research will acknowledge Heiltsuk as an integral part of ecosystems [Guiding Principle]
Practical: requirements for obtaining approvals and/or funding to develop Indigenous-related research projects	Global (192 UN member states)	Intellectual Property and Genetic Resources, Traditional Knowledge and Folklore (WIPO, 2010)	• Recognize value of Indigenous knowledge (social, economic, intellectual, scientific, ecological, commercial, educational); of equal scientific value as other knowledge systems [Policy Objective 1] • Respect contribution of Indigenous knowledge to conservation, food security, sustainable agriculture, progress of science and technology [Policy Objective 2]
	National (Australia)	Guidelines for Ethical Research in Australian Indigenous Studies (AIATSIS, 2012)	• The rights (as laid out in UNDRIP *Article 31* above) of Indigenous peoples must be upheld and recognized [Principle 2] • Researchers must have a good understanding of the nature of Indigenous knowledge systems and intellectual property [Principle 4]
	Institutional (Canadian universities)	Ethical Conduct for Research Involving Humans (CIHR, NSERC, & SSHRC, 2018)	• Engagement with Indigenous communities is an integral part of ethical research involving Indigenous peoples [Premise] • Researchers should appropriately engage Indigenous communities to involve knowledge holders and systems in research [Article 9.15]

[a]Policy articles and calls to action were paraphrased for brevity; meanings or implications remain unchanged.

Pressure is mounting across spheres (i.e. legal, practical; see Table 2) and scales (institutional to global) to pair Indigenous knowledge systems together with Western scientific practices (Ogar et al., 2020). Regardless of terminological preferences, what we sorely need are approaches that: remedy, rather than reinforce, existing power relations; respect differences, instead of suppress them; and uphold, as opposed to diminish, their unique strengths (Muller, 2012). These latter elements comprise yet another imperative, a moral one (Paton, 1971), to conduct research in a way that promotes social justice and self-determination (Artelle et al., 2019; Held, 2019; Ludwig, 2016). In sum, a plural coexistence holds multiple possibilities within it: (a) improving our understanding of complex systems, with insights and information from multiple knowledges contributing to an enriched picture; (b) conforming to legal norms and practical requirements, without which many research programmes simply would not be advanced by today's funding bodies and research ethics boards; and (c) answering to undeniable moral queries about what is "right" in terms of human rights and equality.

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3 | MODELS OF KNOWLEDGE COEXISTENCE

While as diverse as the ecosystems to which they are inextricably linked, Indigenous worldviews globally share a number of philosophical and spiritual underpinnings (Simpson, 2000). The knowledge held may be highly distinct across groups, but the process through which knowledge is generated predominantly ascribes to a paradigm that is cyclic, interconnected and fundamentally relational (McGregor, 2004a)—where knowledge itself depends on relationships and connections between living beings (including humans) and non-living entities (as above; Wilson, 2008). They tend to embrace both "communitism" (the search for and commitment to Indigenous community and values; Weaver, 1997) and respectful individualism and cultural sovereignty (where individual and cultural differences are upheld and maintained rather than homogenized; Gross, 2003). Indigenous worldviews thus have potentially profound implications for how knowledges can come to be complementary and coexist, rather than compete or be subject to assimilation.

In their formative writing on multiple evidence base (MEB) approaches, Tengö et al. (2014) identify a need for new tools and approaches for co-developing questions, documenting and mobilizing knowledge, and co-producing insights and decisions—all under the guiding principle of valuing diversity in knowledge systems. In their view, "a MEB approach emphasizes the complementarity of knowledge systems and the values of letting each knowledge system speak for itself, within its own context, without assigning one dominant knowledge system with the role of external validator" (Tengö et al., 2014). A key point emerges: each way of knowing should not be assessed by external referents, but rather by internal criteria (Klenk & Meehan, 2015). MEB approaches seek to connect distinct knowledge systems (Alexander et al., 2019), often through parallel lines of Indigenous and Western scientific inquiry (Tengö et al., 2014), but mechanisms and successful examples of this or equivalent approaches in practice, especially in an aquatic or fisheries context, have been few and far between (e.g. Cooke et al., 2020; Laidler, 2006; Mackinson, 2001).

A number of long-standing and/or contemporary Indigenous frameworks, although scarcely represented in the academic literature (and where they are, it is largely at the hand of Indigenous scholars and/or in Indigenous-focused journals), may answer directly to this need. They offer means to conceptualize and operationalize the cross-fertilization and coming together of distinct knowledge systems—epistemic pluralism (Carter, 2017) through an Indigenous lens. Conceptual frameworks are reflective of the knowledge one privileges (Kovach, 2010), and their visualization can guide important research choices (Latulippe, 2015). The subsequent four highly visual and conceptual frameworks (Figure 1; glossary: Table 1) exemplify that highly comparable approaches can arise across distinct and distant Indigenous cultures and suggest that these are likely but a small selection of a much larger number of Indigenous conceptualizations for promoting knowledge coexistence. The following descriptions provide references to key sources—many of which are written by members of the cultures from which they stem (and to which the author team does not belong, with the exception of Elder Dr. Albert Marshall of the Mi'kmaq Nation discussed in Subsection 4).

1. The *Kaswentha* (Haudenosaunee for "Two Row Wampum"; Figure 1a) is a 17th century treaty belt to record an agreement between the Haudenosaunee Confederacy and Dutch settlers in eastern New York (Ransom & Ettenger, 2001). It contains two rows of purple beads that each represents the different vessels of the Dutch (ships) and the Haudenosaunee (canoes). They are surrounded by white beads that symbolize the shared "river" of existence (McGregor, 2002). These distinct vessels

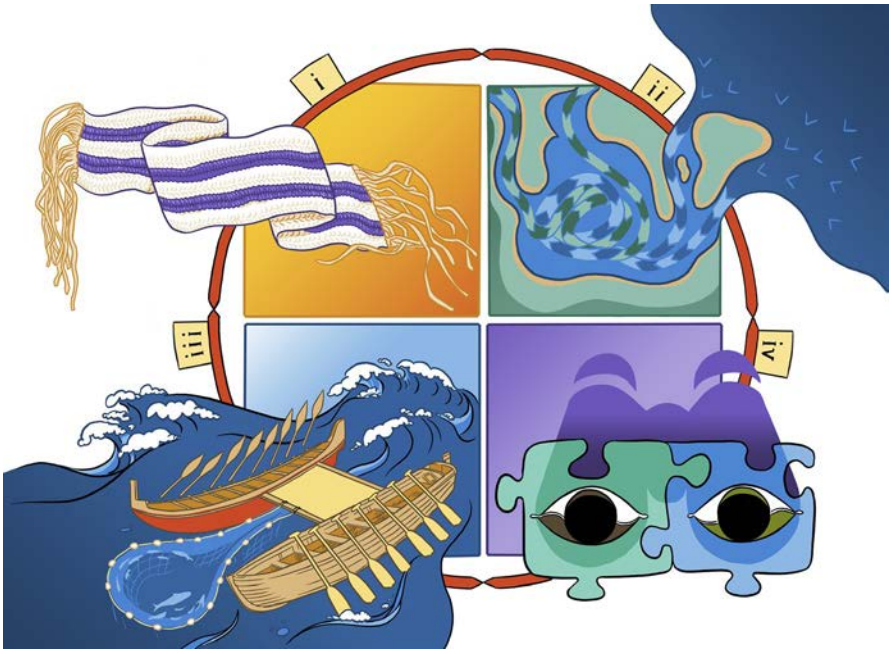


FIGURE 1 Indigenous conceptual frameworks for promoting knowledge coexistence: (i) the "Two Row Wampum" or Kaswentha in Haudenosaunee; (ii) the "Two Ways" or Ganma in Yolngu; (iii) the "Double-Canoe" or Waka-Taurua in Māori; and (iv) "Two-Eyed Seeing" or *Etuaptmumk* in Mi'kmaw. Refer to main text (section 3) for full descriptions of each framework (Subsections 1–4, respectively). Artwork by Nicole Burton [Colour figure can be viewed at wileyonlinelibrary.com]

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remain separate, each containing their own laws, traditions and rights and neither disrupting the integrity or process of the other, though they travel together and work in partnership on common problems (Rathwell et al., 2015). Though a historical model of coexistence, it remains salient today where it is being applied to environmental protection and restoration programmes (Ransom & Ettenger, 2001), water quality monitoring projects (McGregor, 2002) and resource co-management initiatives (Stevenson, 2006).

2. On the north-eastern coast of Arnhemland, Australia, the Yolngu people have a long-standing framework that centres around *Ganma* (a particular confluence of sea water and fresh water; Christie, 2007). The two waters represent distinct knowledge systems that come together, interact, but maintain their separateness akin to isohalines in a lagoon or estuary (Muller, 2012; Figure 1b). Rather than compromising one another and becoming a homogenous whole, this "Two Ways" or "Both Ways" metaphor centres around the creation of a new space where two understandings and knowledges can come together equitably and work in parallel—ultimately creating greater shared understanding (Bat et al., 2014). It is used as a mechanism to this day to ensure that Yolngu are represented equally in the thinking and planning of both land and sea management (Dhimurru Aboriginal Corporation, 2013; Marika, 1999).
3. In *Aotearoa*/New Zealand, the *Waka-Taurua* (Māori for "Double-Canoe") is a contemporary metaphorical framework where two canoes (each representing distinct knowledge systems) are lashed together temporarily for a common purpose (e.g. operating a large seine; Maxwell et al., 2019; Figure 1c). It recognizes inherent differences on both sides and is based on the assertion that respective knowledges, values and actions are not made to fit into each other. As above, there is "negotiated space" (in this case, between canoes) where knowledge systems can interface and innovate (Mila-Schaaf & Hudson, 2009; Smith, 2012). It is embedded within *Kaitiakitanga* (a Māori concept for reciprocal care between people and place; Roberts et al., 1995) and has been applied to uphold Māori and Western scientific knowledges within marine co-management and co-governance (Maxwell et al., 2019).
4. *Etuaptmumk* or Two-Eyed Seeing, as previously introduced, draws together the strengths of mainstream and Indigenous (specifically Mi'kmaw) knowledges (Bartlett et al., 2012; Figure 1d). This binocular framework leads to a "wider, deeper, and more generative field of view" than could be achieved by either perspective or knowledge system in isolation (Iwama et al., 2009). It shares with the above frameworks the notion of working collaboratively across knowledge systems on a common problem (Berkes, 2018), and as with the Double-Canoe, it centres on a cultural conservation concept that of *Netukulimk* where ecological integrity is maintained for the next seven generations (Prosper et al., 2011). It too creates space for common ground and respects differences by reducing us/them dichotomies and breaking down the compartmentalization of knowledge that leads to domination and exclusion (McMillan & Prosper, 2016).

While Two-Eyed Seeing bears substantial resemblance to the other presented frameworks, it is perhaps set apart in its explicit action imperative. Central to Two-Eyed Seeing is the notion that knowledge transforms the holder and that the holder bears a responsibility to *act* on that knowledge (Hatcher et al., 2009). *Netukulimk* implores one to uphold their responsibilities to future generations (Prosper et al., 2011); much like the early conceptual space of conservation biology (Soulé, 1985) but with emphasis here on responsibility to the place from which the knowledge emerges. To do so, *Netukulimk* uses the two perspectives made available through Two-Eyed Seeing processes to improve those very actions (McMillan & Prosper, 2016). This is not to say that the other frameworks do not share similar motivations or implications (recalling *Kaitiakitanga*), but rather that Two-Eyed Seeing uniquely moves beyond "unified-knowledges" as the end goal, to "unified-knowledges-and-here-is-what-we-are-compelled-to-do" as the ultimate realization of the framework. It is perhaps in part due to this assertion that Two-Eyed Seeing has extended past conceptual spaces, and there are a growing number of concrete examples of Two-Eyed Seeing in practice. The big question is not *whether* Two-Eyed Seeing (or like frameworks) will help us confront challenges in a post-colonial society or amidst environmental crises, but, in the words of Lawless et al. (2013), it is "rather, *how* they might be configured and applied." A significant challenge to date is the lack of pre-existing guidelines as the application of these frameworks depends highly on the specific context and the receptiveness of all actors involved (Denny & Fanning, 2016).

4 | TWO-EYED SEEING IN PRACTICE

To gain insight into how Two-Eyed Seeing approaches can and have been applied in aquatic and fisheries research and management contexts, we examine three recent case-studies that speak directly to the abovementioned need for tools and approaches for: (a) co-developing questions; (b) documenting and mobilizing knowledge; and (c) co-producing insights and decisions (Tengö et al., 2014). Given its place of origin (Eastern Canada; Bartlett et al., 2012), these examples of Two-Eyed Seeing in practice are all Canadian-based, but we draw parallels to other pertinent studies centred in other parts of the world, where possible. The subsequent case-studies each take a holistic approach, considering more than strictly fish- or fisheries-related parameters to include multiple indicators of aquatic ecosystem health (cases 4.1 and 4.2) and broader societal implications for fisheries co-management and co-governance (case 4.3).

4.1 | Co-developing questions in the Slave River Delta

This first case-study centres on the theme of developing power neutrality in the research process (Figure 2a). In response to a co-developed set of questions, the collaborative author team of

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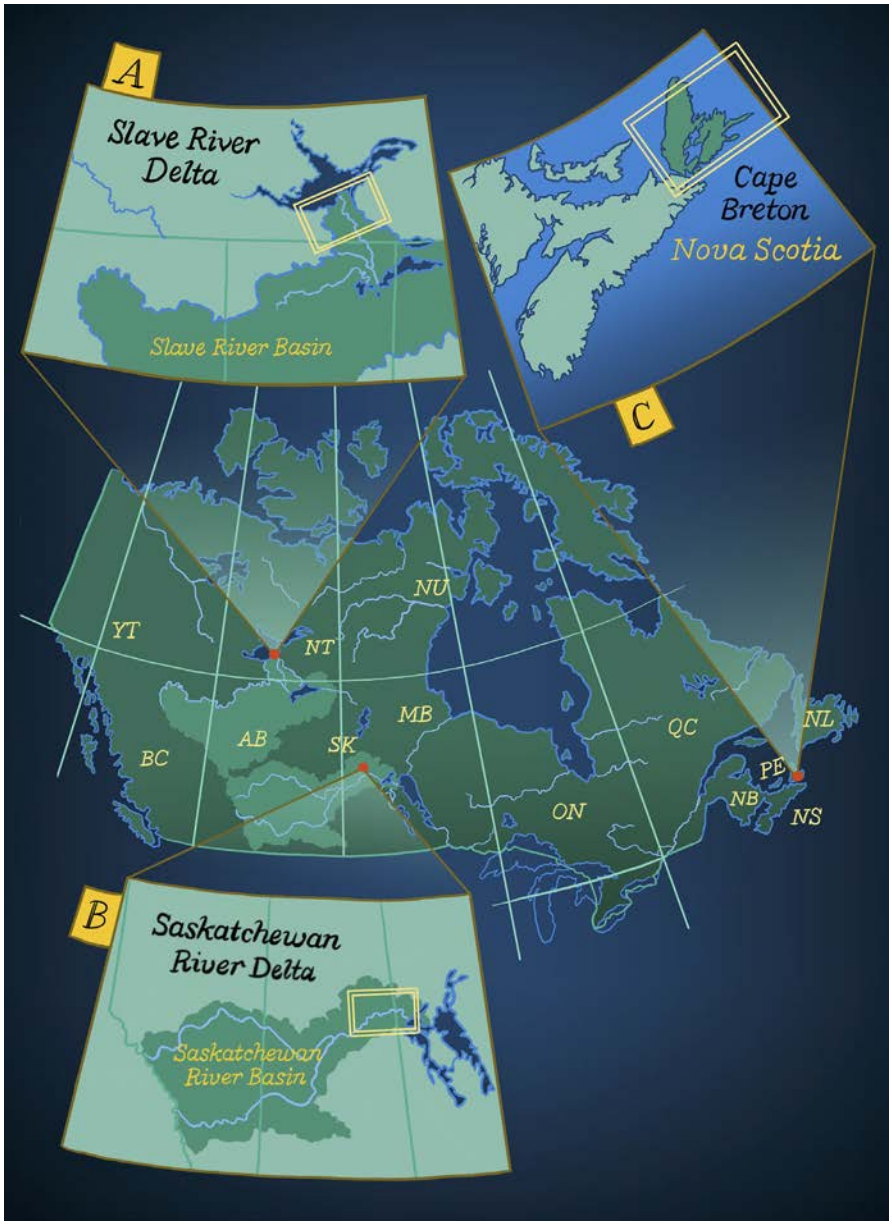


FIGURE 2 Map of Canada illustrating the location of the three case-studies operationalizing Two-Eyed Seeing: (a) Slave River Delta; (b) Saskatchewan River Delta; and (c) *Unama'ki*/Cape Breton. The landmass depicted here involves complex intersections of Indigenous territories and language groups with similarly diverse place names––we present names in English only because we cannot do this diversity justice in the scope of this diagram. Refer to main text (section 4) for full descriptions of each case-study (Sections 4.1–4.3, respectively). Artwork by Nicole Burton [Colour figure can be viewed at wileyonlinelibrary.com]

Mantyka-Pringle et al. (2017; comprising Indigenous community members, academics, and other groups) employed a participatory modelling approach (Bayesian belief networks, BBNs) as the central methodology for operationalizing Two-Eyed Seeing.

In the Slave River Delta in the Northwest Territories of Canada, significant resource development activity upstream (e.g. oil sand operations in northern Alberta, the W.A.C. Bennett Dam in northern British Columbia) is having profound impacts on ecosystem health and societal well-being downstream (Dagg, 2016). This is a place where hunting and fishing comprise a vital part of Indigenous life—for example, in one Slave River community (Fort Resolution), 66% of all Indigenous peoples participated in hunting and fishing in 2013, and 92% of all households ate meat or fish derived from those activities that year (NWTBS, 2014). In direct response to growing community concerns about the health of fish specifically, a diversity of "actors" in the region (three First Nations, three Métis organizations, two towns, a college and research institute, and various territorial and federal government agencies) united to create the Slave River and Delta Partnership (SRDP) in 2010. Their main goal was to develop community-based monitoring activities throughout the region, for which they solicited the help of multiple academic partners (six universities; Dagg, 2016). At an aquatic ecosystem health workshop in 2011, the SRDP and various academics co-developed three key central questions ((a) Is the water safe to drink?; (b) Are the fish and wildlife safe to eat?; and (c) Is the ecosystem healthy?") to which Mantyka-Pringle et al. (2017) offered responses.

At the 2011 workshop, >100 participants identified key indicators of aquatic ecosystem health along two distinct and complementary lines of inquiry: Western science and Indigenous knowledge. Where water quality and fish health could be described, respectively, in terms of "turbidity" (in Nephelometric Turbidity Units) or "fish external anomalies" (number of cysts, tumours, lesions and

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malformations) through a Western scientific lens, they could likewise be understood in terms of "the physical appearance of water" (changes in water visibility or movement over time) or "fish aesthetics" (changes in frequency of lesions or deformities over time) through an Indigenous lens. Data to inform Western science indicators ($n = 19$) were obtained through field observations and document reviews between 2011 and 2015, while key informant interviews with Elders in 2014 (Bradford & Bharadwaj, 2015) formed the basis for Indigenous knowledge indicators ($n = 22$). Two-Eyed Seeing was the core principle that informed how these two knowledge systems (and 41 indicators) would coexist, and BBNs served as the central methodology for operationalizing Two-Eyed Seeing. In 2015, the team led an expert elicitation process where they combined visual, narrative and textual tools to have key knowledge holders (an equal number of Elders, harvesters/fishers, government staff and scientists) to assess the causal links between the indicators and the three guiding questions above. Experts evaluated the following: the importance of indicators and their interactions; the state of indicators compared with the past (low, medium or high); their own level of expertise for each assessment (to populate the BBN with uncertainty estimates); and the resulting model output and behaviour (Mantyka-Pringle et al., 2017).

By bringing together interview transcripts, field data, existing models and expert judgement via participatory modelling, this team was able to provide a power-neutral approach to answering a co-developed set of questions and produce a co-authored report (i.e. Mantyka-Pringle et al., 2017 with the SRDP listed as senior author). Together, they determined a low probability that the social–ecological system is as healthy as it once was, and they found that where multiple Western science indicators were graded as "moderate" compared with the past, Indigenous knowledge indicators were graded as "low"—suggesting either that Western science is less able to detect incremental change given shorter timescales, or an unsubstantiated perception of change by Indigenous knowledge holders, or both (Moller et al., 2004). Notably, as BBNs can readily be updated as new knowledge becomes available, this study serves as but an initial model that can be refined over time. Mantyka-Pringle et al. (2017) add to the growing narrative that BBNs provide an effective means to widen the evidence base (e.g. Ban et al., 2014; Johnson et al., 2013), allowing for both quantitative and qualitative information to come together for a more holistic understanding of a complex system and enabling knowledge-inclusive partnerships to exist and be effective.

4.2 | Documenting and mobilizing knowledge in the Saskatchewan River Delta

This second case-study, Abu et al. (2019), centres on the theme of consilience—the congruence or agreement between the approaches to a topic or question by different knowledge or information systems (Figure 2b). Here, Indigenous knowledge, archival records and information collected using modern scientific instruments are brought together using the Two-Eyed Seeing framework, and their consilience is examined for a vast array of hydrology, fish and wildlife, and vegetation indicators of ecosystem change.

The Saskatchewan River Delta—North America's largest freshwater delta (10,000 km^2)—shares a similar context with the example above, where upstream anthropogenic activities (primarily the E.B. Campbell, Gardiner and Nipawin Dams) have profoundly reshaped system hydrology and fish and wildlife populations, provoking both community concern and the 2012 formation of a collaborative community–academic partnership in response (Patrick, 2014). One of the main goals of the partnership centres on finding ways for Indigenous communities and academic researchers to work together as equals, where both Indigenous knowledge and Western science are equally valued and unified to improve collective understanding of ecosystem change in the delta. Academic partners from the University of Saskatchewan identified three main questions that they explore in Abu et al. (2019): "(a) How can we learn about long-term social-ecological change from diverse knowledge holders? (b) How can we provide for the coexistence of plural forms of knowledge while engaging in respectful critique? and (c) How can we document the relative contribution each knowledge system provides and explain how each helps to fill in the gaps of the other?"

Through literature review, the authors outline various approaches for bridging knowledge systems (touching on a number of the concepts described here in Sections 2 and 3) and identify Two-Eyed Seeing as the guiding framework that will enable them to address their first two central questions. The article draws on three sources of evidence of ecosystem change in the delta. The first line of evidence was Indigenous knowledge drawn from key informant interviews with Elders and harvesters (inclusive of fishers, hunters and trappers) in 2014, which included accounts of key historical events and perceived changes in the system (Abu & Reed, 2018). Once transcribed and analysed, preliminary results were presented back to the community for review and approval. The second evidence base was archival records from the Provincial Archives of Saskatchewan on key historical events and past system changes, as well as information on resource-related policies (e.g. permits, quotas, regulations) and government correspondence (e.g. letters, petitions). The third form of evidence was instrumental observations (i.e. information collected using scientific instruments such as water gauges, or through field records such as fish-landing data). All three evidence bases included both quantitative and qualitative information that were brought together to address their third guiding questions using a simple but elegant means of examining knowledge congruence (c.f. Jackson et al., 2014) where knowledge systems were indexed as either consistent (in agreement), inconsistent (in disagreement) or an evidence type was lacking for comparison. This was performed for multiple indicators of change in hydrology ($n = 12$), fish and wildlife ($n = 16$), and vegetation ($n = 9$).

Taking this MEB approach guided by Two-Eyed Seeing, this team documented one evidence base (i.e. Indigenous knowledge; Abu & Reed, 2018) and mobilized two others (i.e. archival records and instrumental observations) for a novel and holistic approach to examining

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the state of a complex social–ecological system. They found a high degree of convergence across knowledge systems, where adverse changes in hydrology (83% congruent indicators), fish and wildlife (94%), and vegetation (100%) are reflected across all since the development of upstream dams. Incongruent indicators, as examples, included Indigenous knowledge signalling currently poor water quality (whereas instrumental observations declare it "safe") and a high abundance of northern pike (*Esox lucius*, Esocidae; *wícégāpís* in Cree; whereas instrumental observations find it near zero—but this may be explained by a decline in commercial interest, and thus fish-landing data, for this species). For six out of nine vegetation indicators, pertaining largely to knowledge of berries and other flowering plants, Indigenous knowledge provided the sole source of information available. Given the overall high degree of agreement between knowledge systems (as similarly found in Jackson et al., 2014; Service et al., 2014), Abu et al. (2019) provide further reason to be confident about understanding ecological phenomena through more than a strictly traditional (i.e. Western science) lens.

4.3 | *Towards* co-producing insights and decisions on *Unama'ki*/Cape Breton Island

For this third case-study, Giles et al. (2016), we move beyond examples of uniting disparate knowledges to an instance of bringing together disparate experiences with respect to gaining insights about a fishery and making decisions based on those contrasting understandings (Figure 2c). We also move from Northern and Western parts of Canada to the East Coast where the Two-Eyed Seeing concept came into being in *Mi'kma'ki*—the traditional and contemporary territory of the Mi'kmaq people.

Unama'ki/Cape Breton Island is home to the largest Indigenous community in Atlantic Canada and the largest Mi'kmaw community on the continent: the Eskasoni First Nation (population ~4,000; MacPherson et al., 2016). Located along the Bras d'Or Lakes and surrounded by the Atlantic Ocean, the Eskasoni community is deeply engaged in fishing activities for food, social and ceremonial (FSC) purposes and commercially—with a community-owned and community-operated fishing company that employs >150 fishers and contributes to nearly 10% of Eskasoni's annual revenues (Eskasoni Band Council, 2014). Since 1999, Eskasoni has been home to the *Unama'ki* Institute of Natural Resources (UINR)—representing Eskasoni and the four other Mi'kmaq communities on the island (i.e. Membertou, Potlotek, Wagmatcook, and We'koqma'q)—and this is a group that, consistent with the previous two case-studies, was formed in response to rising community concerns regarding natural resources (especially fisheries) and their sustainability. One of UINR's central goals is to strengthen research and natural resource management while maintaining Mi'kmaq knowledges and worldviews. To this end, they frequently partner with external governments, organizations and universities on key environmental concerns (UINR, 2016). One such partnership, Giles et al. (2016), involved researchers from both Dalhousie University and UINR, as well as commercial fishers and representatives from the Eskasoni First Nation. Together, they examined Indigenous inclusion in policy-level fisheries decision-making in Canada, using Eskasoni's American eel (*Anguilla rostrata*, Anguillidae; *Kataq* in Mi'kmaw) fishery as a model system.

The American eel has been vital to the Mi'kmaq for thousands of years (primarily used now for FSC purposes and largely absent from Eskasoni's commercial fishery; Davis et al., 2004), but it has come under threat in recent decades due to the combined effects of habitat destruction and fragmentation from hydroelectric development, as well as targeted commercial fishery operations and other threats (Cairns et al., 2014). Dramatic declines (65% fewer maturing eels in the Great Lakes and upper St. Lawrence River area between 1996 and 2010) have led the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to list the American eel as threatened in 2012 and prompted its consideration for listing under Canada's 2003 *Species at Risk* Act (SARA).

While SARA states that "the traditional knowledge of the aboriginal peoples of Canada should be considered in the assessment of which species may be at risk and in developing and implementing recovery measures," there are inherent challenges that arise from the attempted "integration" of Indigenous knowledges and values into government level policy, which Giles et al. (2016) examined. Moreover, FSC fisheries are constitutionally protected in Canada and the listing of a culturally significant species such as eel could have profound impacts on community subsistence, well-being, and constitutional and treaty rights. It follows that Mi'kmaq inclusion in the COSEWIC and SARA processes for eel should be a given, but Giles et al. (2016) find minimal evidence that Mi'kmaq were included in the process.

In 2014, using Two-Eyed Seeing as a guiding framework (as UINR does through all its activities; UINR, 2016), Giles et al. (2016) interviewed both Eskasoni eel fishers (about the fishery and linked knowledges)and federal government representatives involved in COSEWIC and SARA assessments (about the process and its "use" of knowledge). They found that despite the existence of an Aboriginal Traditional Knowledge Sub-Committee (ATK SC) within COSEWIC, as well as various other measures within SARA (e.g. the National Aboriginal Council on Species at Risk (NACOSAR) and Aboriginal Funding for Species at Risk (AFSAR), which were not even raised by respondents during interviews), "the full understanding of a Mi'kmaq knowledge system is not reflected in [current] management decisions" (Giles et al., 2016). Additionally, Mi'kmaq eel fisheries were found to be underpinned by the values of kinship, relationality, generosity and *Netukulimk*, whereas the governmental approach to eel fisheries was found to be governed by a Western scientific worldview that instead prioritizes process, compartmentalization, economic benefits and conservation.

Reconciling the two vastly differing approaches to knowing and managing the eel fishery sustainably presents a considerable challenge. From the perspective of government respondents, the barriers are logistical (citing: no formal process for "integration"; concerns around data ownership), conceptual (no space in

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the process for cultural or spiritual components; the two systems operating on incompatible time scales—immediate vs. seven generations) and communication-based (using different languages and interpretations; unresolved historical traumas and issues of mistrust between the Mi'kmaq and the Canadian Government). Nevertheless, the authors report "considerable opportunity" for bringing Mi'kmaq knowledge systems to bear on the COSEWIC and SARA processes—highlighting specific mechanisms in their workflow (e.g. ATK SC, NACOSAR, AFSAR) and flagging areas that could be enhanced (e.g. through the inclusion of community advisory boards, scenario-building activities), as well as identifying multiple benefits of doing so *via* a Two-Eyed Seeing approach (i.e. promoting cross-cultural and enriched understandings, fostering mutual respect, and upholding constitutional and treaty rights). Here, we find a critical examination of the involvement of Indigenous peoples and knowledges in policy decision-making and an envisioned path for meaningful and equitable co-governance based on a Two-Eyed Seeing approach—similar arguments and scenarios have been built around the Two Row Wampum model (see Stevenson, 2006), the Two Ways philosophy (see Muller, 2014), and the Double-Canoe framework (see Maxwell et al., 2019).

Two-Eyed Seeing has had visible traction in co-developing questions, documenting and mobilizing knowledge, and co-producing insights, and it holds promise for guiding policy decision-making in fisheries. But, without clear evidence here of the latter coming to full fruition (i.e. true decision co-production), this calls into question whether the mutual understanding generated through Two-Eyed Seeing is of much consequence if it is not then reflected in policy decision-making, which ultimately determines how a fishery is managed, studied, perceived and utilized. It also raises the issue of whether Indigenous knowledge systems are only being valued here because they are supported by and in strong congruence with Western science—but continued colonial sentiment throughout governing bodies prevents their full and equitable inclusion into policy decision-making.

There needs to be a fundamental rethinking in how we come to know and manage fisheries that allows space for multiple ways of knowing if we are to fulfil our obligations (legal, practical, moral, as discussed in Section 2) and achieve its co-benefits. As examples, the inclusion of Indigenous knowledge systems in fisheries research and management has been shown to: offer technological shifts that improve fisheries selectivity and sustainability (Menzies & Butler, 2007); enhance early warning systems for sea state forecasting (Sethi et al., 2011); reverse declines in the abundance and size of exploited species (Frid et al., 2016); yield otherwise inaccessible ecological insights such as missing baseline information (Eckert et al., 2018; Marin et al., 2017); and play a critical role in the improvement and the collective adherence to fisheries policy (Berkes, 2018; Johannes et al., 2000). However, rarely are the past and present impacts of colonialism on these knowledge systems and their power recognized, let alone rectified, which is both "practically and politically dangerous" (Butler, 2006) for all of the reasons presented herein.

5 | RE-ENVISIONING FISHERIES RESEARCH AND MANAGEMENT

The last decade has seen significant strides made in decolonizing research and methodologies (Held, 2019; Kealiikanakaoleohaililani & Giardina, 2016; Smith, 2012; Wilson, 2008) and in defining Indigenous worldviews *as* research method—as a defensible paradigm to guide scholarly inquiry (Kovach, 2010; Latulippe, 2015; McGregor et al., 2018). Held (2019) brings together many of these and additional works as she defines an Indigenous research paradigm in terms of its own philosophical assumptions (i.e. ontology, epistemology, axiology, methodology) and in relation to other major paradigms that inform primarily social inquiry (i.e. positivist, post-positivist, constructivist, transformative and pragmatic research paradigms). From this foundation and informed by philosophical examinations of conventional fisheries alternatives (Berkes, 2001, 2003) and the case-studies above, we can collate the purposes, main assumptions and worldviews that underpin Western and Indigenous approaches to fisheries research and management (see Table 3), and identify avenues for ontological, epistemological, axiological and methodological transformation in fisheries that allow for the full operationalization of Two-Eyed Seeing.

Instead of "fishing-as-business" (Berkes, 2003), Indigenous fisheries are often driven by ethics of sustainability (e.g. *Netukulimk*, *Kaitiakitanga*), protecting the present and future well-being of fish, people and place (Maxwell et al., 2019; McMillan & Prosper, 2016; Prosper et al., 2011; Roberts et al., 1995). While modern fisheries scientists acknowledge uncertainty in their models and projections (e.g. credibility envelopes) and contextualize their findings as being based on the best available evidence at the time, subject to change as new data arise, their discipline historically stems from a realist ontology (that there is but one knowable reality), an objectivist and empirical epistemology (where research findings are "true"), a values-free axiology (where influences and biases are denied) and an experimental and top-down methodology (through which hypotheses are verified and findings universal). In contrast to the more conventional fisheries notions, Indigenous fisheries ascribe to a relativist ontology (where multiple socially constructed realities exist), an intersubjective epistemology (that respects multiple ways of knowing and forms of knowledge), a values-centred axiology (where relational accountability is key), and a participatory and contextualized methodology (that is knowledge-inclusive and its findings specific to place; Held, 2019). The former is characterized by reductionism, positivism and "expert-knows-best" science, while the latter adopts complex systems thinking and is inclusive of local knowledge systems (Berkes, 2003). This culminates, on the one hand, in a Western scientific perspective that is founded upon a utilitarian worldview where humans are in control of nature (as described in Section 1), and an alternate perspective that humans are part of ecosystems, on the other—where, in the latter case of Indigenous fisheries, it is human actions rather than natural systems that are subject to governance and structure (Berkes, 2001, 2003). The aim here again is

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Paradigm dimensions	Conventional fisheries	Indigenous fisheries
Purpose	Fishing-as-business	Sustainable livelihoods; collective well-being
Ontology	Realist; one knowable reality	Relativist; multiple socially constructed realities
Epistemology	Objectivist; empirical truth	Intersubjective; multiple forms of knowledge
Axiology	Values excluded; influence denied	Values included; centre relational accountability
Methodology	Experimental; top-down	Participatory and knowledge-inclusive; place-based
Worldview	Control nature; utilitarian	Humans indivisible from nature; relational

TABLE 3 Philosophical assumptions historically underpinning conventional and Indigenous fisheries approaches and worldviews

Adapted from Held (2019) and informed by Berkes (2001, 2003).

not to pit one approach against the other or to place them at irreconcilable odds, but rather to highlight their distinctiveness given that both have individual strengths in specific contexts.

Frameworks such as Two-Eyed Seeing that enable parallel lines of inquiry to come together require an openness to other ways of being and knowing on both sides that historically has not been reflected in the mainstream approach to fisheries research and management (Denny & Fanning, 2016; Figure 3). As made evident by the case-studies above, knowledge coexistence "for the benefit of all" (Marshall et al., 2015) depends on who is at the table and their receptiveness to alternate modes of knowing and generating knowledge. From these case-studies, there are clear actionable steps that emerge that can inform other research programs moving forward (Figure 4). For instance, in Mantyka-Pringle et al. (2017) and Abu et al. (2019), Indigenous knowledge and Western science were clearly placed on equal footing, with both serving as evidence bases to inform

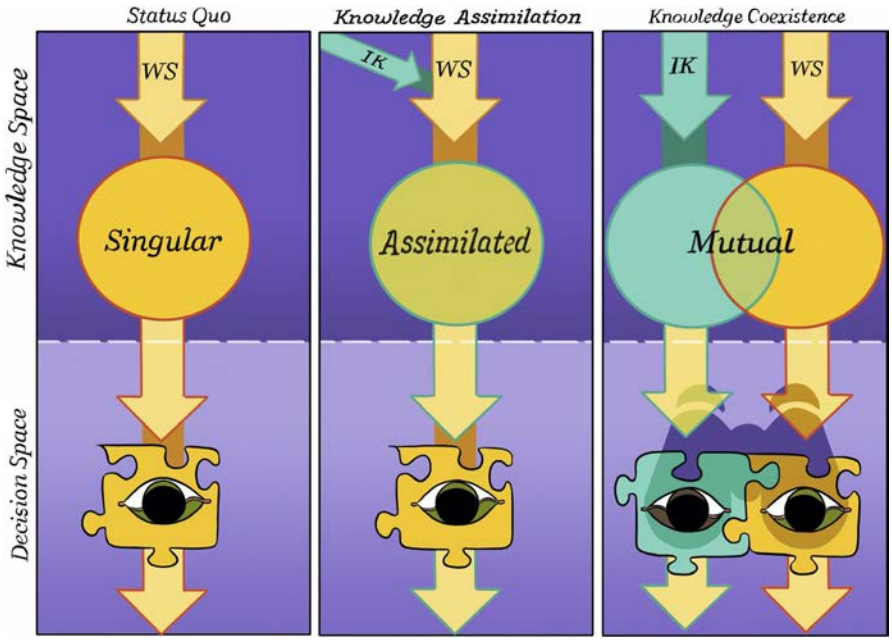


FIGURE 3 A conceptual framework detailing the flow of knowledge (IK, Indigenous knowledge; WS, Western science) that underpins researchers' understandings or views of reality, and ultimately guides their research and management decisions, as classified under three main archetypes. Status Quo (left) depicts a "one-eyed" approach that accepts solely Western science as a valid knowledge system, producing a singular understanding that informs decision-making. Knowledge assimilation (centre) is typical of many management approaches that incorporate Indigenous knowledge into Western science for an improved understanding to inform decision-making, ultimately producing another "one-eyed" approach (however, the reverse situation can also occur whereby Indigenous peoples utilize Western scientific approaches to inform their decision-making that is guided principally by Indigenous knowledge; also "one-eyed" but in the inverse orientation). Lastly, Knowledge coexistence (right) shows an approach where Western science and Indigenous knowledge contribute in parallel to produce a mutual understanding from which context-specific decisions are formed—this reflects an approach that is congruent with Two-Eyed Seeing (represented here by the same symbology shown in Figure 1). Artwork by Nicole Burton [Colour figure can be viewed at wileyonlinelibrary.com]

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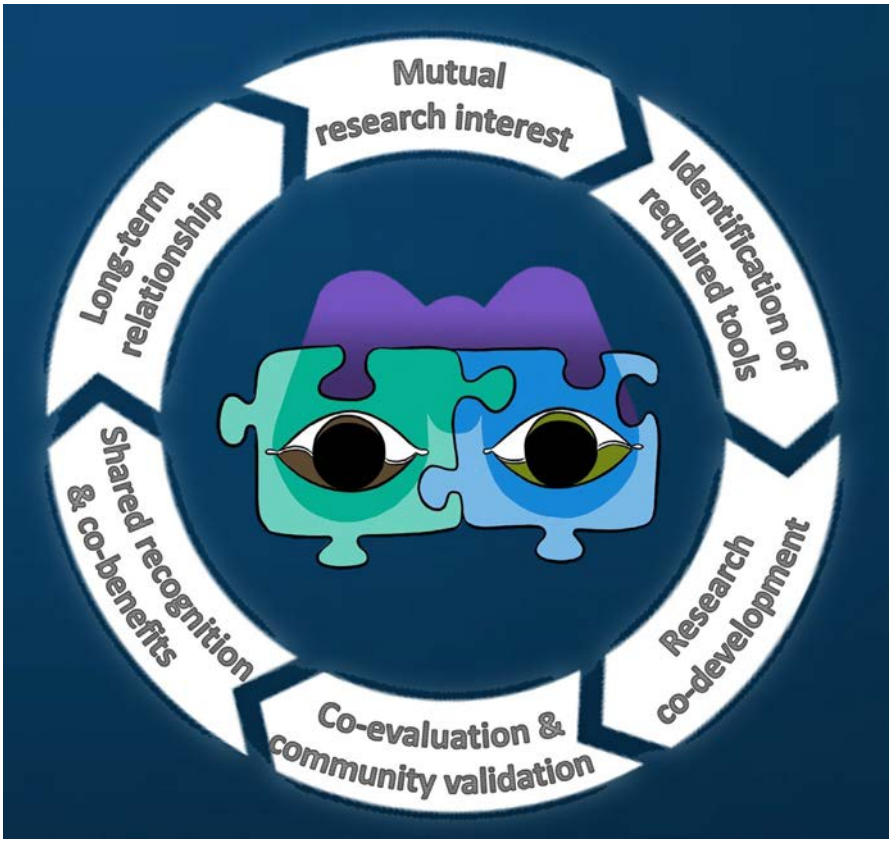


FIGURE 4 A stepwise framework for applying Two-Eyed Seeing to research, reflecting a summary of beneficial steps taken in three case-studies explored herein. The asterisks emphasize the need for a mutually recognized knowledge gap or research potential as the starting point for this cyclical process that can only be fully realized through the conceptualization of a given research programme as a relationship to be maintained and honoured over the long term [Colour figure can be viewed at wileyonlinelibrary.com]

various indicators of aquatic ecosystem health. In the case-studies presented above, most approaches were highly participatory, being co-developed, co-run and/or co-evaluated by the collaborative teams conducting the research, with evaluations primarily measured against internal rather than external referents (e.g. experts evaluating their own expertise and model output in Mantyka-Pringle et al., 2017; researchers bringing their preliminary interview results back to the community for review and approval in Abu et al., 2019). All studies were set in motion by communitism—where Indigenous communities identified the original need(s) and invited external partners in accordingly, which was reflected in co-authorship (UINR partners in Giles et al., 2016; and the SRDP as a collective in Mantyka-Pringle et al., 2017) or acknowledgements (Abu et al., 2019). Each study created a unique current or future pathway for Two-Eyed Seeing in their context, and all are poised for operation in the long term. They demonstrate the context-dependent nature of this framework, and that solutions are not one-size-fits-all scenarios—in fact, knowledge unification was achieved through a multiplicity of mechanisms that matched their individual circumstances.

The prevailing paradigm that was conducive to Two-Eyed Seeing in all three case-studies shares many parallels with Indigenous fisheries approaches and worldviews (Table 3). Each study respected multiple realities (reflective of a relativist ontology), considered multiple knowledges as valid and equal (an intersubjective and pluralistic epistemology where experiential and relational knowledge is equally valued), embraced relational accountability by promoting respectful representation and reciprocity (a value-centred axiology), and carried out highly inclusive and situated research processes (a participatory and place-based methodology). Holding space for multiple perspectives and seeing value in multiple teachings through respectful individualism is an adaptive feature of many Indigenous knowledge systems (Berkes, 2018), and it is a principle that is shared across many Indigenous groups, as was made evident by the plurality of models for knowledge coexistence (Section 3). This may be why Two-Eyed Seeing and other Indigenous knowledge coexistence frameworks seem to be so readily embraced by Indigenous knowledge holders and community members (Bartlett et al., 2012) where there is perhaps less of a paradigm shift required "to use both these eyes together" than for those that ascribe strictly to a Western scientific tradition.

The case-studies also highlight some challenges that need to be overcome if conventional fisheries management and research are to embrace Two-Eyed Seeing. The Slave and Saskatchewan River Delta case-studies, while both very successful, are relatively small in scale compared with the spatial extents of many fisheries. Perhaps part of their success is because they are localized, each clearly linked with specific Indigenous management areas, and about mostly FSC fisheries. The success of Two-Eyed Seeing in these case-studies illustrates that it can be done in small-scale fisheries that have to date largely been ignored by conventional fisheries management and science. The American eel case-study, with commercial interests, has been more challenging (Giles et al., 2016) and has focused on one small part of the eel's range. Fully embracing the concept of Two-Eyed Seeing at the same scale

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as the range of fish species, fisheries and/or management areas would require coordination of many Indigenous peoples and other interests spanning many governments and knowledge types. Such possible mismatches of scale for some species and fisheries may be an obstacle to the uptake of Two-Eyed Seeing for commercial fisheries that focus on wide-ranging species. However, examples do exist demonstrating how such frameworks can and have led to legislated spatial closures for larger scale commercial fisheries (Ban et al., 2018). But even if most initial examples of Two-Eyed Seeing in fisheries are relevant to small-scale fisheries, improvement in such fisheries is needed (Hilborn et al., 2020) and much learning can come from such case-studies and lead to future attempts to apply Two-Eyed Seeing more broadly to commercial and industrial fisheries.

A useful thought exercise at this stage is to conceptualize how this vision could be applied to a specific fishery or other aquatic issue (e.g. development of species at risk recovery plan; siting of a protected area). How would a relativist ontology, pluralistic epistemology, value-centred axiology, and participatory and place-based methodology change the context's current and future state? How would linked practices and policies reflect the interdisciplinary, cross-cultural and pluralistic nature of Two-Eyed Seeing? This exercise could veritably provide a study unto itself, and so for the purposes of the present argument, we can instead take the existing groundwork that has been laid by Giles et al. (2016) who put forward a set of recommendations to improve Mi'kmaq input into the current Western-dominant approach to American eel fisheries and their management. Specifically, they lay out many eeling practices (e.g. sharing eels with Elders, family and community members; being highly selective during summer eeling) and corresponding management recommendations (e.g. minimum FSC level ensured; size limits for summer eeling, respectively) that they wish to be reflected in the forthcoming update to the American eel Integrated Fisheries Management Plan (IFMP) for the Maritimes region of Canada. The Department of Fisheries and Oceans Canada (DFO) is currently in negotiations with various Indigenous organizations and communities to update the IFMP appropriately, and the authors flag this as an "opportunity to explore the complementarity among the First Nations and Western scientific approaches to management while allowing for the value systems and beliefs among the different knowledge systems to be respected" (Giles et al., 2016). It is critical to note, however, that the differing worldviews underpinning Mi'kmaq and Western decision-making processes currently produces distrust and frustration on both sides, and while the authors still see "considerable opportunity" for Two-Eyed Seeing in this context, there may be many comparable cases where such an approach is wholly inappropriate to apply. For instance, as Indigenous Nations increasingly return to self-determination, there needs to be a commensurate rise in the state's confidence in the capacity of these peoples to "manage" fisheries without federal oversight (or that of another colonial force). This relinquishing of power to Indigenous process and management rights is also imperative as many post-colonial nation states grapple with reconciliation. Two-Eyed Seeing will never fit a context in which both sides are not willing partners, which may well be the case where Indigenous Nations exercise fishing rights legislated constitutionally, in treaties and/or through international legal norms (e.g. the United Nations Declaration on the Rights of Indigenous Peoples, UNDRIP Articles 25, 32.2 and 32.3).

Along a similar vein, cases may often arise where predictions and/or results are incongruent or unaligned. For instance, in both Mantyka-Pringle et al. (2017) and Abu et al. (2019), water quality was found to be in a "worse" state based on Indigenous knowledge indicators compared with Western scientific indicators, which graded water quality more moderately. A viable explanation for this trend is that through a Western scientific lens water with levels of chemical contamination below a certain threshold is considered safe to drink (a universal truth based on objectivism), whereas through an Indigenous knowledge lens, any departure from a past known state is being noted so the substantial changes in water quality being signposted by Elders are strongly suggesting otherwise (Mantyka-Pringle et al., 2017). Such discrepancies are in fact informative as they provide a fuller understanding of a complex system where Indigenous knowledge systems may exhibit higher sensitivity to environmental perturbation making them early detectors of ecological change (Berkes, 2018). Though not generally supported by the case-studies presented herein, there may of course be instances where predictions or results point in completely opposing directions—but, as with northern pike in Abu et al. (2019), these disconnects may again be illuminating and indicative of multiple realities existing within a system (e.g. where a high local abundance is being reported by local knowledge holders, and few fish landings are being reported coincident with declining commercial interest in this species). In many cases, access to multiple knowledge types may itself be a luxury, and drawing from multiple evidence bases may be the only means of filling critical knowledge gaps (e.g. as with vegetation indicators in Abu et al., 2019). Additionally, some nations may choose not to engage with colonial governments due to histories of violent colonization, and resulting relationship fractures and distrust.

Conflicting interpretations of recent events and information abound in complex fisheries systems (e.g. Newfoundland's northern cod (*Gadus morhua*, Gadidae) fishery; Finlayson, 1994), and if we continue to subscribe to the notion that knowledge is free from social process, or that scientific interpretations are not socially constructed to a large extent, then we are choosing to uphold the *status quo* or Western approach to fisheries research and management that has led us to this current state of many fisheries failing both ecologically and socially (Pauly et al., 2002). Rounding out our understanding and approach to fisheries to include other knowledges and ways of knowing is no longer an issue of awareness or method, as exemplified here, but rather the barriers are time (to build the requisite relationships), a general lack of incentives (little provocation away from inaction), and entrenched systems of political power

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or unsubstantiated perception of knowledge hierarchies. As common in co-management schemes (Chuenpagdee & Jentoft, 2007), the precursor to each case-study was environmental perturbation followed by a need for innovative approaches to understand and manage the aquatic environment—are we then to wait for the global disruption of all fisheries, large and small, before we choose to depart from the safety of the *status quo*? Our collaborative departure from this *status quo* can instead be a shared choice—an action imperative—generated through an equitable Two-Eyed Seeing approach which leverages many tools and perspectives towards imagining better futures for fisheries and humanity.

6 | CONCLUSIONS

Two-Eyed Seeing offers a legitimate, decolonial approach for working on "wicked" fisheries problems or other aquatic environmental challenges where singular solutions are near impossibilities, and emphasis must instead be placed on engaging in "interactive communication and learning among stakeholders, where norms and values are played out and where different ethics, ideologies, and epistemologies are active" (Jentoft & Chuenpagdee, 2009). Through its action imperative and cooperative foundation, Two-Eyed Seeing values collective over individual action and collaborative learning or "co-learning" (Bartlett et al., 2012) where once disparate and polarized groups or knowledge holders are united, bringing together their respective understandings, insights and skills to bear on a common or shared problem. They learn from one another and in doing so produce a collectively enriched picture of a complex system. Two-Eyed Seeing is a framework that very much centres on *process* rather than *outcome*, and it is actualized in its unending pursuit of responsibilities to those beings—all beings—now and seven generations ahead (McMillan & Prosper, 2016). Improving how fisheries and aquatic ecosystems are studied and managed would not be an end point *per se*, but rather a transformative and ongoing action that can be brought about through Two-Eyed Seeing that remedies power relations, respects differences and upholds unique strengths instream with its uniting of knowledges and ways of knowing. The approach outlined here also has tremendous merit and relevance to other complex environmental problems or issues beyond the aquatic realm, and we challenge our readers to personally take on the action imperative of applying the Two-Eyed Seeing framework to the context—fisheries, aquatic or otherwise—in which they study, work and live.

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DATA AVAILABILITY STATEMENT

This does not apply to the present article as no data sets were generated or analysed in the course of this work.

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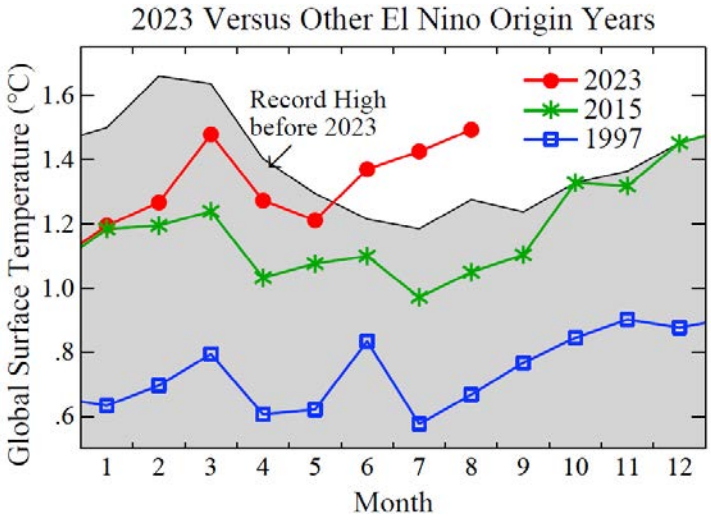


Fig. 1. Global temperature (relative to 1880-1920 mean for each month) during the El Nino origin year for the 1997-98, 2015-16 and 2023-24 El Ninos. The impact of El Nino on global temperature usually peaks early in the year following the year when the El Nino originated.

Global Warming is Accelerating. Why? Will We Fly Blind?

14 September 2023

James Hansen, Makiko Sato, Reto Ruedy, and Leon Simons

Abstract. Global temperature in the current El Nino exceeds temperature in the prior (2015-16) El Nino by more than the expected warming (0.14℃ in 8 years) for the global warming rate since 1970 (0.18℃/decade). Proximate cause of accelerated warming is an increase of Earth's Energy Imbalance (EEI), but what caused that? Indirect evidence points to a decline in the cooling effect of human-made aerosols. Failure to measure aerosol climate forcing is partly compensated by precise monitoring of EEI details. However, there are no adequate plans to continue even this vital EEI monitoring – which will become even more important as humanity realizes its predicament and the fact that we must cool the planet to avoid disastrous consequences and restore a bright future for young people – let alone plans for adequate aerosol monitoring.

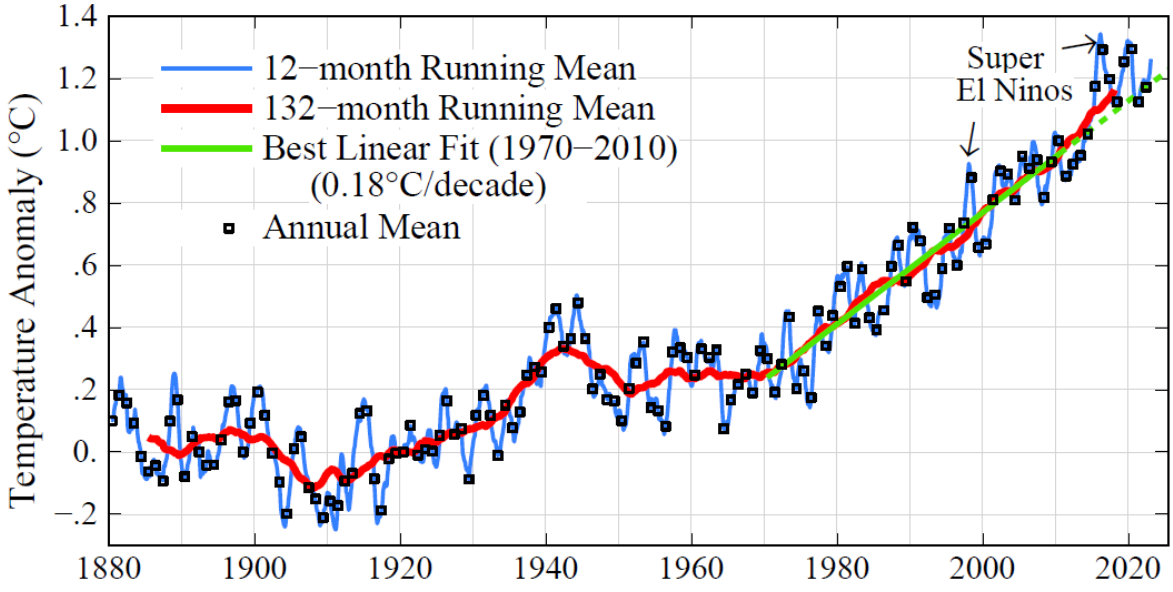


Fig. 2. Global temperature relative to 1880-1920 based on the GISS analysis.[1,2]

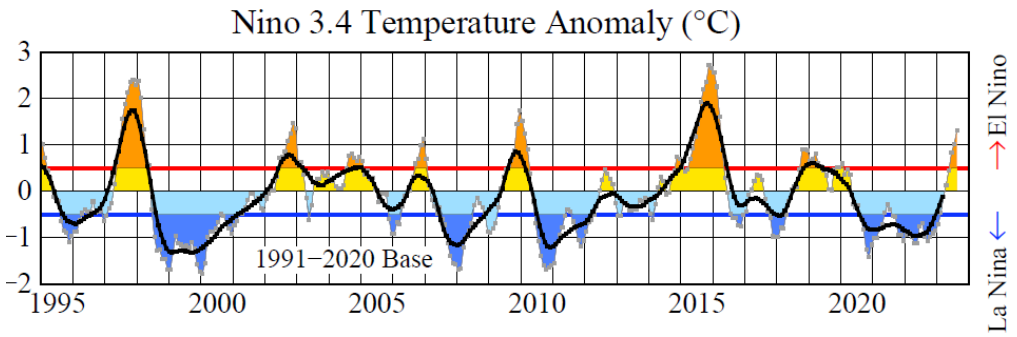


Fig. 3. Temperature in the tropical Pacific region used to define El Nino strength. El Nino (La Nina) is nominally defined to occur when Nino 3.4 is > 0.5℃ (< –0.5℃).

Suspicion that global warming was accelerating was created by the warming rate between the 1997-98 and 2015-16 El Ninos.[3] The rate of warming between those super El Ninos was 0.24℃/decade, exceeding the 1970-2010 rate of 0.18℃/decade (Fig. 2). So far, the present El Nino, only 8 years after the 2015-16 El Nino, suggests substantial further increase in the rate of global warming. It is too soon to say how strong the present El Nino will be, but its seasonality is normal (Fig. 3). Global temperature anomalies lag the Nino3.4 index by several months, so it is also early to estimate the peak warming, which is expected to occur in the first half of 2024. However, global temperature in the first few months of the El Nino is so extreme (Fig. 1) it is now almost certain that the 12-month running mean temperature will exceed 1.5℃ by May 2024 or earlier.

The proximate cause of the global warming is Earth's energy imbalance (EEI): there is more energy coming in (absorbed sunlight) than energy going out (heat radiated to space). EEI increased greatly in the past decade (Fig. 4). The imbalance so far in the 2020s (1.36 W/m^2) is almost double the rate (0.71 W/m^2) during the calibration period (mid-2005 through mid-2015) in which satellite data[4] for EEI (with great precision in temporal change) are put on an absolute scale via decadal-mean in situ (Argo float) ocean heat storage data.[5] The principal mechanism for global warming over the past century has been the reduction of Earth's outgoing heat radiation caused by increasing greenhouse gases, which makes the atmosphere more opaque at infrared wavelengths that emit heat radiation. Heat radiation to space thus arises from higher, colder, levels, which reduces energy loss to space, causing the planetary energy imbalance and therefore global warming.

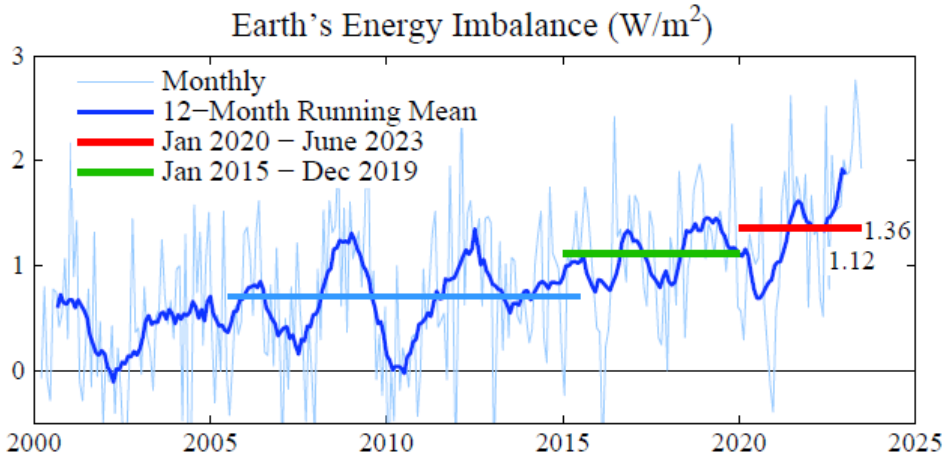


Fig. 4. 12-month running-mean of Earth's energy imbalance from CERES satellite data[4] normalized to 0.71 W/m^2 mean for July 2005 – June 2015 (blue bar) from in situ data.[5]

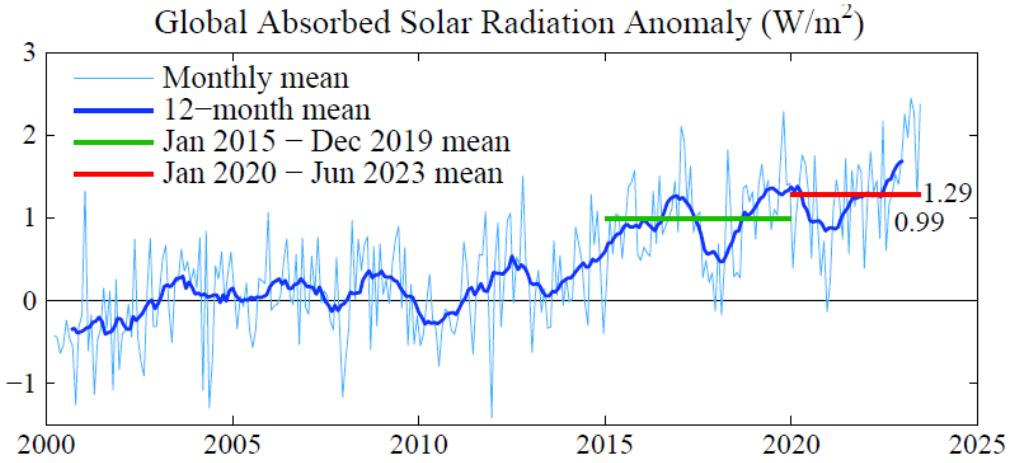


Fig. 5. Global absorbed solar radiation (W/m^2) relative to mean of the first 120 months of CERES data. CERES data are available at http://ceres.larc.nasa.gov/order_data.php Global absorbed solar radiation anomalies are 0.99 and 1.29 W/m^2 in the indicated intervals.

However, greenhouse gases are not the cause of increased EEI since 2015. How do we know? The (CERES) satellite instrument measures both the change of emitted heat radiation and the change of reflected solar radiation. The change since 2015 is a decrease of sunlight reflected by Earth, thus an increase of solar radiation absorbed by Earth (Fig. 5). Absorbed solar radiation in 2015-2019 was 0.99 W/m^2 greater than in the calibration period (2005-15), and since January 2020, the imbalance is even greater (1.29 W/m^2). Increased EEI did not occur because of an increase of solar irradiance. On the contrary, during the 5 years 2015-19 the Sun's brightness declined by an amount decreasing absorbed solar radiation by about 0.15 W/m^2, followed by an increase since 2020 of about 0.2 W/m^2 (Fig. 6, right scale). Changes of sea ice area affect EEI, but sea ice changes in the past decade have been small, except the decrease of Southern Hemisphere sea ice in the past 2 years.[6] The Hunga Tonga volcanic eruption in early 2022 also affects the past two years. Jenkins *et al.*[7] estimate that water vapor injected into the stratosphere caused a small warming forcing (+0.12 W/m^2), but Schoeberl *et al.*[8] found that the cooling effect of stratospheric aerosols injected by Hunga Tonga yielded a net cooling effect, with forcing peaking in mid-2022 at about –0.5 W/m^2. Averaged over 2022, Hunga Tonga may have been about –0.3 W/m^2, but by today it is smaller.

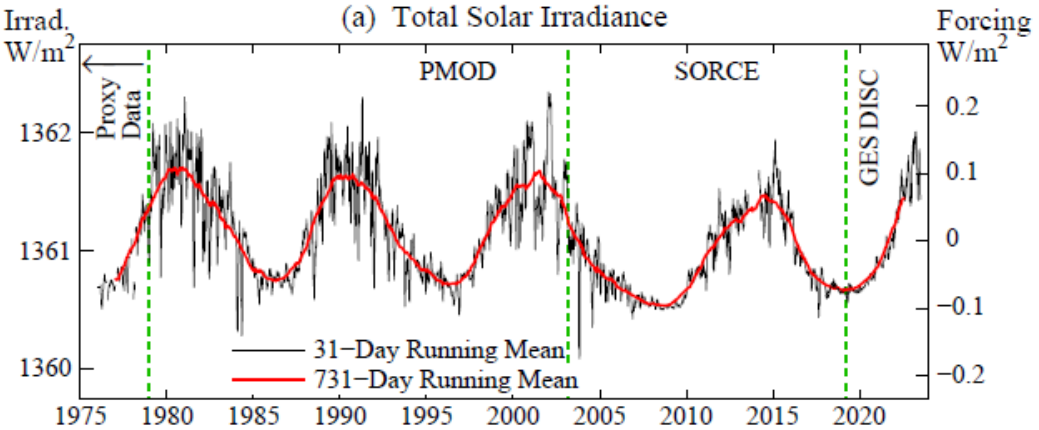


Fig. 6. Solar irradiance and climate forcing, the latter being 0.175 ×irradiance change, where 0.175 = (1 – Earth's albedo)/4, where Earth's albedo = 0.3. Data sources: Physikalisch Meteorologisches Observatorium, Davos, University of Colorado Solar Radiation and Climate Experiment, and Total Irradiance Monitor on the International Space Station (GES DISC).

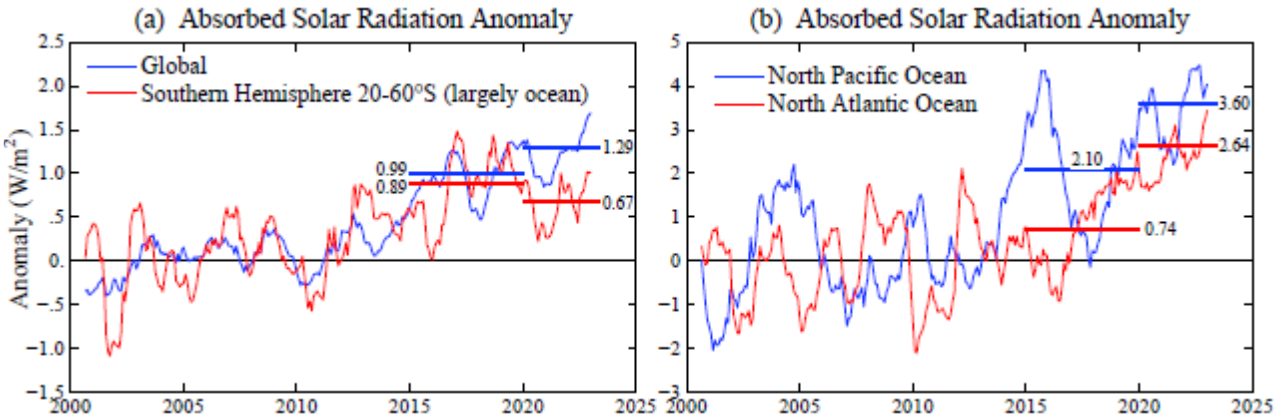


Fig. 7. Absorbed solar radiation for indicated regions relative to first 120 months of CERES data. Southern Hemisphere 20-60°S is 89% ocean. North Atlantic is (20-60°N, 0-60°W) and North Pacific is (20-60°N, 120-220°W). Data source: http://ceres.larc.nasa.gov/order_data.php

We conclude that, although the solar and Hunga Tonga forcings are not negligible, they do not account for the large, persistent increase of absorbed solar radiation since 2015. The only known mechanism capable of such a large forcing is a decrease of cloud albedo. Indeed, we concluded elsewhere[9] that decreased particulate air pollution in the past decade should cause such a decrease of cloud albedo and thus an acceleration of global warming in the post-2010 period. The most distinct and probably the most effective aerosol reduction is due to limitations on the sulfur content of ship fuels imposed by the International Maritime Organization (IMO) in January 2015 and strengthened in January 2020. The change of global absorbed solar radiation suggests that the 2015 change had the larger effect, but that appearance may be misleading. Clouds, and thus planetary albedo (reflectivity), have a large natural variability, e.g., cloud change correlated with the Pacific Decadal Oscillation (PDO). The PDO shifted to its positive phase in 2015, which favors decreased cloud cover and increased global absorption of solar radiation.[10] The PDO shifted back to its negative phase in 2020 (Fig. 8), which favors increased clouds and reduced absorption of solar radiation. Yet the post 2020 EEI has increased (Fig. 4), as has absorbed solar radiation (Fig. 5).

The upshot is strong indirect evidence that an ongoing decrease of particulate air pollution is in the process of increasing absorption of solar energy by Earth, which adds to greenhouse gas global warming. We predict at least a 50 percent increase of the post-2010 global warming rate, compared to the 1970-2010 rate of 0.18℃/decade.[9] This is a partial payment in return for the Faustian bargain that humanity made when it chose to build its economies on fossil fuel energy.[11]

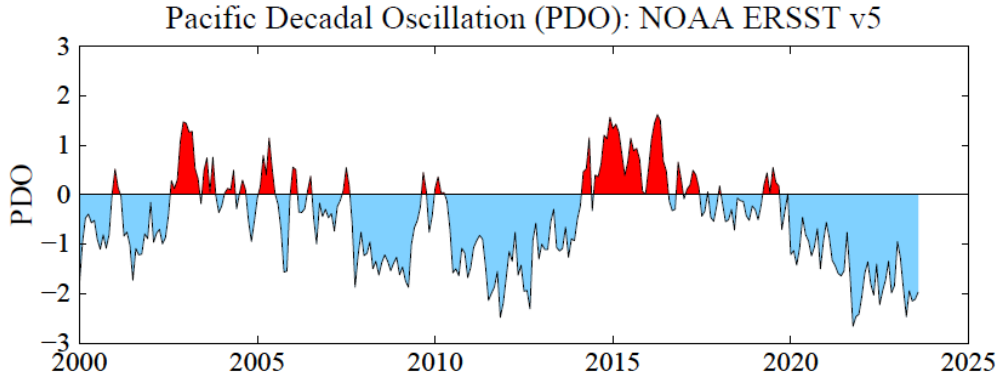


Fig. 8. Pacific Decadal Oscillation.[12]

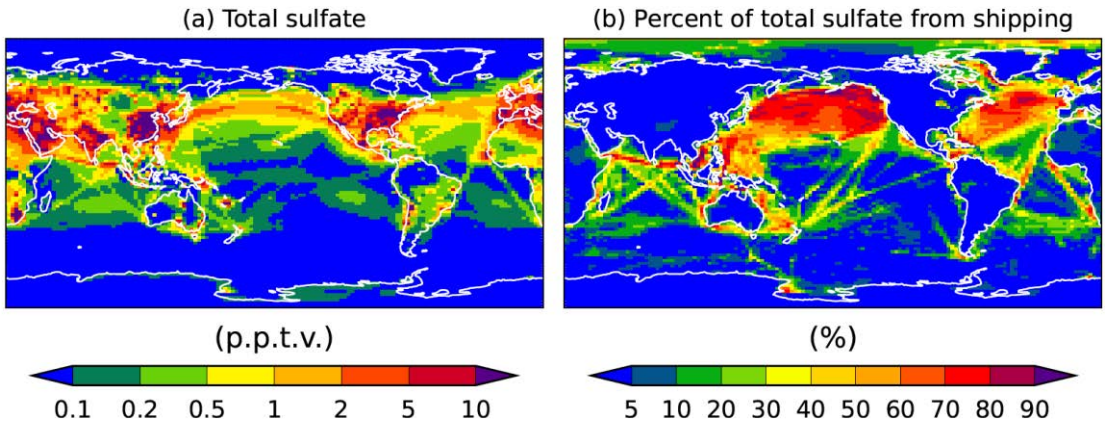


Fig. 9. Total sulfate (parts per trillion by volume) and percentage of total sulfate provided by shipping in simulations of Jin et al.[13] prior to IMO regulations on sulfur content of fuels.

Absorbed solar radiation measured by the CERES satellite instruments, together with the IMO regulations on ship sulfate emissions, provides another indirect way to evaluate aerosol effects. The fraction of total sulfate emissions that arise from ships is large in the North Pacific and North Atlantic (Fig. 9), so study of that region should help quantify the aerosol effect. Fig. 9b suggests that the aerosol effect on cloud albedo is large, although a longer record is needed to overcome the "noise" due to natural variability of clouds.

"This is crazy," you must be saying, "why don't you measure the aerosol climate forcing, instead of this round-about inference via detailed effect on EEI and absorbed solar energy?" Good question. The short answer is that we (the first author and others) tried, but, in career-long failure could not persuade NASA to fly a small satellite with the two instruments (a high precision polarimeter and an infrared spectrometer) needed to monitor the aerosol and cloud microphysics that define the aerosol climate forcing.[14] The short explanation is that NASA preferred large, slow, multi-billion dollar missions as needed to support the budgets of the large NASA Centers. Throw in a climate-denier NASA Administrator, who, in angry response to our persistence, struck out the first line of the NASA Mission Statement "To Understand and Protect the Home Planet."[15]

It's still worth pursuing aerosol and cloud monitoring of the required precision, but the most urgent task is assuring continuation of the CERES or CERES-like monitoring of Earth's radiation balance. As yet there are no firm adequate plans for long-term continuation of these observations. NASA tends to think of itself as an agency that develops scientific and instrumental techniques, while long-term observations should be carried on by others. However, long-term observations are the climate science. It is crucial that NASA make plans to continue these essential measurements.

Measurements in the ocean are equally essential. The Argo program that distributed about 4,000 autonomous, deep-diving floats around the world ocean needs to be continued and enhanced. More measurements are needed especially in the polar regions where some of the most significant climate changes are beginning to occur, changes that will affect the entire planet. The U.S. National Atmospheric and Oceanic Administration (NOAA) has provided a large fraction of the Argo floats, but many other nations contribute; the programs should continue their development.

Without such data, we will be flying blind into a future fraught with dangers. At the very least, we owe young people the knowledge of what we are getting them into.

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PRIMARY RESEARCH ARTICLE

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Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model

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Abstract

Understanding how species might respond to climate change involves disentangling the influence of co-occurring environmental factors on population dynamics, and is especially problematic for migratory species like Pacific salmon that move between ecosystems. To date, debate surrounding the causes of recent declines in Yukon River Chinook salmon (*Oncorhynchus tshawytscha*) abundance has centered on whether factors in freshwater *or* marine environments control variation in survival, and how these populations at the northern extremity of the species range will respond to climate change. To estimate the effect of factors in marine and freshwater environments on Chinook salmon survival, we constructed a stage-structured assessment model that incorporates the best available data, estimates incidental marine bycatch mortality in trawl fisheries, and uses Bayesian model selection methods to quantify support for alternative hypotheses. Models fitted to two index populations of Yukon River Chinook salmon indicate that processes in the nearshore and marine environments are the most important determinants of survival. Specifically, survival declines when ice leaves the Yukon River later in the spring, increases with wintertime temperature in the Bering Sea, and declines with the abundance of globally enhanced salmon species consistent with competition at sea. In addition, we found support for density-dependent survival limitations in freshwater but not marine portions of the life cycle, increasing average survival with ocean age, and age-specific selectivity of bycatch mortality in the Bering Sea. This study underscores the utility of flexible estimation models capable of fitting multiple data types and evaluating mortality from both natural and anthropogenic sources in multiple habitats. Overall, these analyses suggest that mortality at sea is the primary driver of population dynamics, yet under warming climate Chinook salmon populations at the northern extent of the species' range may be expected to fare better than southern populations, but are influenced by foreign salmon production.

KEYWORDS
Bayesian estimation, Chinook salmon conservation, climate change, environmental regulation of survival, life cycle models, marine and freshwater mortality, salmon assessment, Yukon River

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1 | INTRODUCTION

Predicting species' responses to ongoing and future climate change hinges on understanding the role of past environmental variation (Stenseth et al., 2002). However, it is challenging to disentangle the influence of multiple interacting factors on population processes that occur at varying scales in time and space (Levin, 1992). Compounding this challenge is the need to identify critical periods in the life cycle where inter- and intra-specific density-dependent capacity limitations result in survival bottlenecks, and thereby govern population dynamics. To robustly identify the relationship between local- and regional-scale climate and physical processes and observed variation in survival rates, it is necessary to develop statistical models capable of testing alternative hypotheses while also accounting for anthropogenic impacts such as direct or incidental harvest of exploited species. Quantifying environmental regulation of survival is even more challenging for species that cross ecosystem boundaries and migrate between distinct habitats (Piou & Prevost, 2013).

One example is salmon, whose anadromous life history necessitates the evaluation of both freshwater and marine processes on survival, and where harvest in directed fisheries and capture as non-target bycatch requires a holistic approach to quantifying both natural and anthropogenic sources of mortality. Pacific salmon play a unique and important role in ecosystems of the North Pacific. Their migrations move energy and nutrients between marine and freshwater or terrestrial environments (Helfield & Naiman, 2001; Hocking & Reynolds, 2012; Holtgrieve, Schindler, & Jewett, 2009), providing seasonal subsidies for a wide range of species (Bilby, 1996; Field & Reynolds, 2011; Hilderbrand et al., 1999; Scheuerell, Moore, Schindler, & Harvey, 2007). Chinook salmon (*Oncorhynchus tshawytscha*) populations returning to the Yukon River of Alaska provide vast cultural and economic value to indigenous people of the region that subsist on the resource (Brown & Godduhn, 2015). Although northern latitude ecosystems like the Yukon River basin are experiencing some of the most rapid climate change on the globe (IPCC, 2014), we know little about how Chinook salmon populations in Alaska are likely to respond to climate change relative to populations in the southern portion of the species' range (Michel et al., 2015; Ward, Anderson, Beechie, Pess, & Ford, 2015; Yates et al., 2008; Zabel, Scheuerell, Mcclure, & Williams, 2006; Zeug, Albertson, Lenihan, Hardy, & Cardinale, 2011). Flowing more than 3,000 km from Canada to the Bering Sea (Eiler, Masuda, Spencer, Driscoll, & Schreck, 2014), the Yukon River is the fourth largest drainage in North America (855,000 km^2), and until recently was the largest producer of Chinook salmon in the region (Carey, 1980; Gilbert & O'malley, 1921). During the period 1961–2014, the annual harvest averaged 128,740 Chinook salmon and total run size (catch plus those fish that had the opportunity to spawn) averaged near 300,000 fish between 1982 and 1997 (JTC, 2016, Schindler et al., 2013). However, Chinook salmon returns to the Yukon watershed declined by 45% between 1998 and 2010 relative to the preceding 1982–1997 period (Schindler et al., 2013).

This recent period of low Yukon Chinook salmon production has resulted in severe limitations to commercial and subsistence fisheries in the region and difficulty in meeting international treaty obligations for Chinook salmon escapement to Canada, and prompted their listing as a stock of yield concern by the Alaska Board of Fisheries in 2000. The total harvest of Yukon Chinook salmon by both United States and Canadian users declined by 57% after 1997 (JTC, 2016). Among user groups, the US commercial harvest of Yukon Chinook salmon has experienced the largest decline (74%) during the post-1997 period, with complete closure of Alaskan commercial fisheries for Yukon Chinook salmon in 2012 (JTC, 2016). Difficulty meeting the minimum number of spawning individuals required for portions of the Yukon River since 2008 has also resulted in severe restriction of Alaska subsistence harvest, to below the level deemed necessary by the Alaska Board of Fisheries for rural native communities, threatening both food security and a way of life maintained for millenia (Brown & Godduhn, 2015; Schindler et al., 2013). These reductions in Chinook salmon subsistence fishing opportunities combined with low return abundance of chum salmon (*O. keta*), has necessitated the designation of the Yukon River as either a fishery disaster or economic disaster nine times since 1997 by NOAA Fisheries.

Given the importance of subsistence and commercial fisheries for Yukon River Chinook salmon, and the difficulty in managing these fisheries equitably in a trans-boundary river, there is intense interest in understanding the factors driving variation in Chinook salmon survival in both freshwater and marine environments and how populations are likely to respond to future climate change. To date, most studies have examined the effect of freshwater or marine processes in isolation, although salmon span ecosystem boundaries. Neuswanger, Wipfli, Evenson, Hughes, and Rosenberger (2015) evaluated whether a range of habitat variables in the *freshwater* environment could explain observed recruitment patterns for two index stocks of the Middle Yukon, finding that lower productivity of these populations was associated with increased water discharge in natal rivers during juvenile rearing, and postulated that this effect resulted from reduced foraging efficiency during high flow events. Taking a broader perspective, Ohlberger, Scheuerell, and Schindler (2016) investigated coherence in Chinook salmon population dynamics across space, using Dynamic Factor Analysis methods to identify shared trends in the productivity of 15 Alaskan Chinook salmon populations across time and to estimate the influence of indicators in both freshwater and marine environments. With respect to the productivity of the Middle Yukon stocks (the focus of our paper), Ohlberger et al. (2016) found a negative effect of ice out date, a negative but nonsignificant effect of Russian Chinook salmon catch, and a positive but nonsignificant effect of the North Pacific Gyre Oscillation (NPGO).

Evaluation of marine mortality sources for Yukon Chinook salmon has primarily focused on the impact of bycatch in other Bering Sea and Aleutian Islands fisheries (Stram & Harrington, 2009). To quantify the impact of bycatch in the Bering Sea pollock (*Gadus chalcogrammus*) trawl fishery on western Alaska Chinook salmon production, Ianelli and Stram (2014) created an adult equivalency (AEQ)

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model to estimate region-specific impact rates, or proportional losses in Chinook salmon returns after accounting for subsequent age- and year-specific natural mortality. Bycatch mortality was estimated to have averaged 853 (range: 300–1,717) Chinook salmon per year for the Middle Yukon between 1994 and 2012, peaking in 2007. AEQ bycatch mortality for the Upper Yukon during this period averaged 1,771 (610–3,024), representing an annual impact rate (i.e., percent of foregone returns) of 1.74% (0.79–4.03%) for this group of populations (Ianelli & Stram, 2014). Thus, while bycatch does reduce the total number of potentially surviving fish, it does not appear to be the primary driver of declining salmon returns to the Yukon River basin. However, the impact of bycatch mortality in the context of environmentally driven survival variation has not been evaluated.

While successful in testing specific hypotheses about the drivers of variation in Yukon River Chinook salmon production, these previous analyses either: (a) only evaluated hypotheses pertaining to the freshwater environment (Neuswanger et al., 2015), (b) evaluated the influence of anthropogenic (Ianelli & Stram, 2014) or natural (Neuswanger et al., 2015) factors in isolation, (c) did not incorporate potential data sources including juvenile indices of abundance and bycatch numbers and age composition to inform estimation (Ohlberger et al., 2016), or (d) did not account for the influence of observed changes in female age composition and sex ratio over time (JTC, 2016, Schindler et al., 2013) on spawning potential.

In light of these previous analyses, our goal was to evaluate competing hypotheses about the natural and anthropogenic drivers of variation in Yukon Chinook salmon survival in *both* freshwater and marine environments and assess the strength and location of density-dependent capacity limitations, utilizing all available sources of juvenile and adult abundance, age composition, and bycatch data to inform estimation. To accomplish this goal we constructed a novel Bayesian stage-structured population dynamics model, which used Bayesian model selection methods to quantify the level of support from the data for each candidate covariate (O'hara & Sillanpaa, 2009) and Bayesian model averaging (Hoeting, Madigan, Raftery, & Volinsky, 1999; Raftery, Madigan, & Hoeting, 1997) to account for model structural uncertainty in predictions. Finally, we quantified the influence of climate and other factors by simulating the expected differences in survival resulting from fixed changes in the value of each environmental factor, while accounting for both estimation and model structural uncertainty.

2 | MATERIALS AND METHODS

2.1 | Population dynamics model

The population dynamics model tracked cohorts of Chinook salmon from specific brood years forward in time across sequential life stages. The number of Chinook salmon surviving through the current stage (s) depended upon the abundance of individuals from brood year y, surviving the previous stage s-1, of population p ($N_{y,s\text{-}1,p}$), and the year, stage, and population-specific survival rate $SR_{y,s,p}$:

$$N_{y,s,p} = N_{y,s-1,p} SR_{y,s,p} \quad (1)$$

Survival rate though each life stage (Figure 1) was represented by a Beverton-Holt transition function (Moussalli & Hilborn, 1986).

The Beverton-Holt equation (Beverton & Holt, 1957) provides a useful approximation for density-dependent survival of individuals, and has been utilized in a wide range of life cycle models for Chinook salmon (see Scheuerell et al., 2006, Honea et al., 2009, and Battin et al., 2007). The survival rate was calculated as:

$$SR_{y,s,p} = \frac{p_{y,s,p}}{1 + \frac{p_{y,s,p} N_{y,s-1,p}}{k_{s,p}}} \quad (2)$$

where the productivity parameter ($p_{y,s,p}$) represented the maximum survival rate in the absence of density-dependent compensation, and the capacity parameter ($k_{s,p}$) described the maximum number of individuals that could potentially survive through the stage.

Stage and population-specific productivity parameters ($p_{y,s,p}$) were treated as time-varying functions of the environmental covariates under evaluation. Each productivity parameter was an inverse-logit function of a basal productivity $\beta_{s,p,0}$, or the average survival rate at low density across years (in logit space), and the sum of covariate effects

$$p_{y,s,p} = \frac{1}{1 + \exp\left(-\beta_{s,p,0} - \sum_{c=1}^{Nc_{s,p}} \beta_{p,c} X_{t,c}\right)}$$
$$t = y + \delta_c \quad (3)$$

where covariate c values at time t ($X_{t,c}$) were multiplied by coefficients ($\beta_{p,c}$) describing their respective influence on stage and population-specific survival rates. The parameter δ_c defined the difference between the brood year y and the calendar year t in which the cohort interacted with each covariate, and $Nc_{s,p}$ was the number of productivity covariates linked to each population in each stage (See Table 1 for a description of covariates and stage associations, Supporting Information Figure S1 for the time series of covariate values).

The Chena and Salcha Chinook salmon populations of the Middle Yukon River were selected as index populations given the breadth of data available and their use in previous evaluations of Yukon River Chinook salmon production dynamics (see Neuswanger et al., 2015 and Ohlberger et al., 2016). These populations are among the largest contributors to the total US Chinook salmon production in the Yukon River and have been extensively monitored for decades (Brown, Finster, Henszey, & Eiler, 2017). Individuals from these populations primarily spend 1 year in freshwater before migrating to sea in the spring and summer (brood year + 2) and remain at sea for 1–5 years before maturing, primarily returning as 5 and 6-year olds (European Age: 1.3 and 1.4).

The life cycle of these populations was modeled as seven stages describing distinct locations, time periods, or ontogenetic phases: (1) "upstream" tracking survival during juvenile rearing in tributaries in brood year +1, (2) "downstream/nearshore" describing survival

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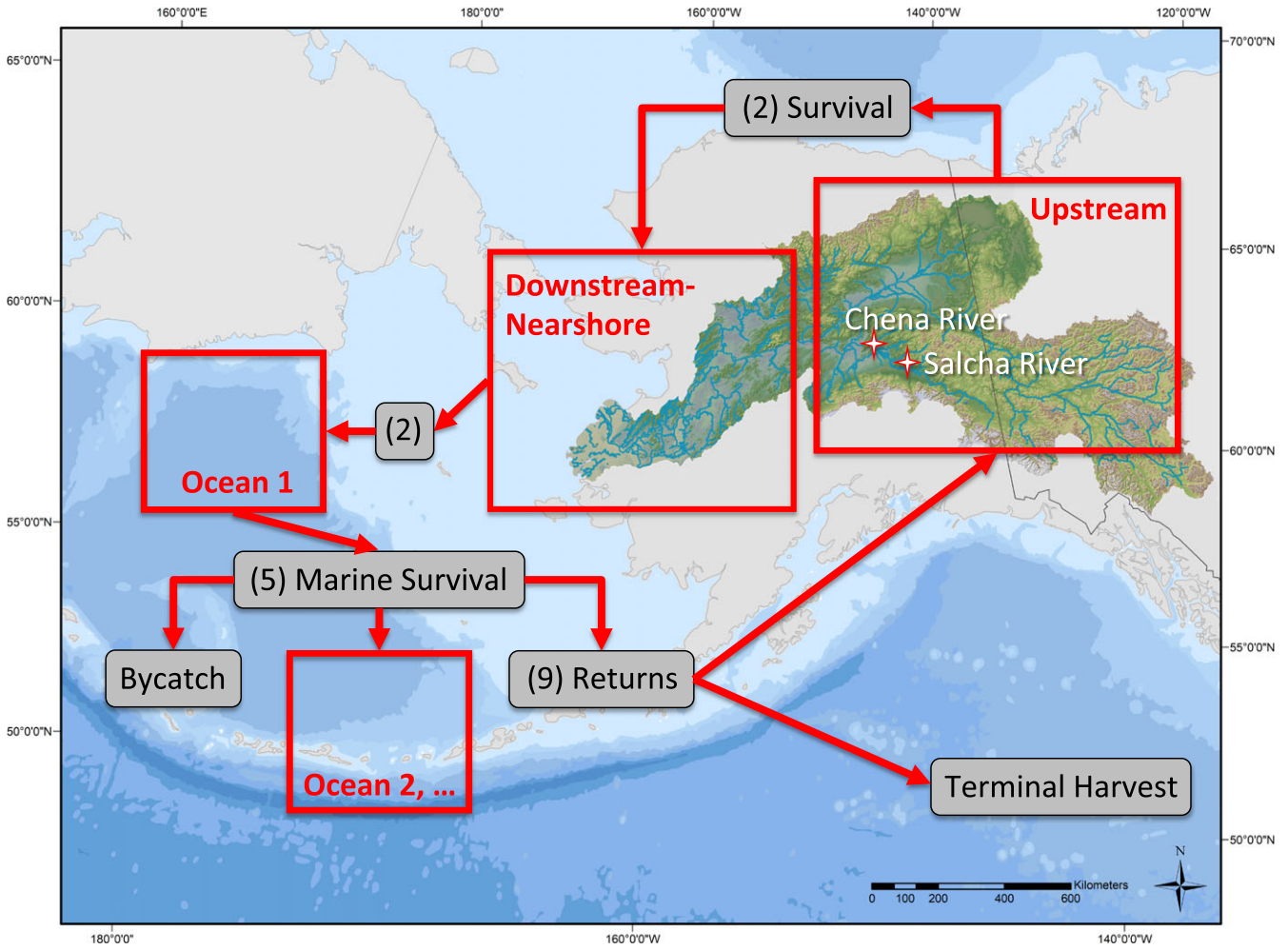


FIGURE 1 Schematic map of the Yukon River Chinook salmon population dynamics model. Red boxes identify model stages and gray boxes describe stage transitions or removals from the system. Numbers in parenthesis reference model equations described in the text. It should be noted that red boxes describing model stages are meant to generally reflect model structure and spatial orientation, but do not reference the exact location of Chinook salmon at any given time

through the Yukon mainstem and early ocean entry (brood year +2) prior to the juvenile offshore survey, and (3–7) separate stages representing survival through five potential years at sea (Figure 1). Two capacity parameters ($k_{s,p}$) were estimated for each population, one for the freshwater (1–2) and the other for the marine (3–7) model stages, based on the a priori expectation that capacity limits should be different in these two environments. Conversely, separate basal productivities ($\beta_{s,p,0}$) were estimated for each freshwater stage (1 and 2) and the first marine stage (3), while the basal productivities for subsequent marine stages (4–7) were a linear function of the basal productivity in the first marine stage (3),

$$\beta_{s\in 4:7,p,0} = \beta_{s=3,p,0} + \omega_p(s-3) \tag{4}$$

where ω_p is the change in basal productivity across marine stages. The formulation of marine basal productivities (Equation 4) allowed for a monotonic change in marine survival as Chinook aged, while reducing the number of estimated parameters by three. In addition, this permitted us to test the hypothesis that the base survival rate for Chinook salmon changed as a function of growth at sea, independent of time-varying environmental effects.

The abundance ($N_{y,s,p}$) of Chinook salmon cohorts was tracked forward in time across model stages based on predicted survival rates (Equations 2 and 3), independent of whether the stage was in the freshwater or marine portion of the life cycle. However, for marine model stages it was also necessary to account for both the maturation process and bycatch mortality in the BSAI pollock fishery (Ianelli & Stram, 2014; Stram & Ianelli, 2014). Given that natural and bycatch mortality are operating concurrently, this was represented as a continuous process (Doubleday, 1976; Pope, 1974). The number of individuals surviving through an ocean stage:

$$\begin{aligned} N_{y,s,p} &= N_{y,s-1,p}e^{-(S_{a,p}F_{t,p}+M_{y,s,p})}(1-\phi_{a,p}) \\ M_{y,s,p} &= -\ln(\mathrm{SR}_{y,s,p}) \end{aligned} \tag{5}$$

was a function of time-varying natural mortality ($M_{y,s,p}$) and the instantaneous fishing mortality rate ($F_{t,p}$) in calendar year t for population p, scaled by the ocean-age a

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TABLE 1 Description of environmental covariates. Months are the period for which each covariate is derived, while the brood year offset describes the difference between the year of covariate influence and the brood year for each cohort. Covariate values were standardized based on the mean and standard deviation (*SD*) of each time series

Covariate	Description	Months	Data Origin	Website	Stage	Brood Year Offset	Mean	SD
chena.discharge	Average monthly discharge for Chena River (cfs^{-1})	May - August	USGS Guage #15493000: CHENA R NR TWO RIVERS AK	http://waterdata.usgs.gov/nwis/inventory?agency_code=USGS&site_no=15493000	Upstream	1	1354	415
salcha.discharge	Average monthly discharge for Salcha River (cfs^{-1})	May - August	USGS Guage #15484000: SALCHA R NR SALCHAKET AK	http://waterdata.usgs.gov/nwis/inventory?agency_code=USGS&site_no=15484000		1	3062	824
ice.tanana	Date of ice out on Tanana River at Nenana (DOY)		Nenana Ice Classic: Tanana River Ice Annual Breakup Dates, Version 1. 1960-2015. Boulder, Colorado USA. NSIDC	http://nsidc.org/data/NSIDC-0064/versions/		1	121.8	5.9
temp.incub	Average air temperature during incubation (°F)	November - February	Western Regional Climate Center	http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak2968		0	-2.43	3.91
temp.juvi	Average air temperature during juvenile rearing (°F)	May - August				1	57.43	1.78
ice.yukon	Date of ice out on Yukon River at Dawson, YT (DOY)			http://www.yukonriverbreakup.com/statistics	Downstream/ Nearshore	2	125.2	4.7
wind.stress.spring	Along-peninsula component of the wind stress in spring ($N\ m^{-2}$)	May - June	Atmosphere Indices, Bering Climate, at_UPWs.nc Stabeno et al. (2002)	http://www.beringclimate.noaa.gov/data/index.php		2	0.03	0.07
wind.mixing.june	Mean wind mixing index at M2*	June - July	Atmosphere Indices, Bering Climate, at_WndMix.nc Stabeno et al. (2001)			2	0.0152	0.0048
se.bs.may.sst	Mean May sea surface temperature in the southeastern Bering Sea	May	Ocean Indices, Bering Climate, oc_MaySST.nc			2	2.18	0.85
arctic.dipole.winter	Winter Arctic Dipole index	December - February	Climate Indices, Bering Climate, in_ADIwin.nc			2	0.02	0.54
slp.spring	Mean spring sea level pressure in the Bering Sea	April - June	Atmosphere Indices, Bering Climate, at_BSPIsp.nc			2	1101	2.1
ice.retreat	Ice Retreat Index: Number of days with ice cover after March 15 at the M2*	March - May	Ocean Indices, Bering Climate, oc_IRI.nc Hunt et al. (2011)		Ocean 1	3	17.29	17.51
winter.prib.temp	Sea surface temperature at the Pribilof Islands (°C)	January - March	Ocean Indices, Bering Climate, oc_PISST.nc			3	-0.058	0.29
m2.fav.wind	Number of days with winds between 4.8 and 9.5 m/s from at M2*	May - mid-July	Atmosphere Indices, Bering Climate, at_NODM2.nc Megrey and Hinckley (2001)			3	37.06	4.49
slp.winter	Mean winter sea level pressure in the Bering Sea	December - March	Atmosphere Indices, Bering Climate, at_BSPIw.nc			3	1006.27	2.01
npgo	Annual average North Pacific Gyre Oscillation index		Di Lorenzo et al (2008)			3	0.11	1.06
wind.stress.winter	Along-peninsula component of the wind stress in winter ($N\ m^{-2}$)	November - April	Atmosphere Indices, Bering Climate, at_UPW.nc			3	0.01	0.05
arctic.oscillation	Winter Arctic Oscillation Index	December - February	Climate Indices, Bering Climate, in_AO.nc			3	0.18	1.02
el.nino	Winter multivariate ENSO index	December - January	Climate Indices, Bering Climate, in_ENSO.nc			3	0.19	0.66
alaskan.index	Alaska Index, relative to 1961-2000 index values	December - March	Climate Indices, Bering Climate, in_AI.nc			3	0.17	0.86
jpn.hat.chum	Japanese hatchery chum abundance (millions)		Ruggerone and Irvine (2015), North Pacific Anadromous Fish Comission	http://www.npafc.org/new/publications/Documents/PDF%202015/1594(USA+Canada).pdf		3	56.44	14.57
pink.total	Total North Pacific pink salmon abundance (wild + hatchery, in millions)					3	388.08	103.43

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specific selectivity ($S_{a,p}$). The calendar year t was the brood year plus an offset for the specific stage ($t = y + \rho_s$), the ocean age was the current stage s minus the number of freshwater stages ($a = s - n_{fw}$), and φ_a was the ocean-age specific probability of maturing. The age-specific maturation probability was represented by a modified logistic function:

$$\phi_{a,p} = \frac{1}{1 + e^{\lambda_p(5-a)+\ln(1/0.99-1)}} \quad (6)$$

where λ_p was a population-specific parameter controlling the maturation schedule, and estimated from the age composition data and assumed to be time-invariant. This simplified logistic function ensures the majority of remaining individuals mature in their fifth year at sea so as to agree with the maximum marine residency observed in these populations and simulated in the model, and requires estimation of one less parameter than the standard logistic function.

Immature and maturing Yukon River Chinook salmon are caught in Bering Sea and Aleutian Islands groundfish trawl fisheries. Bycatch of Chinook salmon in the BSAI pollock trawl fishery was calculated as,

$$C_{t=y+\rho_s,a=s-n\,f_w,p} = C_{y,s,p} = \left(\frac{S_{a,p}F_{t,p}}{M_{y,s,p} + S_{a,p}F_{t,p}}\right) N_{y,s-1,p}\left(1 - e^{-(S_{a,p}F_{t,p}+M_{y,s,p})}\right) \quad (7)$$

and described by brood y or calendar t year, and stage s or ocean age a, with appropriate offsets. Chinook salmon bycatch data from BSAI trawl fisheries were not available prior to 1991 to inform estimation of bycatch fishing mortality rates ($F_{t,p}$); therefore, annual fishing mortality rates were treated as random effects drawn from a population-specific lognormal distribution.

$$F_{t,p} \sim \log\text{normal}(\mu_p, \nu_p) \quad (8)$$

Hyperparameters μ_p and ν_p are the lognormal mean and variance describing the expected distribution of annual bycatch fishing mortality rates, effectively specifying the bycatch rate in the absence of observation, and were estimated from the data.

The number of individuals returning to spawn, termed "spawners", ($R_{t,a,p}$) was calculated as the number surviving marine and bycatch mortality who then matured, less those caught in terminal commercial, recreational, and subsistence fisheries,

$$R_{t=y+\rho_s,a=s-nf_w,p} = N_{y,s-1,p}e^{-\left(S_{a,p}F_{t,p}+M_{y,s,p}\right)}\left(\phi_{a,p}\right)\left(1 - U_{t,p}\right) \quad (9)$$

where $U_{t,p}$ is the year-specific terminal harvest rate estimated by Savereide and Huang (2014) for the Chena and Salcha populations. $U_{t,p}$ was estimated outside of our model and assumed to be known without error. The number of returning individuals $R_{t,a,p}$ was the model-predicted spawning abundance.

The number of eggs produced for a given number of returning individuals was a function of the observed sex ratio, or the female proportion of the spawning abundance for each population in each year $\pi_{t,p}$, and average observed age-specific fecundity $f_{a,p}$.

$$E_{t,p} = \pi_{t,p}\sum_{a=1}^{5}\left(R_{t,a,p}f_{a,p}\right) \quad (10)$$

Population-specific fecundity at age $f_{a,p}$ was found by regressing observed fecundity (Jasper & Evenson, 2006) against length for each population and predicting fecundity for the average observed length of each ocean age class. The abundance of juveniles in the next cohort that survived to the end of the first stage was simply the total egg production ($E_{t,p}$) multiplied by the appropriate survival rate.

Both the terminal harvest rate and age-specific fecundity were estimated outside of our model and assumed known without error and treated as fixed constants.

The abundance of juveniles in the next cohort that survived to the end of the first stage was simply the total egg production ($E_{t,p}$) multiplied by the appropriate survival rate (Equation 11). Population dynamics were modeled for brood years 1980–2007 (return years: 1983–2014). Spawning abundances prior to the beginning of the time series of escapement observations (1980–1986) were needed to seed the initial population dynamics and were estimated as independent parameters based on their contribution to escapement in subsequent years.

$$N_{y=t,s=1,p} = S_{y,s=1,p}E_{t,p} \quad (11)$$

2.2 | ESTIMATION METHODS AND DATA

The population dynamics model was fit to available data using Bayesian methods, and implemented in JAGS (Plummer, 2013) using the R2jags (Su & Yajima, 2015) package in R. Models were fit to data for each population separately, with five chains run for 1,000,000 iterations with a thinning rate of 1/500. The initial 500,000 iterations were discarded as a burn-in period. Convergence of the chains was diagnosed using the Gelman-Rubin statistic (Brooks & Gelman, 1998) and visual inspection of the coherence in the distribution of posterior samples from each chain.

A primary goal of this analysis was to integrate all available sources of data in our assessment of Yukon Chinook salmon population dynamics. Therefore, estimation of model parameters was informed by fitting to five separate data types with appropriate likelihoods. Two indices of abundance were available for the Chena and Salcha populations: (i) spawning abundance ($A_{t,p}$) of population p in year t from mark-recapture experiments and counting tower observations (Savereide & Huang, 2014), and (ii) absolute abundance of juvenile Chinook salmon from the Bering Aleutian Salmon International Survey ($J_{t,p}$), operated by the NOAA Alaska Fisheries Science Center since 2003 (Murphy et al., 2016). The juvenile index of abundance provided by Murphy et al. (2016) was not specific to the Chena and Salcha populations, so this index needed to be scaled based on available data. Genetic stock identification (GSI) data (J. Murphy, unpublished data) was used to translate the total juvenile catch per unit effort into an index of juvenile Chinook salmon from the Middle Yukon River (MYR). Population-specific indices of juvenile abundance were calculated from the MYR index based on the observation that an average of 42.7% of radio-tagged MYR Chinook salmon returned to the Tanana drainage (Eiler et al., 2014), and the average proportion of total Tanana escapement to the Chena (0.397)

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and Salcha (0.603) rivers. Observation error for both adult and juvenile indices of abundance was assumed log-normally distributed,

$$\begin{aligned}\ln(A_{t,p}) &\sim \text{Normal}\left(\ln\left(\hat{A}_{t,p} = \sum_{a=1}^{5} R_{t,a,p}\right), \sigma^2_{\text{adult},p}\right)\\ \ln(J_{t,p}) &\sim \text{Normal}\left(\ln\left(\hat{J}_{t,p} = N_{y=t-\rho_{s=2},s=2,p}\right), \sigma^2_{\text{juvenile},p}\right)\end{aligned} \tag{12}$$

with log-normal variance parameters for the juvenile ($\sigma^2_{\text{juvenile},p}$) and adult ($\sigma^2_{\text{adult},p}$) indices estimated from the data. The model was fit to spawning abundance data 1987–2010 and the juvenile index of abundance 2003–2009.

Chinook salmon bycatch data for the BSAI pollock fishery were available from the North Pacific Fisheries Management Council and total annual bycatch was allocated to MYR bycatch using GSI data (Guthrie, Nguyen, & Guyon, 2016; Ianelli & Stram, 2014), and scaled to the population level as described above. Bycatch observation error was assumed log-normally distributed, when fit to bycatch data 1991–2010,

$$\ln(c_{t,p}) \sim \text{Normal}\left(\ln\left(\sum_{a=1}^{5} C_{t,a,p}\right), \sigma^2_{\text{bycatch},p}\right) \tag{13}$$

where $c_{t,p}$ is the observed bycatch in calendar year t scaled to the population level, and $\sigma^2_{\text{bycatch},p}$ is the population-specific log-normal variance parameter estimated from the data.

Age composition data were available from samples of both adult Chinook salmon on the spawning grounds and BSAI bycatch (Ianelli & Stram, 2014). Bycatch at age was calculated by Ianelli and Stram (2014) based on time-area stratified and combined age-length keys and bycatch length compositions from the fishery observer program. The estimation model was fit to age composition data for spawning adults 1987–2010 and bycatch 1991–2010 assuming the sampling process is best described by a Dirichlet-multinomial mixture,

$$\begin{aligned}\widehat{P}_{i=\text{adult},t,a,p} &= R_{t,a,p} / \sum_{a=1}^{5} R_{t,a,p}\\ \widehat{P}_{i=\text{bycatch},t,a,p} &= C_{t,a,p} / \sum_{a=1}^{5} C_{t,a,p}\\ \alpha_{i,t,a,p} &\sim \text{Dirichlet}\left(w_i \cdot \widehat{P}_{i,t,a,p}\right)\\ S_{i,t,a,p} &\sim \text{Multinomial}\left(a_{i,t,a,p}, \sum_{a=1}^{5} S_{i,t,a,p}\right)\end{aligned} \tag{14}$$

where $\widehat{P}_{i,t,a,p}$ are the model-predicted age composition proportions from sample type i, $S_{i,t,a,p}$ are the spawning ground or bycatch compositions, and w_i is the weighting parameter for each sample type. The Dirichlet-multinomial likelihood has been advanced as a superior alternative to traditional multinomial likelihood for compositional data, because it allows for the overdispersion associated with the sampling process (Francis, 2014; Thorson, Johnson, Methot, & Taylor, 2016). Following the suggestions by Francis (2011), we chose to fix the weighting parameters at a level that reduced conflict between abundance and age composition data ($w_{i=\text{adult}} = 50, w_{i=\text{bycatch}} = 5$), rather than using model-based estimates of w_i that tended to preferentially fit age composition data. Optimal fixed values for Dirichlet-multinomial weights were found by iteratively fitting the model while increasing weights, until the point that the model's ability to fit the two abundance indices was negatively impacted. While there is still extensive debate within the stock assessment literature about optimal methods for the weighting of composition data (see. Francis, 2017; Hulson, Hanselman, & Quinn, 2012; Punt, 2017), we believe the iterative method employed here provides a reasonable balance for inference from both age composition and abundance data.

2.3 | BAYESIAN MODEL SELECTION

To select the most parsimonious set of explanatory covariates (Table 1, Supporting Information Figure S1) and generate predictions that are robust to model structural uncertainty, we used Bayesian model selection methods. Specifically, we employed a random effects version of the indicator variable method described by Kuo and Mallick (1998), where the covariate influences in Equation (3) ($\beta_{p,c}$) are the product of the estimated covariate effect ($\varepsilon_{p,c}$) and an indicator variable ($\tau_{p,c}$):

$$\begin{aligned}\beta_{p,c} &= \tau_{p,c}\varepsilon_{p,c}\\ \tau_{p,c} &\sim \text{Bernouli}(\upsilon_p)\end{aligned} \tag{15}$$

The indicator variable is Bernoulli distributed with a population-specific prior inclusion probability of υ_p that was estimated as a hyperparameter (Table 2). For each sample from the posterior, $\tau_{p,c}$ takes a value of 0 or 1, functionally including or excluding that covariate in each step. As such, the average value of $\tau_{p,c}$ across posterior samples represents the inclusion probability for each covariate for each population, or the weight of evidence from the data for its inclusion. For this analysis, we implemented a random effects version of the Kuo and Mallick (1998) method by placing a hyperprior on γ_p, the standard deviation of the normal prior on covariate effects $\varepsilon_{p,c}$ (Table 2). It has been suggested that the random effects prior structure is optimal because it helps in combatting Lindley's paradox (Lindley, 1957) and the resulting potential for underselection of candidate variables (Lawrence, Gramacy, Thomas, Buckland, & Freckleton, 2013; Link & Baker, 2006). In their review and comparison of Bayesian variable selection methods, O'hara and Sillanpaa (2009) found the random effects version of the Kuo and Mallick (1998) method to be unbiased and have lower variance in estimated effects, when compared to alternative Bayesian model selection methods. Most importantly, Raftery et al. (1997) highlight that ignoring model structural uncertainty results in underestimation of uncertainty in quantities of interest, and Bayesian model averaging across a set of models is likely to result in better inference than any single model in most cases (Hoeting et al., 1999; Madigan & Raftery, 1994).

2.4 | PRIORS

Prior distributions for estimated model and hyperparameters (Table 2) were chosen to be uninformative or weakly informative when transformations were considered. The exception was the hyperprior for the prior on covariate inclusion probability υ_p, which

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was Beta distributed to scale 0–1 with an expected value of 0.2 (95% probability range 0.03–0.48). By assuming this weakly informative prior on υ_p, rather than using a fixed value, we allowed the model to learn about the optimal degree of sparsity in terms of covariate inclusion while providing a moderate penalty on overfitting. The prior specified for ω_p, the change in basal productivity across ocean stages (Equation 4), was normally distributed around zero indicating an a priori hypothesis of no change in survival across marine years.

2.5 | COVARIATES

The environmental covariates included in this analysis (Table 1, Supporting Information Figure S1) represent a priori hypotheses for the processes driving variation in Yukon River Chinook salmon survival rates. We evaluated five covariates describing four hypotheses about survival during incubation and early juvenile rearing, each relating to habitat conditions and the onset of primary production in spring, as approximated by the date of ice breakup. Separate water discharge data were available for the Chena and Salcha rivers, while all other covariates were not stock specific. Covariates for the downstream and nearshore stage addressed conditions in the lower Yukon River and the Bering Sea at ocean entry, prior to the juvenile offshore survey (Table 1, Supporting Information Figure S1). These included the date of Yukon River ice out in the year of ocean entry, the Arctic Dipole Index during the months preceding ocean entry, and the Bering Sea sea level pressure (SLP) and sea surface temperature (SST) in the spring of ocean entry. Also explored were springtime wind stress, which quantifies transport of nutrient-rich waters through Unimak Pass (Stabeno, Reed, & Napp, 2002), and the level of wind mixing in June, which plays an important role in determining whether nutrient-rich water from lower in the water column will be moved into the photic zone and foster continued plankton blooms during the summer (Stabeno, Bond, Kachel, Salo, & Schumacher, 2001).

Marine environmental covariates quantified a wide range of oceanographic, atmospheric, climatic, and biotic factors (Table 1, Supporting Information Figure S1). Oceanographic processes included the timing of ice retreat in the southeastern Bering Sea, given implications for the timing and biomass of the spring plankton bloom and trophic structure of the Bering Sea (Hunt et al., 2002, 2011), and winter SST at the Pribilof Islands given its observed influence on western Alaska Chinook salmon growth (Mcphee, Leon, Wilson, Siegel, & Agler, 2016; Siegel, Mcphee, & Adkison, 2017) and correlation with recruitment of several groundfish species (Mcfarlane, King, & Beamish, 2000) as potential prey. Covariates related to the marine atmosphere included SLP and wind stress during the first winter at sea given their observed importance for ecosystem productivity, and the duration of May–early June wind vectors in the southern Bering Sea (at the NOAA-PMEL M2 OA mooring: 56.87°N, −164.06°W) that promote favorable feeding conditions for larval pollock (Megrey & Hinckley, 2001). Marine climate-related covariates included the North Pacific Gyre Oscillation (Di Lorenzo et al., 2008), which is correlated with fluxes in salinity, nutrients and *chlorophyll-a* concentrations, the Arctic Oscillation Index describing dominant trends in North Pacific SLP, and the Alaska Index which measures the atmospheric circulation driving variation in ice cover.

Two covariates were included to test the hypothesis that competition with other salmonid species in the marine environment may influence survival: the return abundance of Japanese hatchery chum salmon (*Oncorhynchus keta*) and the total North Pacific return abundance of pink salmon (*Oncorhynchus gorbuscha*; hatchery and wild). Return abundances were included rather than hatchery releases because we believe the return abundance better quantifies potential competition, compared with hatchery releases which are separated from the period of potential interaction in the Bering Sea by the period of highly variable early marine survival.

All covariates were z-standardized by subtracting the mean and dividing by the standard deviation of the 1980–2010 time series. The covariates included in these analyses were prescreened to ensure that absolute Pearson correlation among covariates did not exceed 0.6 (Table 1, Supporting Information Figure S1).

2.6 | SENSITIVITY ANALYSIS: SURVIVAL RATES AND POPULATION PRODUCTIVITY

We conducted a sensitivity analysis to compare the effects of different covariates on expected survival and population productivity (recruits-per-spawner), while accounting for model structural uncertainty (e.g., inclusion probabilities), estimation uncertainty, bycatch mortality, and survival through subsequent life stages. We simulated Bayesian model averaged predictions by: (a) Drawing 5,000 sets of model parameters from the joint posterior to preserve posterior correlation (including indicator variables controlling parameter inclusion), (b) Simulating survival through one complete life cycle for each of these parameter sets while iteratively increasing each covariate by one standard deviation from its long-term mean, and (c) Comparing results to a "base case" with all covariates at their long-term (31-year) mean. In all scenarios the average spawning abundance, proportion of females, age of females, and adult harvest rate were used, as well as the predicted mean for the distribution of hierarchical bycatch fishing mortality rates.

3 | RESULTS

Estimated effects and inclusion probabilities for covariates together suggest that variation in the survival of the Chena and Salcha populations is better explained by processes in the marine rather than the freshwater environment. A comparison of model predictions to the observed data for both populations (Figure 2) shows that the model generally captured the variation in all data sources with reasonable accuracy and limited bias. Of note is a tendency for the model to underpredict the proportion of 2-ocean individuals in the escapement of both populations, and to a lesser extent

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TABLE 2 Estimation model parameter descriptions and specified priors

Parameter	Description	Prior
$\beta_{s\in 1:3,p,0}$	Basal productivity for stages 1–3	$\sim \text{Normal}\left(0, 1.5^2\right)$
ω_p	Slope of basal productivity across marine stages	$\sim \text{Normal}\left(0, 0.5^2\right)$
$\varepsilon_{p,c}$	Environmental covariate effect	$\sim \text{Normal}\left(0, {\gamma_p}^2\right)$
γ_p	Standard deviation of prior distribution on covariate effect*	$\sim \text{gamma}(1, 1)$
$\tau_{p,c}$	Covariate indicator variable	$\sim \text{Bernouli}(\upsilon_p)$
υ_p	Prior inclusion probability for covariate indicator variable*	$\sim \text{Beta}(2, 8)$
$k_{s\in(1:2,3:7),p}$	Basal capacity in log space	$\sim \ln\left(\text{Uniform}\left(10^3, 10^7\right)\right)$
λ_p	Maturation parameter	$\sim \text{Uniform}(0, 5)$
μ_p	Log-normal mean for bycatch mortality rate distribution*	$\sim \text{Uniform}(0, 4)$
ν_p	Log-normal standard deviation for bycatch mortality rate distribution*	$\sim \text{Unifrom}\left(10^{-3}, 2\right)$
$F_{t\in 1983:2014,p}$	Bycatch fishing mortality rate	$\sim \text{lognormal}(\mu_p, \nu_p)$
$S_{a\in 1:4,p}$	Bycatch selectivity for 1–4 years at sea	$\sim \text{Uniform}(0, 1)$
$R_{t\in 1980:1986,a,p}$	Initial spawning abundance	$\sim \text{Uniform}\left(1, 10^4\right)$
$\sigma_{\text{adult},p}$	Log-normal *SD* for spawning abundance observation error	$\sim \text{Uniform}(0, 5)$
$\sigma_{\text{juvenile},p}$	Log-normal *SD* for juvenile index observation error	$\sim \text{Uniform}(0, 5)$
$\sigma_{\text{bycatch},p}$	Log-normal *SD* for bycatch observation error	$\sim \text{Uniform}(0, 5)$

Note: * indicates model hyperparameters. Population-specific capacity parameters $k_{s,p}$ are estimated for the grouped freshwater (1–2) and marine (3–7) stages.

the proportion of 2 and 3-ocean individuals in the age composition of bycatch.

3.1 | Estimated covariate effects

Covariate effects describe the direction and magnitude of influence each environmental factor is predicted to have on Chinook salmon survival (Figure 3a,b). Generally, there was greater uncertainty in the estimated effect of covariates in the upstream relative to downstream/nearshore and marine stages. While the direction of covariate effects was similar for the two populations, the magnitude of these estimated effects sometimes differed. Strong (95% CI not overlapping zero) negative effects of ice-out date on the Yukon River in the year of ocean entry and of Japanese hatchery chum abundance and strong positive effects of wintertime temperatures at the Pribilof Islands during the first winter at sea are estimated for both populations (Figure 3a,b). During the first year at sea, increased duration of winds, which is favorable for juvenile Pollock growth on the Bering Sea shelf (Megrey & Hinckley, 2001), is also estimated to have a strong positive effect on survival of Chena Chinook salmon, while a higher North Pacific Gyre Oscillation index is associated with increased survival of the Salcha population (Figure 3b).

The effect of wind stress along the Alaska Peninsula in both spring and winter was estimated to be negative for both populations, indicating that marine survival is higher during periods of stronger easterly winds along the peninsula (negative wind stress values), which support a greater flux of nutrient-rich waters northward through Unimak Pass and into the Bering Sea (Stabeno et al., 2002). The two populations differed in the sign of covariate effects for the date of ice out on the natal tributary (Tanana River) in the year of emergence, for wintertime SLP, and for the Arctic Oscillation index; however, in all three cases the effects were not strong, with 50% or 95% CIs overlapping zero (Figure 3a,b). While the direction and magnitude of covariate effects are informative, they must be considered in conjunction with covariate inclusion probabilities (below).

3.2 | Model selection: covariate inclusion probabilities

The estimated inclusion probability for each environmental covariate (Figure 3c,d) describes the weight of evidence from the data for each hypothesis and can be loosely interpreted as 'significance' for a given covariate. For the Salcha population, high (>0.75) inclusion probabilities are estimated for 3 of 21 candidate covariates: Yukon River ice-out date, Pribilof Island wintertime temperature, and Japanese hatchery chum abundance. A larger proportion of covariates exhibited strong support from the data (five of 21) for the Chena population, including the three selected for the Salcha population, plus the Arctic Dipole index during the winter prior to ocean entry and the strength of favorable winds onto the Bering Shelf during the first winter at sea (Figure 3c,d). The prior probability of covariate inclusion (υ_p) was updated from its prior expectation (0.2) by each population's data likelihood, with estimated values of 0.38 (95% CI: 0.17–0.63) for the Chena River and 0.35 (0.15–0.60) for the Salcha River.

3.3 | Sensitivity analysis: covariate effects on survival

Covariate effects were quantified by simulating population dynamics while iteratively adjusting covariate values. Figure 4 illustrates both

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the percent difference in egg-to-adult survival (a, b) and expected recruits-per-spawner (c, d) when each covariate is increased by one standard deviation from its long-term average while fixing all other covariates at their respective averages. For each 6.6-days later Yukon River ice breakup occurs (1 *SD* from long-term mean), survival is predicted to be 31.0% lower on average for Chena Chinook salmon, and 28.6% lower for the Salcha population. Chena Chinook salmon survival at ocean entry is also found to be closely associated with variation in the Arctic Dipole wind pattern, with each one standard deviation increase in the index predicted to result in a 27.3% increase in egg-to-adult survival. For wintertime temperature at the Pribilof Islands, each 0.29°C increase is predicted to raise survival of Chena Chinook salmon by 32.4% and Salcha Chinook salmon by 22.6% on average. Competition with Japanese hatchery chum salmon is predicted to have a large impact on survival of both Chinook salmon populations. For each 14.6 million increase in chum adult returns, egg-to-adult survival is expected to be 30.2% lower on average for Chena and 18.9% lower for Salcha Chinook salmon (Figure 4a,b).

3.4 | Habitat capacity, age-specific marine survival, and bycatch selectivity

In addition to environmental effects, other model parameters provide insights into Yukon River Chinook salmon habitat capacity, patterns in marine survival and bycatch mortality. Capacity parameters describe density-dependent limitations on Chinook salmon survival due to intraspecific competition, and were estimated for the upstream and downstream/nearshore (first and second) stages separately from the marine stages. While no capacity limitation is discernable for the marine stages, well-defined capacities for the early life history stages (1–2) are estimated for both populations (Figure 5d,e). In addition to capacity limitations, the population dynamics model also allowed for changes in marine survival as Chinook salmon grow in the ocean through the slope parameter ω_p. Estimates of ω_p are positive for both populations, +0.59 with 95% CI of 0.16–1.31 for the Chena River and +0.50 (0.16–1.04) for the Salcha River, indicating strong evidence for increasing marine survival of Chinook salmon with ocean age (Figure 5c).

Additional marine mortality resulting from BSAI Pollock fishery bycatch was estimated by fitting to bycatch age compositions and Chinook salmon bycatch numbers scaled to the population level. Selectivity of bycatch mortality is estimated to increase with ocean age in both populations, with extremely low bycatch potential for 1-ocean individuals (Figure 5b). In practice, the selectivity of 5-ocean individuals was fixed to be equal to that of four-ocean individuals to improve convergence. Age-specific differences in capture probability may be due to the size-specific selectivity of the gear itself, or more plausibly due to differences in the degree of spatial overlap between salmon and the trawl fleet, with 1-ocean individuals distributed further north and thus at lower risk.

4 | DISCUSSION

Understanding how populations will respond to future environmental change is necessary for risk assessment and conservation planning, yet is contingent upon disentangling the effect that co-occurring natural and anthropogenic factors have on survival. Leveraging all available life history information in a framework that explicitly incorporates multiple sources of uncertainty, our analysis reveals a prominent role of physical and biological drivers in the marine ecosystem. These include interspecific competition with foreign-reared salmon, a very limited effect of bycatch mortality, and evidence that Yukon River Chinook may be subject to density-dependent capacity limitations from intraspecific competition in freshwater but not marine portions of the life cycle. Despite including a wide range of candidate covariates throughout the Chinook salmon lifecycle, we found support for only a small subset of these hypotheses, but this subset was able to explain much of the variation in observed abundance and age composition for these populations (Figure 2).

The only freshwater covariate with strong support from the data was the date of ice breakup on the Yukon River in the year of outmigration, with earlier ice break-up associated with higher juvenile survival. This result is consistent with findings by Ohlberger et al. (2016) and suggests that increased warming of the Yukon River earlier in the season and corresponding earlier onset of primary and secondary production have positive survival benefits for juvenile Chinook salmon. The ecological mechanisms and agents of selection underpinning the association between earlier break-up and survival are unknown, but presumably earlier spring break up results in reduced starvation mortality in early spring, enhanced growth opportunity affording increased survival at ocean entry, beneficial shifts in outmigration timing, or a combination of the above. Although data on how migration timing varies among years is limited for this system, there is mounting evidence that variation in the timing of Chinook salmon ocean entry can have large implications for early marine survival (Satterthwaite et al., 2014; Scheuerell, Zabel, & Sandford, 2009).

The positive association between Chinook salmon survival during the first winter at sea and SST at the Pribilof Islands (Figure 4) suggests that warmer temperatures foster enhanced productivity of these two Chinook salmon stocks. Siegel et al. (2017) provide a potential mechanistic explanation for this relationship, finding a positive correlation between marine temperature and growth of other Chinook salmon populations in this region and suggesting this may result in reduced risk of size-selective marine mortality (Farley, Murphy, Moss, Feldmann, & Eisner, 2009; Murphy et al., 2013). However, our results indicating a positive association between marine survival and temperature for these Chinook salmon populations in the northern portion of Alaska, contrast with findings by Sharma and Liermann (2010) of a net negative association between SST and recruitment of west coast Chinook salmon between Southeast Alaska and Oregon. The idea that salmonid stocks in northern regions respond differently to climate forcing when compared to their conspecifics at southerly latitudes is well established (Hare,

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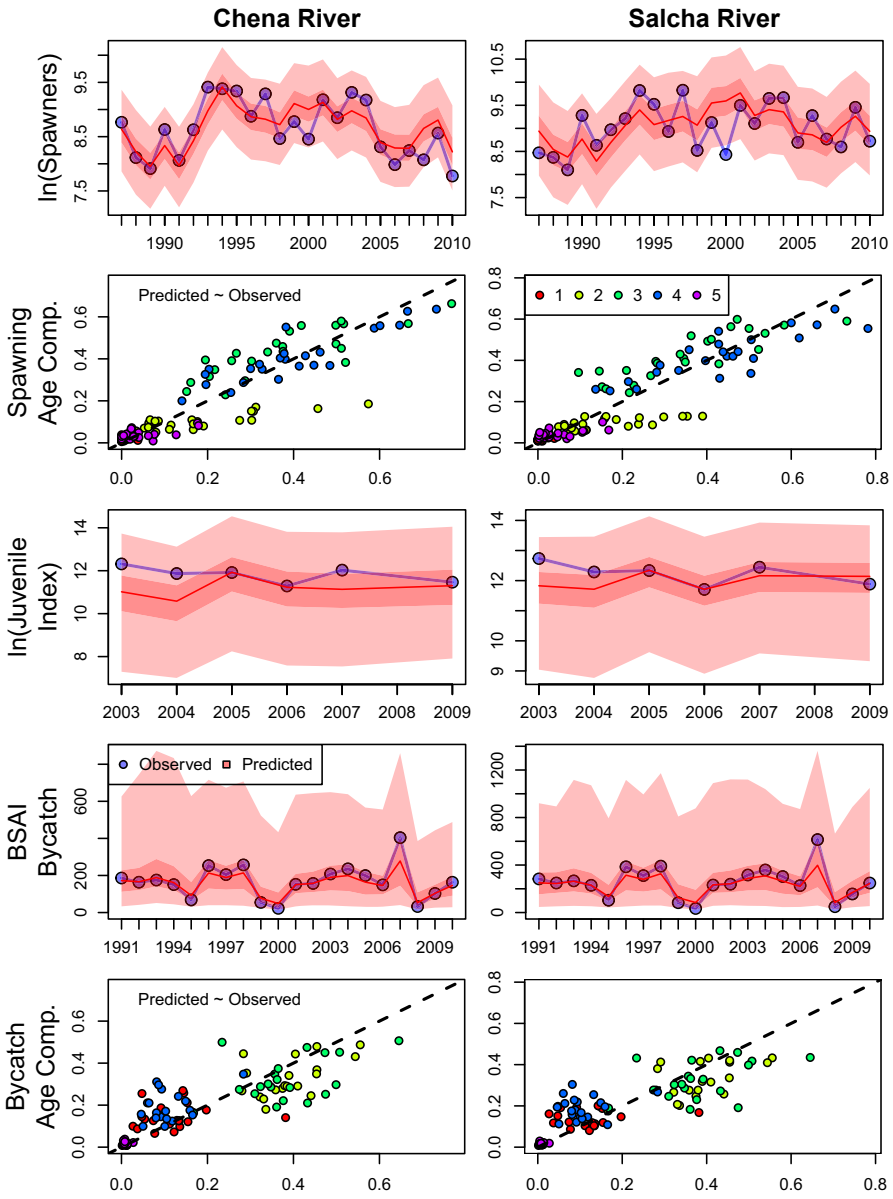


FIGURE 2 Comparison of model predicted adult (spawner) and juvenile abundance indices, bycatch numbers, and age composition, with observed data. Adult and juvenile abundance indices and bycatch data are presented as blue points, with red lines and shaded regions describing the median, 50%, and 95% credible intervals for the posterior predictive distribution. Model fits to age composition data are presented as a comparison of observed and predicted proportions by year and ocean age (year in the ocean). For age composition data, observed proportions are on the *x*-axis, predicted proportions are on the *y*-axis, and each point represents a year-by-age class combination. Points falling on the dashed 1:1 line indicate a predicted and observed proportions are equal

Mantua, & Francis, 1999) however, with cooler SST correlated with greater upwelling in the south (Wells, Grimes, Field, & Reiss, 2006; Wells, Grimes, & Waldvogel, 2007). Regardless of the underlying mechanism(s), support for a positive wintertime SST effect implies that a warmer Bering Sea under some climate change scenarios (IPCC, 2014) might enhance future Yukon River Chinook salmon marine survival.

These positive associations between survival and both earlier ice break-up in freshwater and warmer marine temperature conditions during the first winter at sea together suggest that the projected climate warming for this region (Chapin et al., 2014; IPCC, 2014) may enhance survival of Yukon River Chinook salmon at specific points in the lifecycle, at least for modest increases in the short term. More broadly, these results highlight that Chinook salmon populations at the northern extent of the species' range are expected to respond differently to future climate warming relative to populations in the Pacific Northwest (Battin et al., 2007) and California (Thompson et al., 2012), where responses to a warming climate are predicted to be negative. This aligns with the sentiments of Mantua, Crozier, Reed, Schindler, and Waples (2015) that, "the impacts of future climate warming on Pacific salmon will be mixed, and context dependent". While our results suggest increased survival with local and

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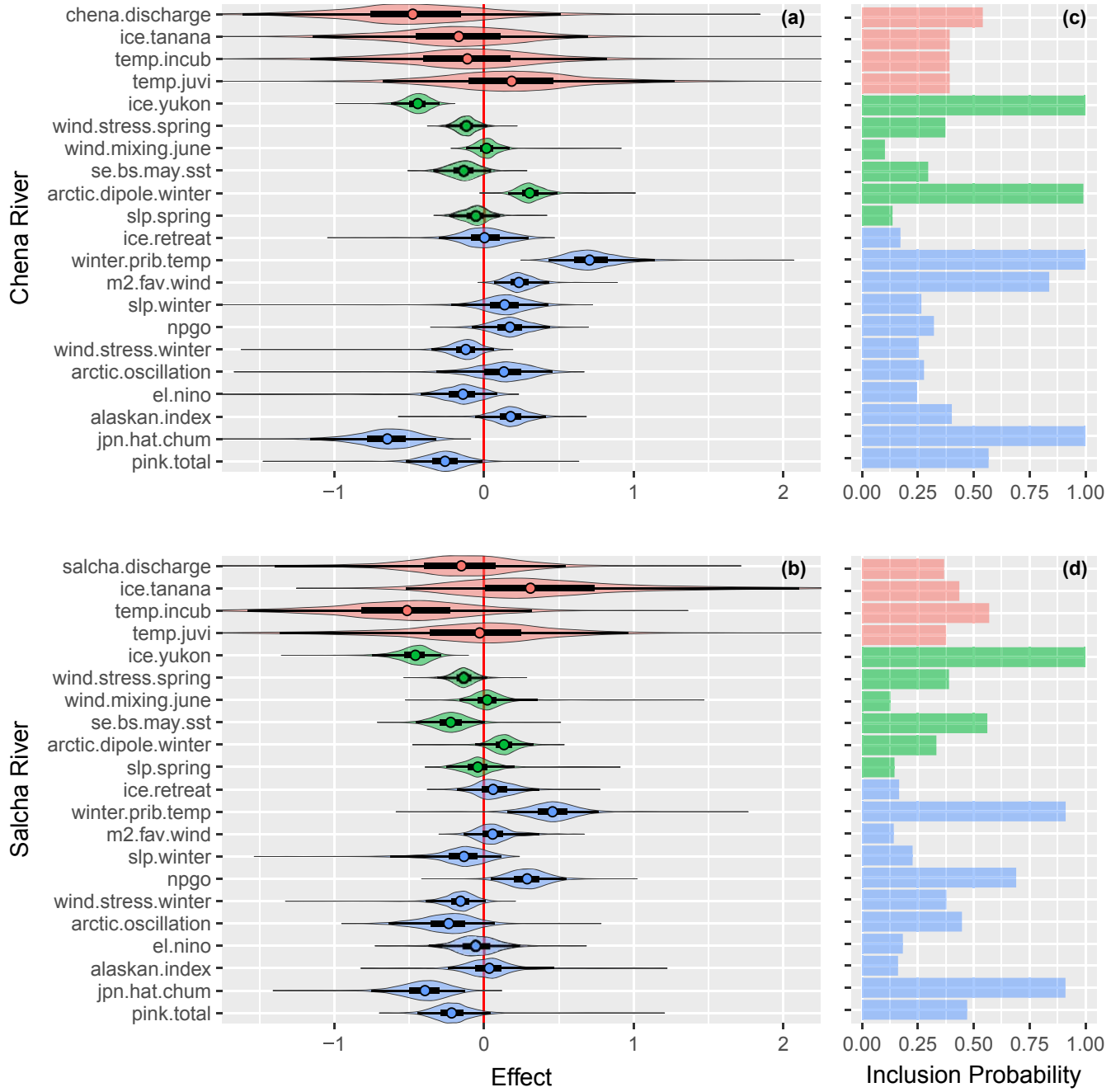


FIGURE 3 Covariate effects and inclusion probabilities. Left panels (a, b) show posterior distributions for covariate effects as caterpillar plots where the point, thick, and thin lines, indicate the median, 50% and 95% credible intervals. Posterior distributions for covariate effects are only samples for which the covariate was included included ($\tau_{p,c} = 1$). Right panels (c, d) show inclusion probability for each covariate. For descriptions of covariates, see Table 1. Colors correspond to model stage, red being upstream, green is downstream/nearshore marine, and blue is offshore marine

regional scale climate warming, it is critical to remember that: (a) these relationships only represent the range of data observed historically and may not fully capture potential nonlinear responses to temperature regimes outside the range of past observations, (b) temperature effects at other points in the lifecycle may have different effects on survival, (c) future climate change will alter aspects of marine and freshwater environments other than temperature, and changes in other habitat variables may have negative impacts, (d) climate-mediated northward shifts in the distribution of marine species (Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Thorson, Pinsky, & Ward, 2016) may result in increased predation risk to juvenile and adult Chinook salmon, and (e) temperature may only be a proxy for the actual driver of survival variation.

In addition to climate effects, the model also detected a negative association between the Japanese hatchery chum abundance and marine survival of Yukon River Chinook salmon (Figure 4a,b). Although

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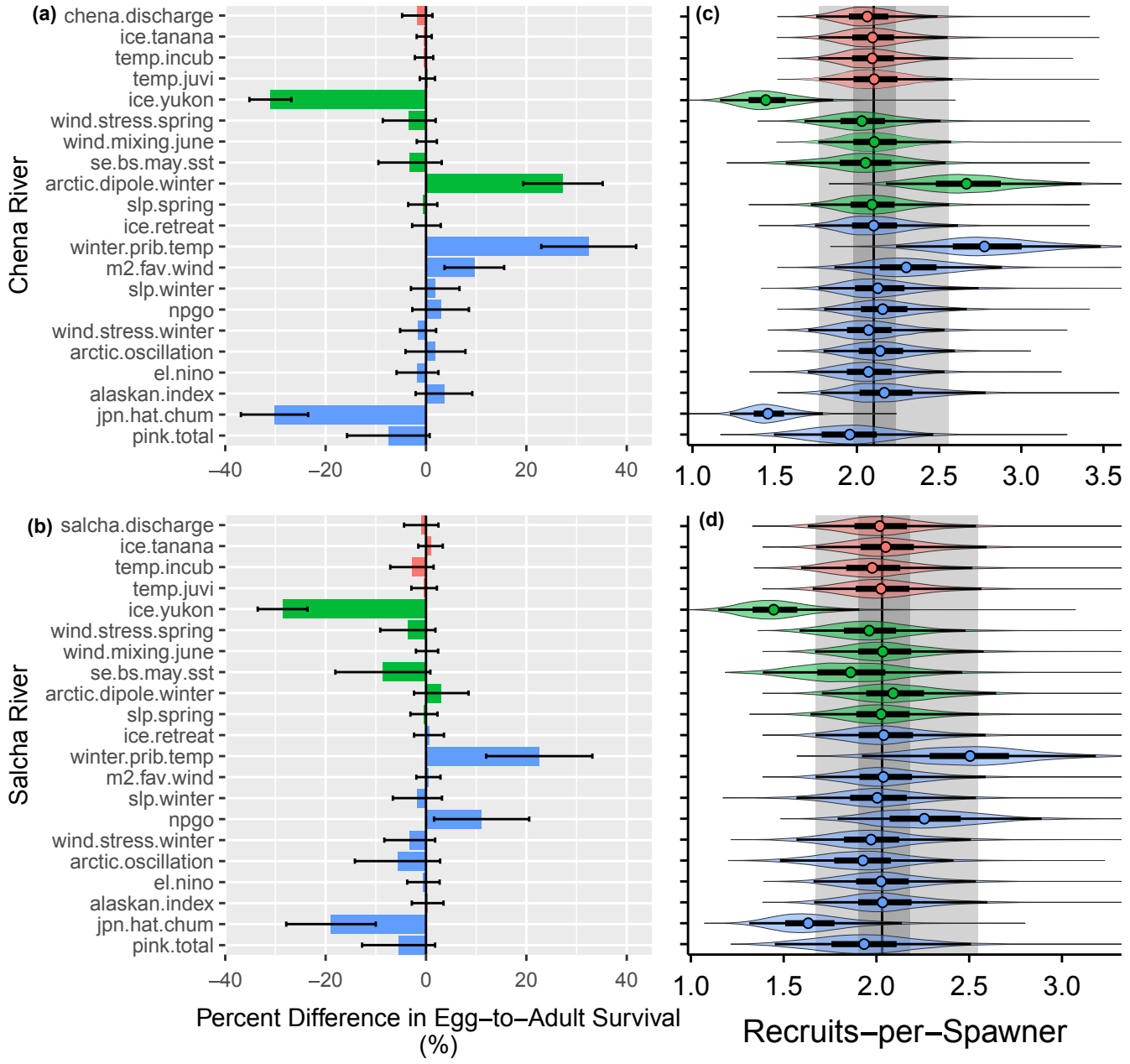


FIGURE 4 Simulated covariate effects. Left panels (a, b) show the expected percent change in egg-to-adult survival when each covariate is increased by +1 standard deviation from its long-term average. Right panels (c, d) show the distribution of expected productivity (recruits-per-spawner) for each simulated case, relative to the base case (all covariates are fixed at their long-term average). The black line, dark, and light gray shaded regions, denote the median, 50% and 95% credible intervals for base case productivity. Colors correspond to model stage (Table 1, Figure 1)

the effect of increased pink salmon abundance was also estimated to be negative for both populations, there was weak support for this hypothesis (Figure 3). The observation of decreasing survival with increasing hatchery production is generally consistent with possible density-dependent effects on survival at different spatial scales during the marine phase for various Pacific salmon species (Peterman, 1982; Ruggerone, Peterman, Dorner, & Myers, 2010). Ruggerone and Nielsen (2005) found that increased pink salmon abundance reduced survival of Puget Sound Chinook salmon and growth of Bristol Bay sockeye salmon through competition for prey resources, while Ruggerone and Connors (2015) found North Pacific pink salmon abundance to be negatively correlated with sockeye survival and size-at-age and positively correlated with later age at maturity. These results suggest that increased hatchery production of chum salmon, whether by Japan or other countries, could reduce Yukon River Chinook salmon survival.

Although with less support from the data, the estimated direction of effects for other environmental covariates is also informative. For example, the effect of wind stress on Chinook salmon survival at ocean entry and during the first winter at sea was negative for both

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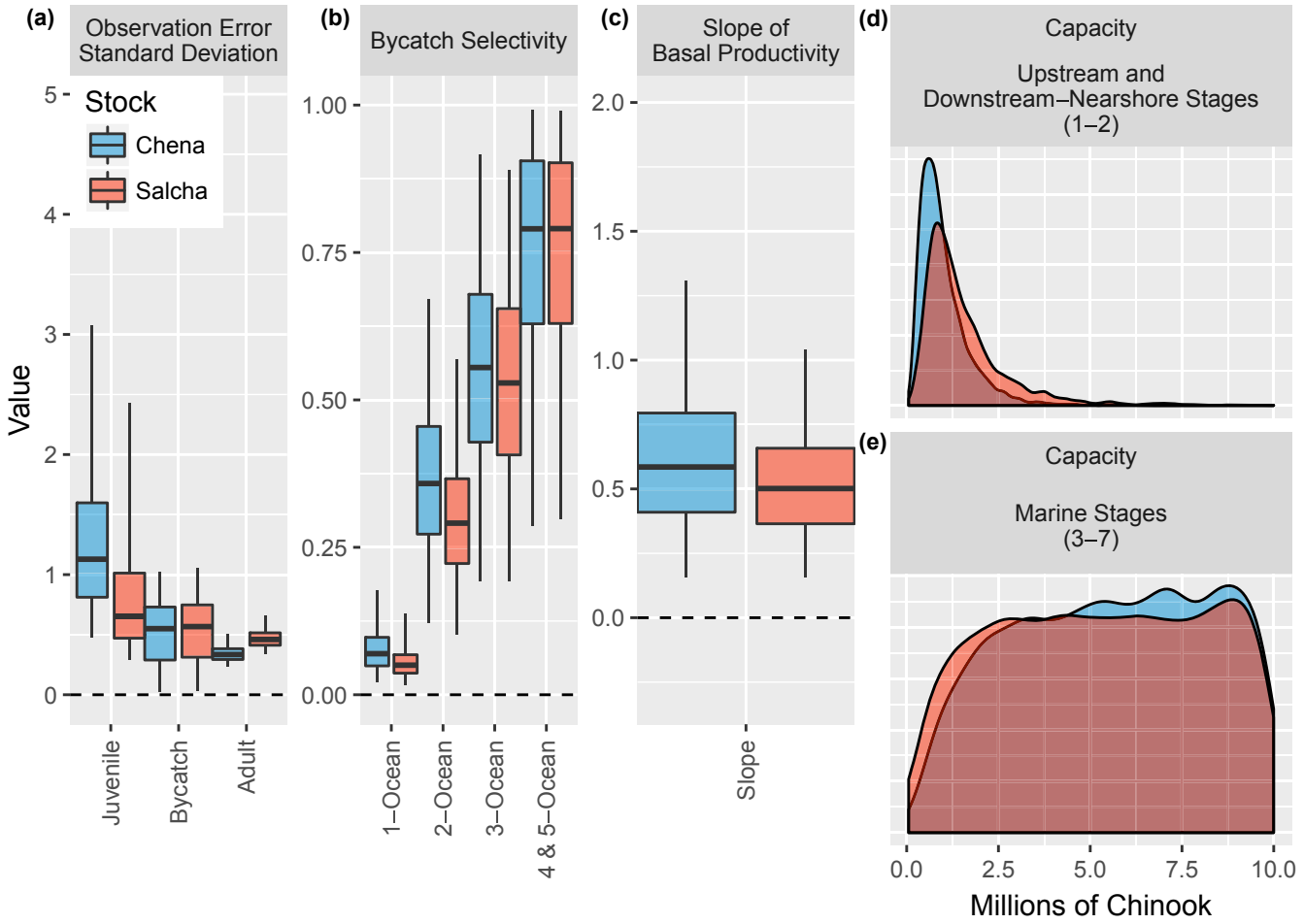


FIGURE 5 Posterior distributions for other population dynamics model parameters: (a) standard deviation of the lognormal observation error for the three indices of abundance $\sigma_{_,p}$, (b) marine bycatch selectivity by ocean age $S_{a,p}$, (c) slope of the change in basal productivity (maximum survival rate) across marine stages ω_p, and (d, e) capacities for upstream and nearshore stages and marine stages $k_{s,p}$

populations (Figure 3a,b). Negative wind stress values denote anomalously strong easterly winds that drive northward transport of nutrient-rich waters through Unimak Pass (Stabeno et al., 2002). Wind-driven northward transport of nutrients, particularly nitrogen, plays an important role in modulating productivity of the Bering Sea food web (Rosenkranz, Tyler, & Kruse, 2001; Stabeno et al., 2002). These negative effects of wind stress on Chinook salmon survival concur with our a priori hypothesis, despite the relatively low inclusion probabilities and limited utility in forecasting future survival. Consistent with Neuswanger et al. (2015), our results suggest increased water discharge in natal streams during the summer following emergence is associated with lower juvenile survival (Figure 3a,b), although discharge also had a low inclusion probability (Figure 3c,d). Neuswanger et al. (2015) hypothesized this negative association with arise from reduced foraging efficiency of juvenile Chinook as a result of increased water turbidity during high flows, though the exact mechanism(s) remain unclear (Neuswanger, Wipfli, Rosenberger, & Hughes, 2014).

Estimated effects of upstream (first stage) covariates had both high uncertainty and low inclusion probabilities (Figure 3), together indicating little evidence that survival to the adult stage has responded in a predictable manner to freshwater environmental conditions early in the life cycle (Figure 4). However, it is important to note that this finding might result from several processes. First, freshwater processes might indeed not drive variation in survival. Second, downstream survival bottlenecks might mask the influence of upstream processes and therefore our ability to discern their effect. Third, the lack of abundance indices for juveniles exiting tributaries and entering the mainstem Yukon (between stages 1 and 2) limits our ability to partition mortality between upstream and downstream/nearshore environments. Finally, we may have failed to include the most relevant freshwater covariates due to the limited monitoring in these large, remote watersheds. In any case, results suggest that future trends in survival are better predicted by marine rather than freshwater conditions, but additional abundance indices for juvenile Chinook as they exit tributaries or for Chinook smolt as they enter the ocean may be of value in improving understanding of population dynamics.

In conclusion, the use of stage-structured models in conjunction with Bayesian model selection methods provides a useful framework for testing hypotheses about, and quantifying the influence of, environmental processes on survival of species at different locations in space and time, throughout their life cycle, and generating

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predictions that are robust to uncertainty in both estimation and model structure. However, these methods are data intensive and are correlative in nature and thus limited by contrast in both covariate and biological data. Applications of these methods to Yukon River Chinook salmon populations suggest that with the exception of variables related to the timing of springtime ice breakup in freshwater, processes in the marine environment better explain survival variation. This does not suggest, however, that freshwater processes are unimportant as these populations' genomes likely reflect site-specific adaptations to selection pressures of freshwater habitats that bolster population robustness and stability (Carlson & Satterthwaite, 2011; Griffiths, Schindler, & Seeb, 2013; Hilborn, Quinn, Schindler, & Rogers, 2003). The maintenance of a rich portfolio of complex, diverse, and interconnected freshwater habitats in the middle Yukon River and beyond should be a conservation goal (Carlson & Satterthwaite, 2011; Griffiths et al., 2014). Finally, results suggesting density-dependent capacity limitations in freshwater indicate that any proposed enhancement programs designed to benefit depressed Yukon River stocks should carefully consider potential impacts on wild populations and probability of success given downstream bottlenecks, while also considering the global connectivity of Pacific salmon rearing in the North Pacific Ocean.

Perhaps most importantly, from the perspective of future climate change, the strong support for positive association between Yukon River Chinook salmon survival and both earlier ice breakup in freshwater and warmer wintertime temperatures at sea suggests that in the short term future climate warming is more likely to have a net positive impact on these Chinook populations at the northern extent of their Pacific range, in contrast with predicted impacts on populations inhabiting southerly portions of the species' range in the North Pacific (Battin et al., 2007; Crozier et al., 2008; Thompson et al., 2012). However, this prediction is based on the range of environmental conditions observed historically and may not be applicable if and when conditions exceed the range of past observations.

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Climate-driven zooplankton shifts cause large-scale declines in food quality for fish

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Zooplankton are the primary energy pathway from phytoplankton to fish. Yet, there is limited understanding about how climate change will modify zooplankton communities and the implications for marine food webs globally. Using a trait-based marine ecosystem model resolving key zooplankton groups, we find that future oceans, particularly in tropical regions, favour food webs increasingly dominated by carnivorous (chaetognaths, jellyfish and carnivorous copepods) and gelatinous filter-feeding zooplankton (larvaceans and salps) at the expense of omnivorous copepods and euphausiids. By providing a direct energetic pathway from small phytoplankton to fish, the rise of gelatinous filter feeders partially offsets the increase in trophic steps between primary producers and fish from declining phytoplankton biomass and increases in carnivorous zooplankton. However, future fish communities experience reduced carrying capacity from falling phytoplankton biomass and less nutritious food as environmental conditions increasingly favour gelatinous zooplankton, slightly exacerbating projected declines in small pelagic fish biomass in tropical regions by 2100.

Zooplankton are a critical component of marine food webs, serving as the primary energy pathway from phytoplankton to fish[1]. Zooplankton are extremely diverse, representing 15 phyla[2] and accounting for ~40% of the world's marine biomass[3]. However, despite their abundance and ecological importance, most ecosystem models resolve few zooplankton groups[4], focusing on phytoplankton or fish, particularly in climate change projections[5,6]. By not adequately resolving zooplankton communities in ecosystem models, major climate-driven changes in marine food webs in response to climate change may be overlooked[7–9]. These changes could have important implications for ecosystem services ranging from biogeochemical cycling[10–12] to fisheries[1,13].

Zooplankton community structure across space and time is determined by how the vastly different functional traits of its members drive interactions between individual zooplankton and their environment[8,14]. Zooplankton functional traits not only govern the relative fitness of individual zooplankton[7,8,15] but also regulate the transfer of energy from phytoplankton to fish[8,14,15]. For example, the number of trophic steps between phytoplankton and fish is partly determined by zooplankton predator–prey mass ratios (PPMRs; the ratio of predator–prey body size). Higher PPMRs mean fewer trophic steps and therefore less energy lost from phytoplankton to fish[16]. Thus, communities dominated by carnivorous copepods (PPMR < 100; Supplementary Table 1) are expected to transfer less energy to higher trophic levels than those dominated by filter feeders such as larvaceans and salps[16] (PPMR > 6 million; Supplementary Table 1). Zooplankton community composition also affects the nutritional quality (carbon content) of food for fish. This is because zooplankton carbon content varies within taxa and by over one order of magnitude across taxa[17], from gelatinous zooplankton (0.5%), through crustaceans (12%), to microzooplankton (15%). Better accounting for

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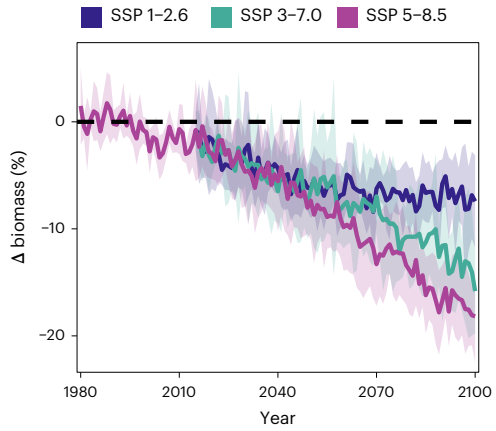


Fig. 1 | Effects of climate change on global zooplankton biomass. Change in global zooplankton biomass (%) for three zooplankton groups from 1980 to 2100, relative to 1980 to 2000, under emission scenarios SSP 1–2.6, SSP 3–7.0 and SSP 5–8.5. Solid lines represent the ensemble mean change in zooplankton biomass and shaded areas are the standard deviation from separate simulations of ZooMSS, each forced by one of five Earth-system models. The horizontal black dashed line indicates no change in biomass, compared to mean biomass in 1980–2000.

the diversity of zooplankton functional traits will therefore improve understanding of energy flow from plankton to fish now and under future climate change.

In this Article, we assess effects of climate change on global zooplankton community composition. We then explore how these climate-driven changes affect small pelagic (planktivorous) fish—the primary predator of zooplankton beyond zooplankton themselves. We use a global marine ecosystem model, the Zooplankton Model of Size Spectra (ZooMSS)[18] (Methods), which resolves phytoplankton, two microzooplankton groups (heterotrophic flagellates and ciliates), seven mesozooplankton and macrozooplankton groups (omnivorous and carnivorous copepods, larvaceans, euphausiids, salps, chaetognaths and jellyfish) and three size-based fish groups (broadly representing small pelagic fish (SPF) ≤100 g; medium pelagic fish 100 g ≤ 10 kg and large pelagic fish 10 kg ≤ 1 t). ZooMSS resolves the nine zooplankton groups on the basis of several traits: the size range of the group, feeding characteristics (PPMR and feeding kernel width) and carbon content[18] (Supplementary Table 1). We focus our analysis on the mesozooplankton and macrozooplankton (hereafter called zooplankton), organizing them into three groups defined by their feeding characteristics—carnivores (chaetognaths, jellyfish and carnivorous copepods), omnivores (euphausiids and omnivorous copepods) and filter feeders (larvaceans and salps). ZooMSS is forced by sea-surface temperature and phytoplankton variables from five coupled model intercomparison project phase 6 (CMIP6) Earth-system models[19] under three future (2015–2100) Intergovernmental Panel on Climate Change shared socioeconomic pathways (SSPs)[20] (SSP 1–2.6, SSP 3–7.0 and SSP 5–8.5) using historical (1980–2014) conditions as a baseline (Methods).

Climate-driven declines in global zooplankton biomass

Global zooplankton biomass declined by 7–16% from 1980 to 2100 (Fig. 1 and Table 1). These declines in zooplankton biomass are within the range of similar studies[21,22] and are primarily caused by projected declines in phytoplankton biomass. Of course, ZooMSS could be within range of other models for the wrong reasons or due to compensation effects (section on Model caveats). Contemporary distributions of zooplankton and small fish biomass at the global level and their future declines show similar spatial and temporal patterns to phytoplankton biomass (Extended Data Fig. 1). This is because in ZooMSS phytoplankton are the primary food source for microzooplankton[23], filter feeders[24] and omnivorous zooplankton[25], which are themselves food for carnivores and SPF[26–28] (Extended Data Fig. 2). Therefore, a decline in phytoplankton means less zooplankton and fish can be supported. Previous modelling and observational studies have also shown that contemporary and future zooplankton biomass is strongly related to phytoplankton biomass over large spatial scales[21,22,29]. Warming acts as an additional driver of biomass decline in ZooMSS by increasing background mortality from senescence, which is not balanced by predation-driven growth. However, since predation-driven growth and mortality processes scale in the same way with temperature across all functional groups in ZooMSS (section on The model), warming is a secondary driver of zooplankton and fish biomass decline compared to decreases in phytoplankton biomass[18,30].

The decline in global biomass (from 1980 to 2100) varied across zooplankton groups (Fig. 2a–c and Table 1). Omnivorous zooplankton biomass exhibited the greatest decline of 8–18%. By contrast, filter feeders experienced a more modest biomass decline of up to 6%. The magnitude of decline of carnivorous zooplankton biomass was even less than filter feeders, decreasing between 1% and 2%. The greater decline in omnivores is a consequence of the relatively greater projected global reductions in nanophytoplankton (2–20 µm) and microphytoplankton (>20 µm) biomass under climate change—both major components of omnivore diets (Extended Data Fig. 2i,k)—in comparison to smaller picophytoplankton (<2 µm)[8,14] (Extended Data Fig. 3a–c).

There was considerable variation in the response of each zooplankton group across ocean biomes (Fig. 2d–l and Table 1). From 1980 to 2100, omnivore biomass declined >25% under both SSP 3–7.0 and SSP 5–8.5 in tropical areas. By contrast, filter-feeder biomass was the least affected by climate change, varying between an increase of 2% in the polar biome (SSP 3–7.0, SSP 5–8.5) and a decrease of 8% in tropical waters (SSP 5–8.5). The magnitude of the change for carnivores was even smaller than filter feeders, with changes varying between a decline of 4% in polar regions under SSP 3–7.0 and SSP 5–8.5 and no change in tropical waters under SSP 1–2.6.

Climate-driven shifts in global zooplankton composition

Biomass declines across the zooplankton groups manifest spatially as disparate shifts in the composition of the zooplankton community (Fig. 3). Under historical (1980–2000) conditions, carnivorous and filter-feeding zooplankton constitute up to 50% of zooplankton in oligotrophic subtropical gyres (Fig. 3a,b) where phytoplankton and zooplankton biomass is lower[31,32] (Extended Data Fig. 1a,b) and picophytoplankton—a major component in the diets of microzooplankton and filter feeders (Extended Data Fig. 2a,c,e,g)—dominate (Extended Data Fig. 4a). By contrast, omnivorous zooplankton constitute 60–90% of zooplankton biomass in polar and upwelling regions (Fig. 3c) where phytoplankton and zooplankton biomass are higher and nanophytoplankton and microphytoplankton are prevalent[31,32] (Extended Data Fig. 4b,c).

Carnivorous and gelatinous filter-feeding zooplankton increase in dominance with climate change, particularly in expanding open-ocean oligotrophic gyres (Fig. 3d–l), with the magnitude of changes increasing with greater future emissions. Under SSP 1–2.6, carnivorous and filter-feeding zooplankton each increased as a proportion of zooplankton biomass by up to 10% across large areas. Omnivorous zooplankton declined by >15% as a proportion of total zooplankton biomass under all emission scenarios, in areas where the relative prevalence of carnivores and filter feeders increased. Within the three groups, patterns of change in individual zooplankton groups were broadly similar (Supplementary Figs. 1d–l, 2c–h and 3c–h).

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Table 1 | Changes in global zooplankton under climate change

	Total zooplankton			Carnivores			Filter feeders			Omnivores		
	SSP1–2.6	SSP3–7.0	SSP5–8.5	SSP1–2.6	SSP3–7.0	SSP5–8.5	SSP1–2.6	SSP3–7.0	SSP5–8.5	SSP1–2.6	SSP3–7.0	SSP5–8.5
Global	−7±3***	−12±5***	−16±4***	−1±2**	−2±5*	−2±6*	−1±2***	−5±4***	−6±5***	−8±4***	−14±5***	−18±4***
Polar	−8±10***	−5±7***	−8±11***	−3±4***	−4±5***	−4±5***	2±3***	1±2	0±2	−8±11***	−5±8***	−8±13***
Temperate	−5±3***	−7±7***	−11±5***	−1±1***	−1±2***	−2±3***	−1±2**	−4±3***	−5±3***	−5±3***	−8±8***	−12±5***
Tropical	−9±6***	−22±10***	−27±10***	0±3	−2±8	−2±10*	−3±3***	−7±7***	−8±8***	−12±8***	−28±12***	−34±11***

Mean (±standard deviation) biomass change (%) in 2080 to 2100, relative to the mean over 1980–2000, for total zooplankton, carnivores (chaetognaths, jellyfish and carnivorous copepods), filter feeders (larvaceans and salps) and omnivores (euphausiids and omnivorous copepods) across SSPs and biomes. Note here that temperate and tropical, respectively, correspond to westerlies and trades Longhurst biomes and global results exclude the coastal biome (Extended Data Fig. 10 provides a map of the biomes). Each mean and standard deviation is calculated over five model simulations, with each simulation using a different Earth-system model to provide environmental forcings. *P* values from two-sided Mann–Whitney non-parametric *U*-tests comparing initial (1980–2000, n=100; 20 years×5 simulations) and final (2080–2100, n=100) biomass change are summarized as: *$0.01<P\leq0.05$, **$0.001<P\leq0.01$ and ***$P\leq0.001$.

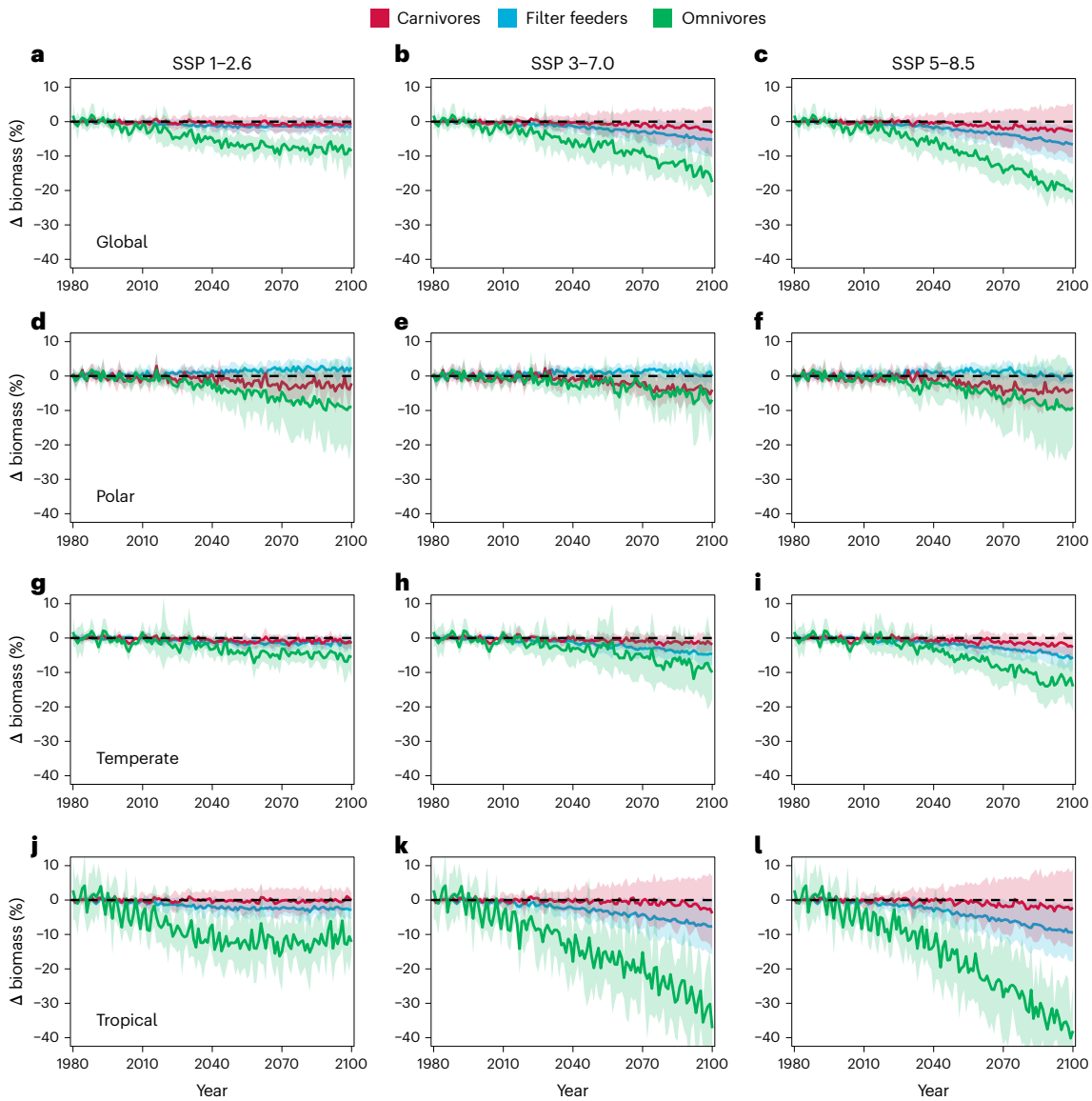


Fig. 2 | Effects of climate change on major zooplankton groups. a–l, Change in biomass (%) for three zooplankton groups (carnivores, filter feeders and omnivores) from 1980 to 2100, relative to 1980 to 2000, under emission scenarios SSP 1–2.6 (**a**,**d**,**g**,**j**), SSP 3–7.0 (**b**,**e**,**h**,**k**) and SSP 5–8.5 (**c**,**f**,**i**,**l**), across global (**a**–**c**), polar (**d**–**f**), temperate (**g**–**i**) and tropical (**j**–**l**) waters. Note here that temperate and tropical, respectively, correspond to westerlies and trades Longhurst biomes and global results exclude the coastal biome; Extended Data Fig. 10 gives a map of the biomes. Solid lines represent the ensemble mean change in zooplankton biomass and shaded areas are the standard deviation from separate simulations of ZooMSS, each forced by one of five Earth-system models. The dashed black line in each plot represents no change from mean biomass in 1980–2000.

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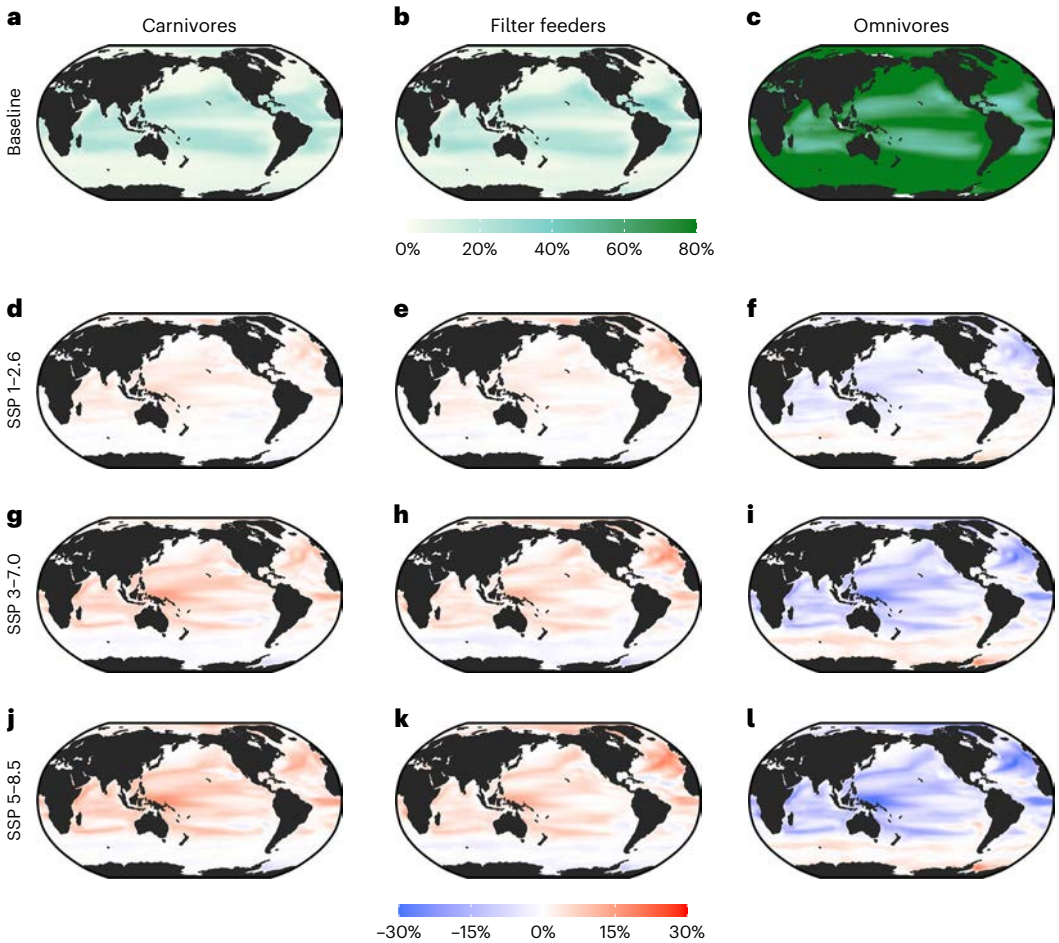


Fig. 3 | Climate-induced shifts in zooplankton community composition. **a**–**c**, The mean baseline percentage of total community biomass in 1980–2000 comprising carnivores (**a**), filter feeders (**b**) and omnivores (**c**). **d**–**l**, Maps of the mean change (%) of total zooplankton community biomass from carnivores (**d**,**g**,**j**), filter feeders (**e**,**h**,**k**) and omnivores (**f**,**i**,**l**) in 2080–2100 relative to 1980–2000 under emission scenarios SSP 1–2.6 (**d**–**f**), SSP 3–7.0 (**g**–**i**) and SSP 5–8.5 (**j**–**l**), across the five Earth-system models used to force ZooMSS.

Since warming affects all zooplankton groups in ZooMSS in the same way (section on The model), projected shifts are driven primarily by changes in phytoplankton size structure. Under climate change, picophytoplankton are projected to increase as a proportion of the phytoplankton community across most the world's oceans[33,34], with corresponding declines in the prevalence of larger phytoplankton (Extended Data Fig. 4d–l). Owing to their massive PPMRs (Supplementary Table 1), filter feeders consume picophytoplankton[25,35] (Extended Data Fig. 2e,g), which are too small for most copepods and euphausiids. Thus, filter-feeding zooplankton can outcompete omnivores in oligotrophic regions[8,14,24]. Carnivores are also projected to increase as a proportion of the zooplankton community because of the greater relative importance of microzooplankton[8,14,36] (Supplementary Fig. 4), which is >50% of their diet (Extended Data Fig. 2m,o). Finally, the greater prevalence of picophytoplankton (Extended Data Fig. 4, left column) and microzooplankton (Supplementary Fig. 4) and projected declines in larger phytoplankton in the future (Extended Data Fig. 4, centre and right column), decreases the total phytoplankton directly available for omnivorous zooplankton[8,14,36], since nanophytoplankton and microphytoplankton are large components of their diet, especially in eutrophic waters (Extended Data Fig. 2i,k).

Within carnivore and filter-feeder groups, jellyfish (Supplementary Fig. 1, right column) and larvaceans (Supplementary Fig. 2, left column) experienced modest declines in some parts of the open-ocean gyres, whereas the other filter feeders (salps) and carnivores (carnivorous copepods and chaetognaths) increased as a proportion of total zooplankton biomass. These unique changes for larvaceans and jellyfish are driven not only by shifts in phytoplankton community size structure but also predator–prey interactions among zooplankton groups. For example, larvaceans are the smallest mesozooplankton (Supplementary Table 1) and their declines in some regions where salps increase as a proportion of the zooplankton are probably driven by increases in predation pressure not balanced by growth, as they become more prevalent in diets of carnivores and SPF as oligotrophic regions expand (Extended Data Fig. 2m,o,q,s). Conversely for jellyfish, their declines in some regions where other carnivores increase are driven by decreases in the prevalence of omnivorous copepods (Supplementary Fig. 3, left column) and larvaceans (Supplementary Fig. 2, left column), which together are >50% of jellyfish diet from oligotrophic to eutrophic waters (Extended Data Fig. 2q).

Evidence for this projected shift from omnivores toward carnivores and gelatinous filter feeders has already been observed in some regions[37,38] and our results suggest that these shifts will intensify under climate change. Only in the Southern Ocean and some subtropical waters where larger microphytoplankton increase as a proportion of the phytoplankton community (Extended Data Fig. 4, right column) is the dominance of omnivorous zooplankton projected to increase (Fig. 3f,i,l). However, effects of climate change on phytoplankton in the Southern Ocean are poorly understood[39], which means our

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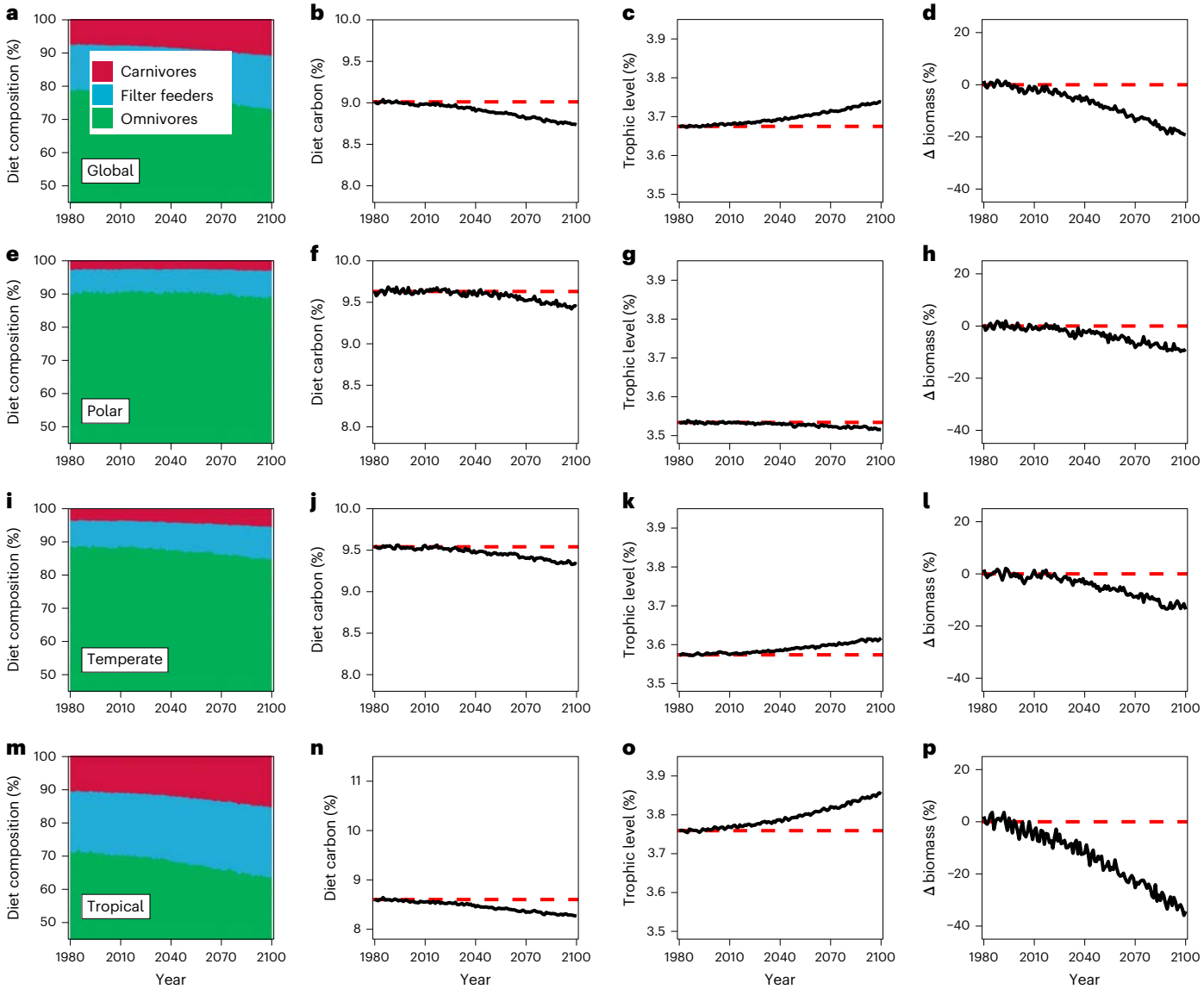


Fig. 4 | Effects of climate change on SPF. a–**p**, Mean change in the diet composition (**a**,**e**,**i**,**m**), diet carbon (**b**,**f**,**j**,**n**), trophic level (**c**,**g**,**k**,**o**) and biomass (**d**,**h**,**i**,**p**) of SPF, relative to 1980–2000 under SSP 5–8.5 in global (**a**–**d**), polar (**e**–**h**), temperate (**i**–**l**) and tropical (**m**–**p**) waters, across the five Earth-system models used to force ZooMSS in this study. Extended Data Figure 10 gives a map of the biomes. Dashed red lines represent the mean in 1980–2000.

projections of zooplankton community shifts in this region are particularly uncertain. Nevertheless, these results represent substantial potential shifts in global zooplankton composition, given that omnivorous copepods dominate total zooplankton biomass[34] and are arguably the most abundant multicellular animals on Earth[35].

Implications for fish

Changes in zooplankton composition can have profound implications for fish[1,13,16,29,36,40]. We thus explored how changes in zooplankton community composition under SSP 5–8.5 affected the diet and trophic level of SPF. SPF have an extremely important ecological role transferring energy to larger fish and form some of the most economically valuable fisheries resources, contributing significantly to global food security[41].

Globally, the proportion of SPF diet comprising omnivorous zooplankton decreased from 79 to 72% between 1980 and 2100, with simultaneous increases in the contribution of filter feeders from 13 to 16% and carnivores from 8 to 12% (Fig. 4a). These changes in SPF diet mirrored shifts in zooplankton community composition (Extended Data Fig. 5a). Yet, despite future declines in omnivorous zooplankton (high PPMRs) and increases in carnivorous zooplankton (low PPMRs) that should lead to longer food chains[8,42,43], the mean trophic level of SPF increased by only ~1.5% globally (from 3.67 to 3.74) and by at most ~2.5% in tropical waters (from 3.76 to 3.86) from 1980 to 2100 (Fig. 4, third column). In contrast, the mean trophic level of omnivorous zooplankton increased by on average 3.5% (from 2.57 to 2.66) in tropical waters and 2.5% (from 2.46 to 2.52) globally (Extended Data Fig. 6, right column). These mean changes conceal greater increases within regions. For example, the trophic level of omnivorous zooplankton increased by ≥15% in some areas in the North Atlantic but ≤8% for SPF in the same areas (Extended Data Fig. 7c,d). The smaller changes in SPF trophic level are because the longer food chains resulting from a rise in carnivores and decline in omnivores are partially offset by the increase in gelatinous filter feeders in the diet of SPF (Fig. 4, first column). Owing to their huge PPMRs and similar body size range to omnivores (Supplementary Table 1), filter feeders are uniquely capable of shunting energy from small phytoplankton to higher trophic levels[32,35,44]. These traits mean that the trophic level of filter feeders in ZooMSS in the future falls within a

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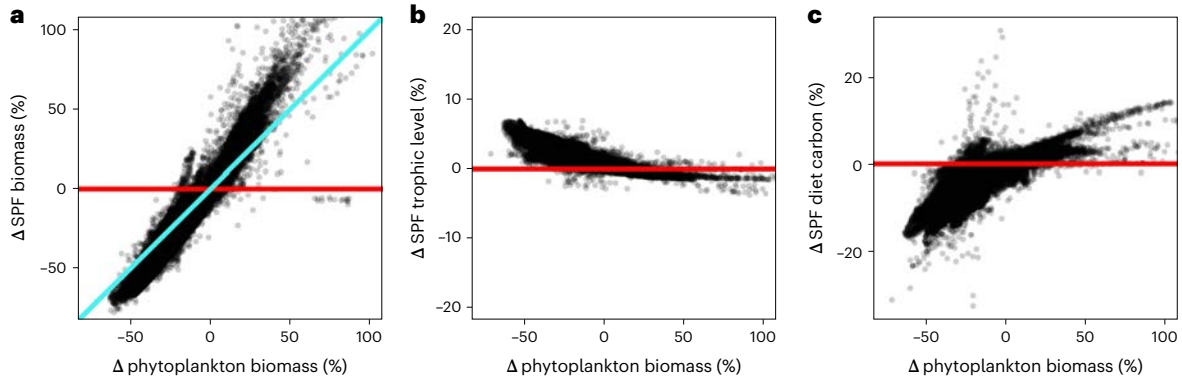


Fig. 5 | Effects of changing phytoplankton biomass on SPF. a–**c**, Mean percentage change in the biomass (**a**), trophic level (**b**) and diet carbon content (**c**) of SPF against the percentage change in phytoplankton biomass, for individual 1° grid squares from 1980–2000 to 2080–2100 under the SSP 5–8.5 emissions scenario across the five Earth-system models used to force ZooMSS in this study. Under the blue 1–1 line in **a**, where the change in phytoplankton biomass is negative is where the decline in SPF biomass is greater than that of phytoplankton. Similarly, above the blue 1–1 line in **a** and where the change in phytoplankton biomass is positive, is where the increase in SPF biomass is greater than that of phytoplankton. The red solid horizontal line in each figure indicates where the percentage change in each SPF attribute is zero.

relatively constant and low range of 2–2.25, while trophic levels of omnivores are more sensitive to shifts in phytoplankton biomass from oligotrophic to eutrophic waters compared to filter feeders (Extended Data Fig. 2 and Extended Data Fig. 6, centre and right column; Extended Data Fig. 7). Our results suggest that the trophic stability of filter feeders will moderate effects of shrinking phytoplankton on future trophic levels of SPF. At the same time, carnivorous jellyfish have large PPMRs relative to other carnivores (Supplementary Table 1), although their large body sizes mean they are more a competitor of SPF than prey (Extended Data Fig. 2q–t). Thus, the role of jellyfish in buffering the effects of climate change on food web length could be minor compared to filter feeders.

The unique role of gelatinous filter feeders in providing an alternative energy pathway between phytoplankton and higher trophic levels has long been suggested[35,44]. However, owing to their fragile bodies, gelatinous zooplankton have been poorly studied because they rapidly disintegrate in the guts of predators or when sampled in nets[24]. New approaches to examining diets of marine predators, such as stable isotope analysis and DNA metabarcoding, show that gelatinous filter feeders are often important prey of many commercial fish species and therefore serve an important role in structuring marine ecosystems[27–29,32]. Our results suggest that the direct energy pathway from small phytoplankton through filter feeders to fish will grow in importance if small phytoplankton become increasingly dominant under climate change[33].

The trend toward gelatinous zooplankton caused a decrease in the carbon content of SPF diets under climate change (Fig. 4, second column). Gelatinous carnivores such as jellyfish and chaetognaths and filter feeders such as larvaceans and salps, are 65–95% less carbon-dense than omnivorous zooplankton such as euphausiids and copepods[17]. As gelatinous zooplankton outcompete carbon-dense omnivorous groups, the carbon content of the diet of SPF decreased by ~3.5% globally, from just over 9% in 1980 to 8.7% in 2100 (Fig. 4b). Although this mean global decline is modest, there was a greater mean reduction of ~4.5% in the tropical biome (1980–2100; Fig. 4n). These shifts in the nutritional quality of SPF diets reflect changes in zooplankton community carbon content in these biomes (Extended Data Fig. 5, right column).

Sudden, climate-driven changes in fish diets have already been observed during the recent marine heatwave in the North Pacific from 2013 to 2016, commonly called the 'Blob', which led to hotter sea-surface temperatures and lower primary production[45]. Decreases in phytoplankton production during the heatwave drove declines in the abundance of carbon-dense euphausiids and increases in carbon-poor gelatinous zooplankton[46], which then manifested as shifts in the diet of SPF[47] as well as declines in their weight and energetic content[47,48]. Coupled with these empirical studies, our results indicate future fish communities in large parts of the world's oceans face not only reduced carrying capacity from falling primary production but also potentially lower carbon diets as reductions in phytoplankton biomass favour less carbon-dense zooplankton communities (Extended Data Fig. 8).

From 1980 to 2100, global SPF biomass is projected to decline by 20% (from 1980 to 2100) under SSP 5–8.5, with declines of ~10–35% within biomes (Fig. 4, fourth column). Similar declines are also projected for total fish biomass (Supplementary Fig. 5). Declines in SPF biomass were slightly greater than phytoplankton in many regions (Fig. 5a), a process known as trophic amplification[22]. To assess whether an increasingly gelatinous zooplankton community played a role in trophic amplification from phytoplankton to fish, we ran ZooMSS with the carbon content of all zooplankton groups held constant at 10%, the same as SPF (Supplementary Table 1). The magnitude of declines in SPF biomass in tropical waters were about 10% smaller (~32% versus ~35%) when zooplankton carbon contents were held constant (Extended Data Fig. 9). At the same time, in temperate waters where there was little change in zooplankton composition, there was almost no difference in the change in SPF biomass (Extended Data Fig. 9c) and in polar waters, declines in fish biomass were slightly larger (Extended Data Fig. 9b) when zooplankton carbon contents were held constant.

Discussion

A general expectation of climate change is that future marine ecosystems will support less fish biomass where primary production decreases[5,30,49,50], while the number of trophic steps between primary producers and fish is expected to substantially increase as mean phytoplankton size declines[42,43]. Our results support the first part of this expectation—less phytoplankton means lower fish biomass (Fig. 5a)—while challenging the expectation that future food webs will be much longer (Figs. 4, third column and 5b). Our results also support another suggestion: lower future phytoplankton biomass will support more gelatinous food webs (Fig. 5c and Extended Data Fig. 8).

In ZooMSS, shifts in phytoplankton size structure are the primary driver of zooplankton composition shifts. However, empirical evidence[18,51] and a recent modelling study[52] suggest that gelatinous filter feeders and carnivore (including jellyfish) biomass may increase because of temperature alone, which is not resolved in ZooMSS. This means that ZooMSS could still underestimate the role of gelatinous

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zooplankton in structuring marine food webs in future, warmer oceans. At the same time, ZooMSS may also underestimate the buffering capacity of gelatinous filter feeders on fish biomass under climate change[33,34] because it does not resolve how gelatinous filter feeders are more easily caught[27] and digested[24] by fish compared to more carbon-dense copepods and euphausiids. Finally, direct human impacts from fishing—also not considered here—have also been suggested to favour carnivorous jellyfish by removing their predators and competitors[53], although this idea remains disputed[54].

Since ZooMSS was designed to project the condition of marine ecosystems over large spatial and temporal scales, it has many simplifying assumptions concerning dynamic processes such as reproduction, seasonality and adaptation (section on Model caveats). This means that we are likely to be underestimating climate effects on marine ecosystems at finer spatial and temporal scales. For instance, decoupling between higher trophic level reproduction and seasonal phytoplankton pulses in polar and temperate regions under climate change could drive increasingly widespread recruitment failures, with cascading effects across marine food webs[55,56]. By using an annual time step, these processes and their effects are not explicitly represented here. Further, as zooplankton and fish groups in ZooMSS are defined by fixed functional traits (Supplementary Table 1), any potential adaptations to changing environmental conditions are also not considered. More broadly, the coupling between phytoplankton and consumers in ZooMSS—and most of the current generation of marine ecosystem models—is incomplete, with models not resolving predation impacts from higher trophic levels on phytoplankton[30]. This lack of coupling means that potential critical pathways of trophic amplification remain unresolved.

Nevertheless, we believe our model is an important step towards resolving the changing role of zooplankton under climate change. Previous studies have highlighted the sensitivity of global higher trophic level biomass to energy flow through the plankton[16,22,57] but at present ZooMSS is the only global marine ecosystem model that resolves zooplankton by multiple functional traits[30]. At the same time, although an increasing number of biogeochemical models now resolve gelatinous zooplankton and their role in carbon sequestration[52,58,59], they do not explicitly represent fish. By bridging the gap between plankton and fish, the trait-based modelling framework used here is a powerful way to generate new insights into how climate change will affect zooplankton and the pivotal role they play in the world's marine ecosystems.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-023-01630-7.

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Methods

The model

We use the ZooMSS (v.2.1)[18], which uses the functional size-spectrum framework[60] to resolve multiple zooplankton and fish groups. In brief, ZooMSS resolves a single phytoplankton community, nine of the most prevalent zooplankton functional groups (heterotrophic flagellates and ciliates, omnivorous and carnivorous copepods, larvaceans, salps, euphausiids, chaetognaths and jellyfish) and three fish groups. The nine zooplankton groups are defined by their size ranges, feeding characteristics (PPMR and feeding kernel width) and carbon content. The three size-based fish groups are defined by their size ranges, broadly representing: small pelagic (planktivorous) fish ≤100 g, medium pelagic fish 100 g ≤ 10 kg and large pelagic fish 10 kg ≤1 t. Other than their asymptotic size, the three fish groups share the same functional traits (feeding characteristics and carbon content), which are unique from the zooplankton groups. A summary of the parameter values used to define the functional traits of the nine zooplankton and three fish communities can be found in Supplementary Table 1. The version of ZooMSS used here has been slightly updated from the previous iteration (v.2.0)[18]. Carbon contents of flagellates, copepods, larvaceans and salps have been updated to better reflect published estimates, and the size range of flagellates has been expanded to incorporate nanoflagellates (<3 µm). These updates result in very minor changes to model outputs compared to the previous iteration. To aid interpretation, in the main text we aggregated the output from the seven mesozooplankton and macrozooplankton types into three summary groups on the basis of their feeding characteristics: omnivores (omnivorous copepods and euphausiids), carnivores (carnivorous copepods, chaetognaths and jellyfish) and filter feeders (larvaceans and salps). Heterotrophic flagellates and ciliates were grouped together as microzooplankton.

Zooplankton and fish growth at any size class is driven by the density of smaller organisms within their preferred prey size range. For predators, growth conversion efficiency—the proportion of consumed food converted into new wet weight biomass—is affected by the carbon content of their prey. Prey groups with larger carbon contents (for example, copepods) contribute more to the growth of their predators when they are consumed than other groups with less carbon (for example, jellyfish). From the perspective of the prey, total predation from larger size classes is the primary source of mortality. Since individuals grow and age over time, senescence mortality is also included, which increases with body size.

ZooMSS is driven by sea-surface temperature and phytoplankton variables (see next section on Environmental drivers). Across the global ocean, zooplankton community composition emerges based on the relative fitness of the different groups. Since temperature affects all groups in the same way, it is a secondary driver of total zooplankton biomass (since background mortality from senescence increases with temperature)and not a major driver of zooplankton composition. Rather, zooplankton composition is primarily driven by shifts in the size structure of the phytoplankton, from oligotrophic to eutrophic waters (Supplementary Fig. 14).

Spatial patterns of zooplankton groups generally agree with observations, as do growth rates of the functional groups[18]. However, the zooplankton abundance modelled in ZooMSS is considerably higher than observations[18]. This could be due to the abundance estimates of zooplankton in ZooMSS including all size classes—eggs, nauplii, larvae, juveniles and adults—whereas observations from nets severely underestimate early life stages and thus abundances[4]. At the same time, total zooplankton biomass from ZooMSS across the global ocean is within the range of two empirical estimates[18,61]. However, this does not mean that ZooMSS could not be within the range of empirical estimates for the wrong reasons or due to compensation effects.

Environmental drivers

ZooMSS is run with sea-surface temperature and phytoplankton variables averaged annually, with a 1° spatial resolution. With respect to phytoplankton variables, at minimum ZooMSS requires surface chlorophyll *a* from Earth-system models or satellite to calculate the size structure of the phytoplankton community. However, where available, mean size-fractionated phytoplankton biomass across the euphotic zone can also be used to calculate continuous phytoplankton size spectra.

Temperature affects the growth and mortality rates of the zooplankton and fish functional groups. Temperature is incorporated into growth and mortality rates with a Q_{10} factor of 2, meaning that for every 10° C of warming, all growth and mortality rates of zooplankton and fish are accelerated twofold. We chose a Q_{10} factor of 2 based on the comprehensive review of zooplankton growth rates[62], which contained >2,500 observations across nine zooplankton taxonomic groups (non-copepod crustaceans, copepods, cnidarians, ctenophores, chaetognaths, pteropods, polychaetes, thaliaceans and larvaceans). They found Q_{10} values ranged from 0.38 to 3.86, with a median of 1.86, although when individual body size was accounted for the median Q_{10} value shifted to 2.31. We selected a Q_{10} factor of 2 for zooplankton and fish since it falls between these two median estimates and is also almost identical to the body-size adjusted Q_{10} value of 1.98 for teleost fish[63].

Chlorophyll *a* sets the total biomass and size structure of the phytoplankton community, since phytoplankton dynamics are not explicitly represented in ZooMSS. Phytoplankton community slope, intercept and maximum size is calculated in several steps. First, we use the algorithm from ref. [64], which estimates the percentage contribution of picophytoplankton (0.2–2 µm equivalent spherical diameter (ESD)), nanophytoplankton (2–20 µm ESD) and microphytoplankton (>20 µm ESD) to total chlorophyll *a* in surface waters. This algorithm describes changes in the phytoplankton community composition across the ocean: picophytoplankton dominate in oligotrophic waters but decline as a percentage of the community as chlorophyll *a* concentration increases; nanophytoplankton are most prevalent in mesotrophic waters; and microphytoplankton are a minor component at low chlorophyll concentration but increase from oligotrophic to eutrophic waters (Supplementary Fig. 12). Second, as the chlorophyll:carbon ratio of phytoplankton varies across the oceans of the world[65], the contribution of each of the three phytoplankton groups to total chlorophyll *a* is then converted to carbon biomass using the empirical relationship from Fig. 1c of ref. [65]. Phytoplankton carbon biomass is converted to wet weight assuming 1 g carbon weight = 10 g wet weight[66]. Last, for each 1° grid cell and each year, phytoplankton community slope, intercept and maximum size are then found analytically using the wet weight biomass of the three phytoplankton groups (see the supplement of ref. [18] for more information). Derived phytoplankton abundance slopes range from −1.2 to −0.77 from waters low to high in chlorophyll *a*, which is similar to ranges reported in empirical studies[67–69].

When size-fractionated phytoplankton carbon biomass variables are available from Earth-system models, the conversion step from chlorophyll *a* to carbon described above is not required, nor the size-fractionation step involving the Brewin algorithm[70]. Using size-fractionated phytoplankton directly from Earth-system models also means that subsurface features of the phytoplankton—such as the deep chlorophyll maximum in stratified waters[71]—are incorporated in continuous phytoplankton size spectra for stratified waters (provided these features are present in the Earth-system model phytoplankton).

Of the five Earth-system models used in this study, size-fractionated and depth-resolved phytoplankton carbon biomass was available from CESM2 and GFDL-ESM4. However, we were only able to use these products from GFDL-ESM4 but not CESM2. This was because there is an inconsistency between overall phytoplankton biomass of CESM2 and the size structure of its phytoplankton community. It is well-established empirically that as total phytoplankton biomass increases, the proportion of the phytoplankton that comes from large size classes increases[8,64,72–74]. In CESM2, this relationship exists but it is relatively weak. For example, for most of the global ocean where

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mean phytoplankton biomass in the euphotic zone is between 0.05 and 0.15 g m^{-3} the proportion of phytoplankton from large size classes can vary between ~10% and 90% in CESM2, before sharply increasing to >90% for waters with phytoplankton >0.15 g m^{-3}. In contrast, the change in the proportion of phytoplankton from large size classes in GFDL-ESM4 increases smoothly from ~2% to 70%, across waters with low to high phytoplankton biomass (Supplementary Fig. 13a). As a result, we found it was not possible to consistently convert small and large phytoplankton biomass from CESM2 to continuous phytoplankton size spectra; total phytoplankton biomass from CESM2-derived continuous size spectra does not match what is provided from the ESM itself, a challenge that is not present with GFDL-ESM4-derived phytoplankton spectra (Supplementary Fig. 13b). Therefore, for GFDL-ESM4, we used size-fractionated and depth-resolved phytoplankton carbon biomass to calculate continuous phytoplankton size spectra but, for CESM2 and the other Earth-system models, we used surface chlorophyll *a* concentration.

To assess how using either surface chlorophyll *a* or size-fractionated phytoplankton could alter our results, we compared changes in the ZooMSS zooplankton community composition for GFDL-ESM4 simulations that have both phytoplankton outputs available under SSP 5–8.5. Spatial patterns of contemporary phytoplankton size structure and zooplankton composition, as well as future changes in both were broadly similar between the two approaches with GFDL-ESM4 (Supplementary Figs. 6–9). However, in polar and tropical biomes, mean climate-driven increases in picophytoplankton as a proportion of the total phytoplankton were lower (~0% versus 2% in polar waters and ~6% versus 8% in tropical waters) when depth-resolved phytoplankton was used compared to surface chlorophyll *a* (Supplementary Fig. 10). This smaller change slightly reduced the increase in the proportion of the total zooplankton from filter feeders (~0% versus 2% in polar waters and ~6% versus 8% in tropical waters) and corresponding decrease in omnivores in these regions (Supplementary Fig. 11). All else being equal, this suggests that increases in the prevalence of gelatinous filter feeders at the expense of omnivores could be attenuated, depending on how phytoplankton community size structure is parameterized. However, uncertainty in projected shifts in plankton composition introduced when alternative inputs are used to calculate the continuous phytoplankton size-spectrum is much smaller than the total uncertainty across the five Earth-system models (Supplementary Figs. 10 and 11).

Model caveats

There are several caveats associated with ZooMSS. First, since ZooMSS is designed to provide insight into the long-term conditions of marine ecosystems over large spatial scales, we have made many simplifying assumptions about dynamic processes such as reproduction, seasonality and predator–prey coupling in the plankton. Zooplankton reproduction is a complex and diverse process, with groups exhibiting a variety of strategies such as binary fission in ciliates[75] and flagellates[76], alternating generations of sexual and asexual reproduction in salps[77] and jellyfish[78], hermaphroditism in chaetognaths[79] and intersexuality in copepods[80]. What is more, since many zooplankton groups time their reproduction to coincide with phytoplankton blooms[81,82] seasonal cycles of boom and bust in the phytoplankton is a major driver of variation of zooplankton productivity, particularly in polar and temperate areas. However, for simplicity, ZooMSS assumes constant recruitment for fish and zooplankton groups, as in some other size-spectrum models[57,83], which keeps the abundances of their smallest size classes fixed, relative to the abundance of other groups in the same size class. By simplifying reproduction and using a yearly temporal resolution for our model inputs, we do not explicitly resolve these reproductive and seasonal processes.

Second, another simplifying assumption in ZooMSS and other global marine ecosystem models is that the phytoplankton community is represented as a static resource because it is driven by external inputs (for example, satellite remote sensing or Earth-system models) and thus has no predation feedback from higher trophic levels[30]. However, at large temporal and spatial scales, the absence of an explicit two-way coupling between phytoplankton and zooplankton in ZooMSS does not lead to unrealistic estimates of zooplankton biomass or growth, since the model can reproduce global zooplankton biomass and growth rates within the range of empirical estimates[18]. Further, global zooplankton biomass declines under climate change are similar in ZooMSS to the range of projections from biogeochemical models that explicitly resolve predator–prey interactions between phytoplankton and zooplankton[21]. Yet, the absence of diverse zooplankton reproductive strategies and phytoplankton dynamics, from predation impacts to seasonal booms and busts, means that the current version of ZooMSS is not suitable for providing insight beyond long-term conditions of marine ecosystems over large spatial scales.

Third, the size structure estimated from the near-surface chlorophyll *a* is assumed to be representative of the phytoplankton community size structure more generally. Using near-surface chlorophyll *a* from four of the five Earth-system models used in this study means that ZooMSS does not resolve phytoplankton communities at the deep chlorophyll maximum layers, which are ubiquitous in low chlorophyll *a*, stratified regions[71] and thus probably underestimates primary producer biomass in oligotrophic regions.

Fourth, and related to the second caveat, where size-fractionated, depth-resolved phytoplankton biomass is not available directly from the Earth-system models, ZooMSS does not resolve phytoplankton size structure through the upper water column. In these instances, we use surface chlorophyll *a* to represent the phytoplankton (where size-fractionated phytoplankton is not available from Earth-system models) because it is a key variable used by algorithms that calculate the global contribution of pico-, nano- and microphytoplankton to total phytoplankton biomass[84]. This includes the algorithm used by ZooMSS, developed by ref. [64], which we selected because it was calibrated using an extensive dataset of 5,841 in situ samples across all basins except the Arctic Ocean. To our knowledge, the algorithm of ref. [74] is the only global algorithm that uses surface chlorophyll *a* to calculate phytoplankton community composition across the entire euphotic zone. However, ref. [74] found that in stratified waters where the deep chlorophyll maximum is a persistent feature, the variation in phytoplankton size structure over 1.5 times the euphotic zone depth from oligotrophic to eutrophic waters was broadly similar to the variation in surface waters (comparing Fig. 6a and c in ref. [74]). Uncertainties remain around how phytoplankton size structure varies with depth at the global scale[74], as well as how phytoplankton at the individual and community level will respond to climate change[64,85,86]. However, it is widely expected that the global dominance of small phytoplankton will increase[34,86,87] as warm, nutrient-poor oligotrophic regions expand[88] and this expectation is the primary driver of the projected climate-driven changes in zooplankton composition in ZooMSS.

Although temperature sensitivity varies among taxa[89], ZooMSS uses a uniform Q_{10} across groups, as is common in many marine ecosystem and Earth-system models[30,34,90–94]. This is because—to the best of our knowledge—a meta-analysis of the temperature dependence of physiological processes related to growth and mortality across broad zooplankton taxonomic groups does not yet exist. Since we use the same Q_{10} across all functional groups, temperature shifts have little effect on the relative competitiveness of different zooplankton groups in ZooMSS. Rather, all else being equal, increasing temperatures will primarily cause declines in biomass for all groups, due to increasing non-predation mortality (for example, senescence) that is not balanced by increases in predation-driven growth.

Finally, ZooMSS is not a hydrodynamic model and thus does not resolve passive (for example, by currents) or active movement of fish or zooplankton. This is a common weakness among other global marine ecosystem models[91–94]. This could bias abundances in certain regions

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due to active movement and migration of apex predators by swimming and by passive transport of zooplankton. Further, the lack of hydrodynamics means that ZooMSS does not include vertical mixing, which could affect zooplankton abundances, although the phytoplankton fields from Earth-system models used to drive ZooMSS do include hydrodynamic processes.

Running the model

Abundances of the zooplankton and fish groups were each governed by separate, second-order McKendrick–von Foerster equations, which we solved numerically using a second-order semi-implicit upwind finite difference scheme[95]. For each 1° cell and for each year, ZooMSS is initialized with the same zooplankton composition[18] and community structure then emerges, on the basis of the relative fitness of the different groups given environmental conditions. Previous sensitivity analysis has shown that total zooplankton biomass from the model is robust to ±50% changes in the initial abundance of each zooplankton group[18].

For each simulation forced with temperature, chlorophyll *a* concentration or size-fractionated and depth-resolved phytoplankton biomass, we run the model for 1,000 years, with a half-weekly time step and the zooplankton and fish community size ranges discretized into 0.1 $\log_{10}$ size intervals. The first 500 years is a burn-in period, allowing the different zooplankton groups to interact and settle from initial conditions. The very large PPMRs of salps, larvaceans and euphausiids means that simulated biomass does not settle to a constant level as the simulation progresses, an effect that has been observed in many theoretical studies[16,96–98]. Rather, model biomass for the different groups settles into a series of repeating cycles through time. To address this, results are obtained by calculating mean diets and biomass over the last 500 years of each simulation for each functional group, to obtain long-term averages over the repeating cycles.

Assessing climate effects on zooplankton

We assess changes in the biomass of omnivores (euphausiids and omnivorous copepods), filter feeders (larvaceans and salps) and carnivores (chaetognaths, jellyfish and carnivorous copepods) as well as resultant changes in zooplankton community composition and implications for SPF, under three future (2015–2100) Intergovernmental Panel on Climate Change SSP scenarios[19] (SSP 1–2.6, SSP 3–7.0 and SSP 5–8.5) using historical (1980–2000) conditions as a baseline. Environmental drivers required to run the model over the historical and three future SSP scenarios were sourced from five CMIP6 (ref. [20]) Earth-system models: CESM2, GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR and UKESM1-0-LL. We chose these five models because they had been previously selected from the larger CMIP6 model cohort to force ecosystem models in the fisheries and marine ecosystem model intercomparison project (FishMIP), of which ZooMSS is a participating model (https://www.isimip.org/protocol/3/).

To assess climate effects across polar, westerlies (temperate) and trades (tropical) Longhurst biomes[99] (Extended Data Fig. 10), we used the Longhurst biome mask from https://www.marineregions.org. Throughout this work, we have renamed the westerlies and trades biomes to temperate and tropical. Climate-driven changes in phytoplankton are highly uncertain, especially in coastal regions[90]. This is because global Earth-system models with 1° spatial resolution—such as the five used in this study—do not properly resolve biogeochemical dynamics in coastal systems[90,100–103]. For example, in the Peru upwelling, downscaled phytoplankton biomass from three different ESMs (CNRM, GFDL and IPSL) were compared with phytoplankton biomass from the same models but at their original (coarser) resolution[103]. From 2005 to 2100 under representative concentration pathway (RCP) 8.5, the coarser resolution models predicted a decrease in chlorophyll (between −11% and −104%), whereas the higher resolution versions projected an increase of between 2% and 17%. Because of this uncertainty, we excluded the coastal Longhurst biome from our results.

Calculating fish diet, trophic level and diet carbon content

The trophic level of SPF (TL_{SPF}) was calculated for all fish with an asymptotic size of 100 g irrespective of life stage, which is because the trophic level of an individual is more related to its body size than life stage[104]:

$$TL_{SPF} = 1 + \sum_j TL_j \times PD_{SPF,j},$$

where TL_j is the trophic level of group j and $PD_{SPF,j}$ is the proportion of the diet of SPF from group j:

$$PD_{SPF,j} = \frac{F_{SPF,j}}{\sum_j F_{SPF,j}},$$

and $F_{SPF,j}$ is the total biomass from group j consumed by SPF. Except for phytoplankton, which have a fixed trophic level of 1, the trophic levels of the different zooplankton and fish groups change with their diet, so we used the Gauss–Jacobi iteration method to solve TL_{SPF}.

SPF diet carbon content, CC_{SPF}, was:

$$CC_{SPF} = \frac{C_j B_{SPF,j}}{\sum_j C_j B_{SPF,j}},$$

where $B_{SPF,j}$ is the total biomass from group j consumed by SPF and C_j is the carbon content of group j, as a proportion of total wet biomass.

Statistical methods

We ran ZooMSS five times in total, with each run forced by one of the five Earth-system models used. These simulations were summarized as means and standard deviations in figures and tables. To verify if mean changes in total zooplankton biomass and the biomass of filter feeders, carnivores and omnivores were significant, P values in Table 1 were calculated using two-sided Mann–Whitney non-parametric U-tests comparing initial (1980–2000, $n = 100$; 20 years × 5 simulations) and final (2080–2100, $n = 100$) biomass changes. Only biomass changes that had significant P values ($P < 0.05$) were discussed in the text.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

ZooMSS environmental inputs were sourced from five climate models from CMIP6 (Methods; climate model data are available from the Earth System Grid Federation here: https://esgf-data.dkrz.de/projects/esgf-dkrz/). ZooMSS model outputs analysed in this study are available at https://doi.org/10.5281/zenodo.7619220 (ref. [105]).

Code availability

ZooMSS model code is available at https://github.com/MathMarEcol/ZoopModelSizeSpectra. The code used to conduct all analysis in this study is available at https://doi.org/10.5281/zenodo.7619220 (ref. [105]).

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Author contributions

R.F.H., A.J.R. and J.D.E. defined the research question for this study. J.D.E. conducted the simulations, with the assistance from R.F.H. R.F.H. drafted the manuscript, with the assistance and feedback from A.J.R., J.D.E., P.S. and J.L.B.

Competing interests

The authors declare no competing interests.

Additional information

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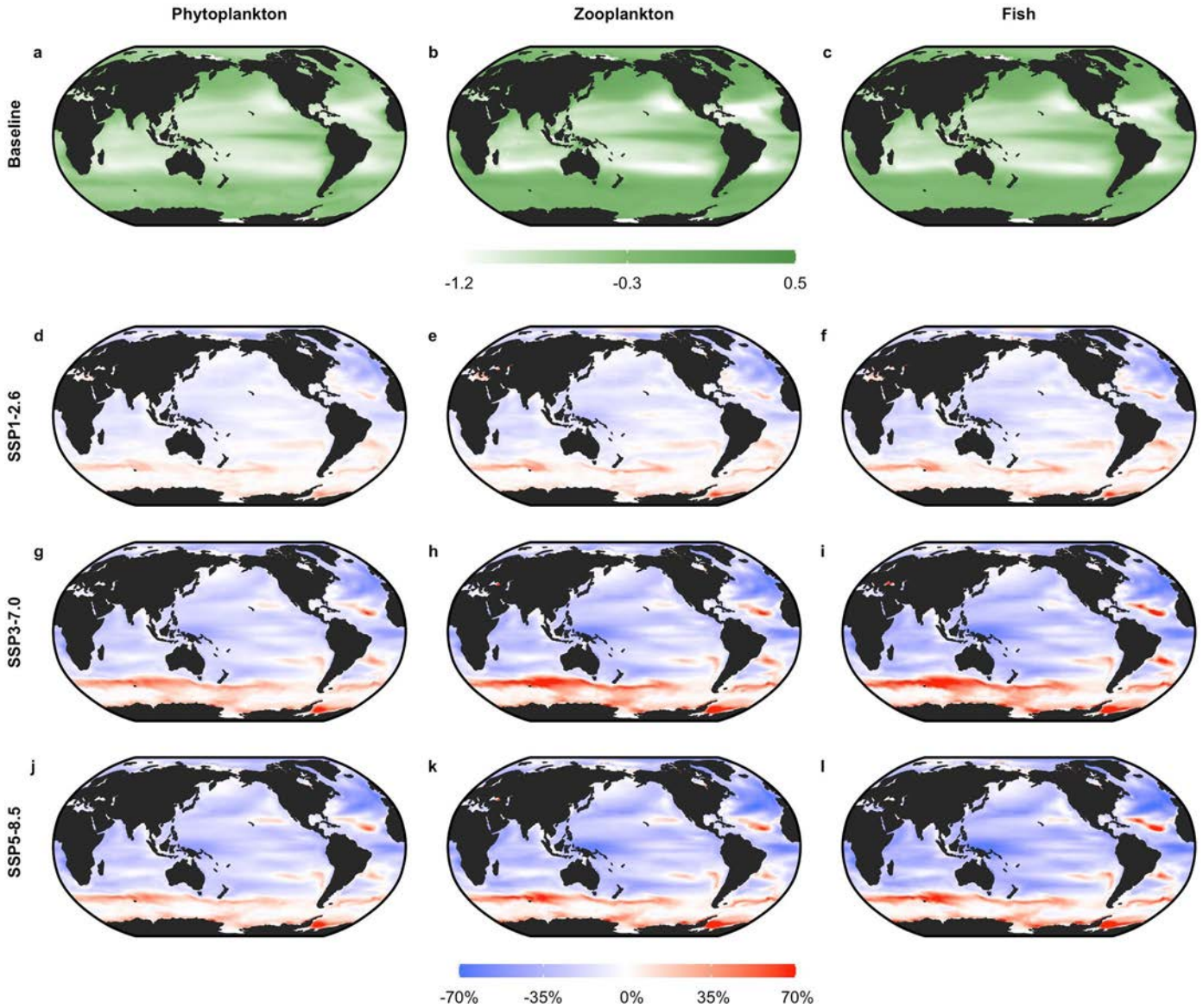
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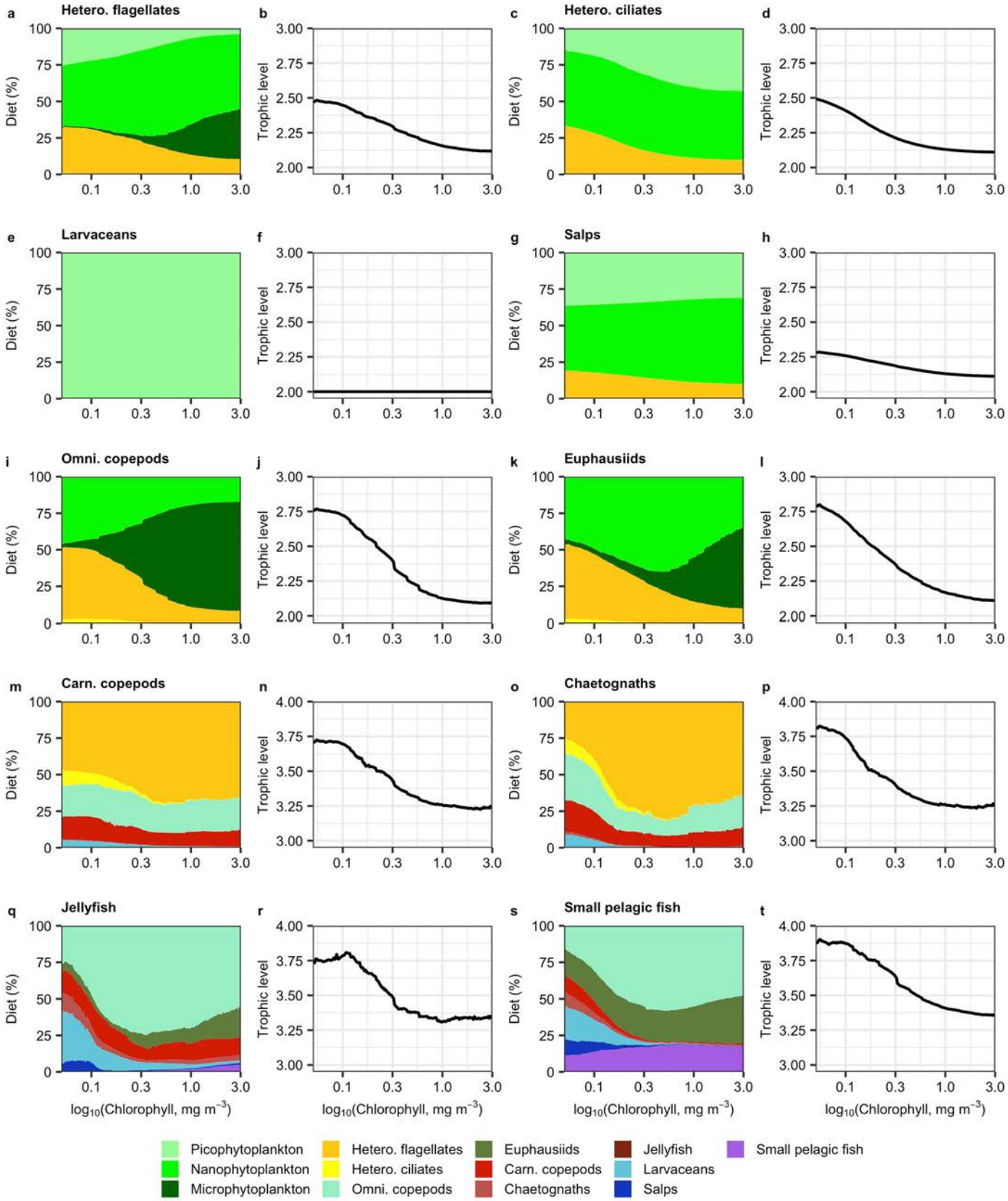
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Extended Data Fig. 1 | Climate-induced shifts in biomass of phytoplankton, zooplankton and SPF. Mean $\log_{10}$ biomass (g m^{-2}) in 1980–2000 of: **a**, Phytoplankton; **b**, Zooplankton (both micro and macrozooplankton); **c**, SPF; (**d**–**l**), Maps of the mean change in the total biomass of: (**d, g, j**), Phytoplankton; (**e, h, k**), Zooplankton; and (**f, i, l**), SPF in 2080–2100 compared with 1980–2000 under emission scenarios SSP 1–2.6 (**d**–**f**), SSP 3–7.0 (**g**–**i**) and SSP 5–8.5 (**j**–**l**), across the five Earth-system models used to force ZooMSS (see Assessing climate impacts on zooplankton in Methods for more information about Earth-system models used in this study).

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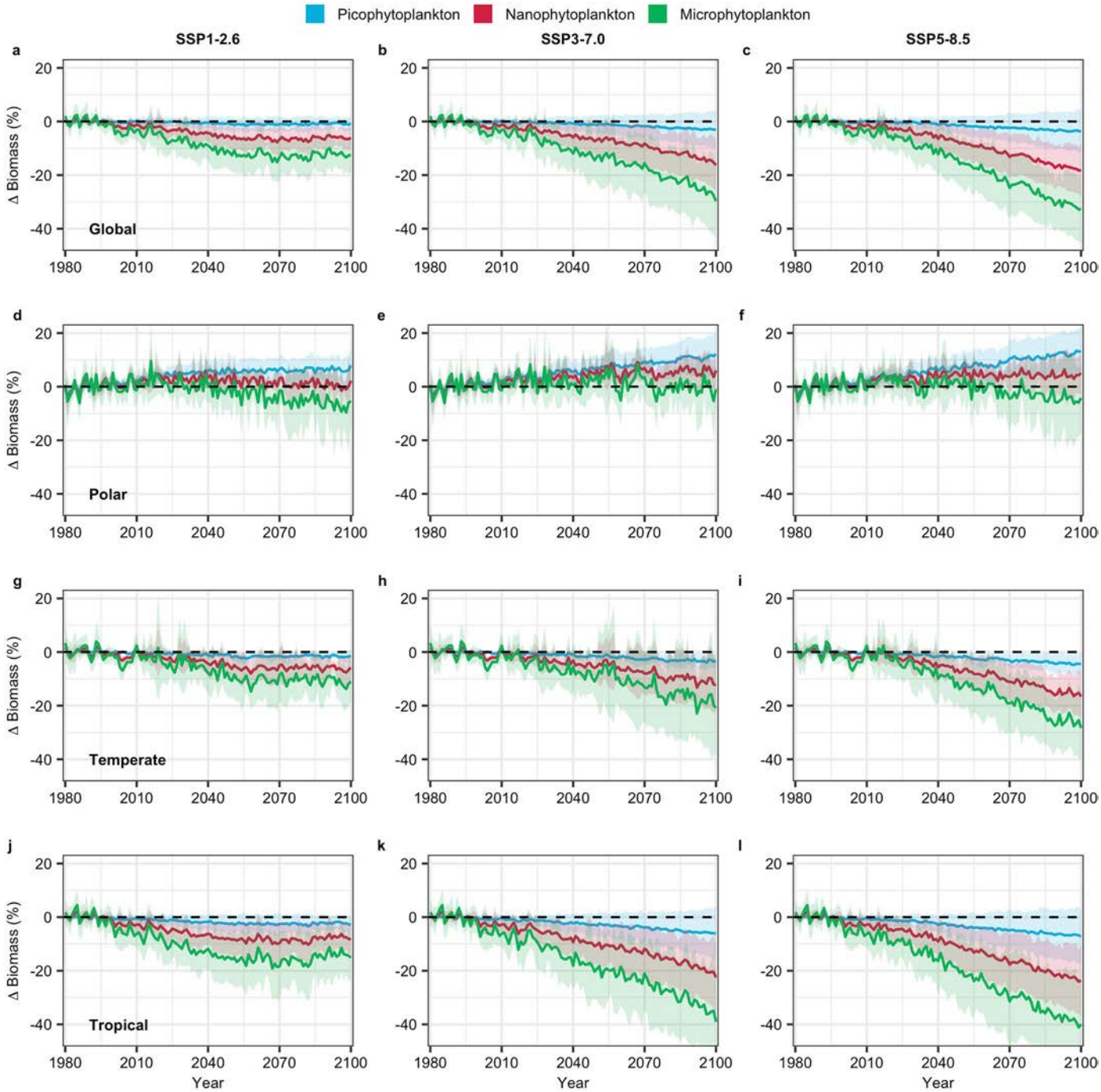
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Extended Data Fig. 2 | Diet composition and trophic level of the 9 zooplankton groups in ZooMSS. Mean diet composition and resultant trophic level across the global chlorophyll gradient from the five Earth-system models used to force ZooMSS for **a, b**, Heterotrophic (Hetero.) flagellates; **c,d**, Heterotrophic (Hetero.) ciliates; **e,f**, Larvaceans; **g,h**, Salps; **i,j**, Omnivorous (Omni.) copepods; **k,l**, Euphausiids; **m,n**, Carnivorous (Carn.) copepods; **o,p**, Chaetognaths; **q,r**, Jellyfish; **s,t**, SPF.

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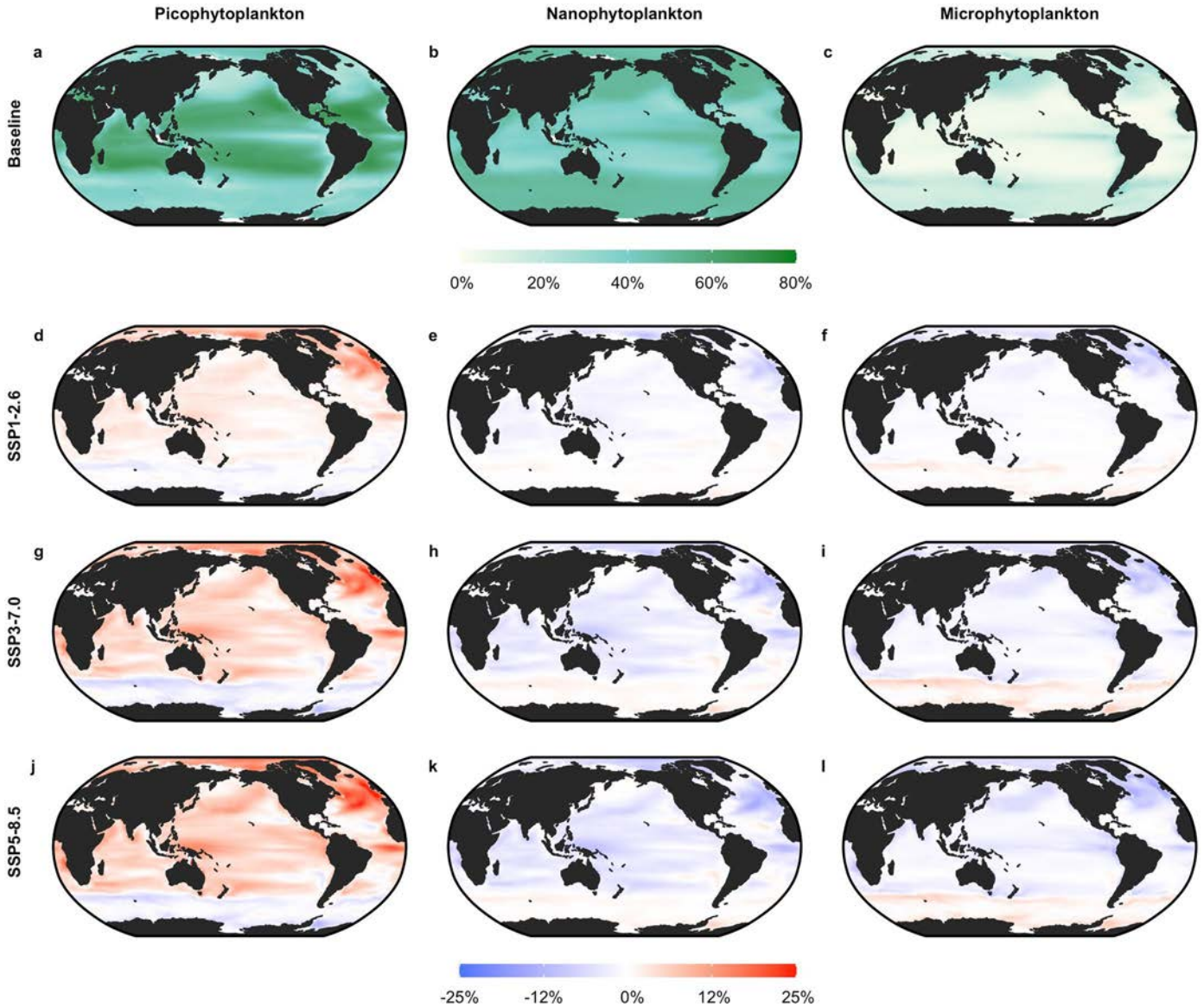
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Extended Data Fig. 3 | Impacts of climate change on the three phytoplankton groups. Change in global biomass (%) for the three phytoplankton groups (Picophytoplankton, 0.2–2 µm ESD; Nanophytoplankton, 2–20 µm ESD; Microphytoplankton, >20 µm ESD) from 1980–2100, relative to 1980–2000, under emission scenarios (**a, d, g, j**) SSP 1–2.6; (**b, e, h, k**) SSP 3–7.0; and (**c, f, i, l**) SSP 5–8.5, across (**a**–**c**) Global; (**d**–**f**) Polar; (**g**–**i**) Temperate; and (**j**–**l**) Tropical waters. Note here that Temperate and Tropical respectively correspond to Westerlies and Trades Longhurst biomes, and Global results exclude the Coastal biome, see Extended Data Figure 10 for a map of the biomes. Solid lines give the ensemble mean change and shaded areas represent the standard deviation for each phytoplankton group across the five Earth-system models used to provide forcings for ZooMSS. The dashed black line in each plot represents no change from mean biomass in 1980–2000.

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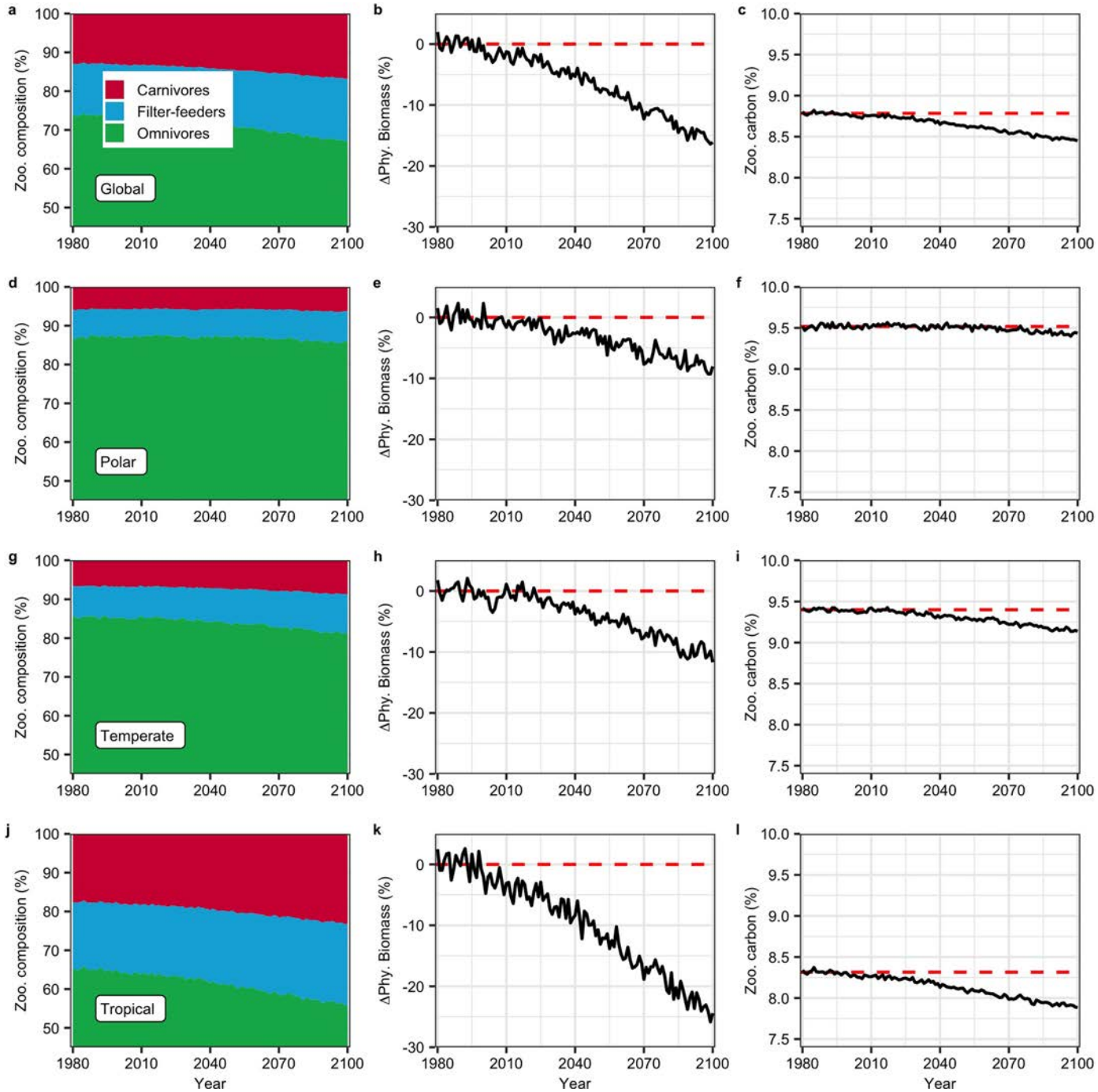
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Extended Data Fig. 4 | Climate-induced shifts in biomass of pico (0.2–2 µm ESD), nano (2–20 µm ESD) and microphytoplankton (>20 µm ESD). The baseline percentage of total phytoplankton biomass in 1980–2000 comprising: **a**, Picophytoplankton; **b**, Nanophytoplankton; **c**, Microphytoplankton. **d**–**l**, Maps of the mean change (%) of total phytoplankton biomass from: (**d, g, j**) Picophytoplankton; (**e, h, k**) Nanophytoplankton; and (**f, i, l**) Microphytoplankton in 2080–2100 relative to 1980–2000 under emission scenarios (**d**–**f**) SSP 1–2.6; (**g**–**i**) SSP 3–7.0; and (**j**–**l**) SSP 5–8.5, across the five Earth-system models used to force ZooMSS.

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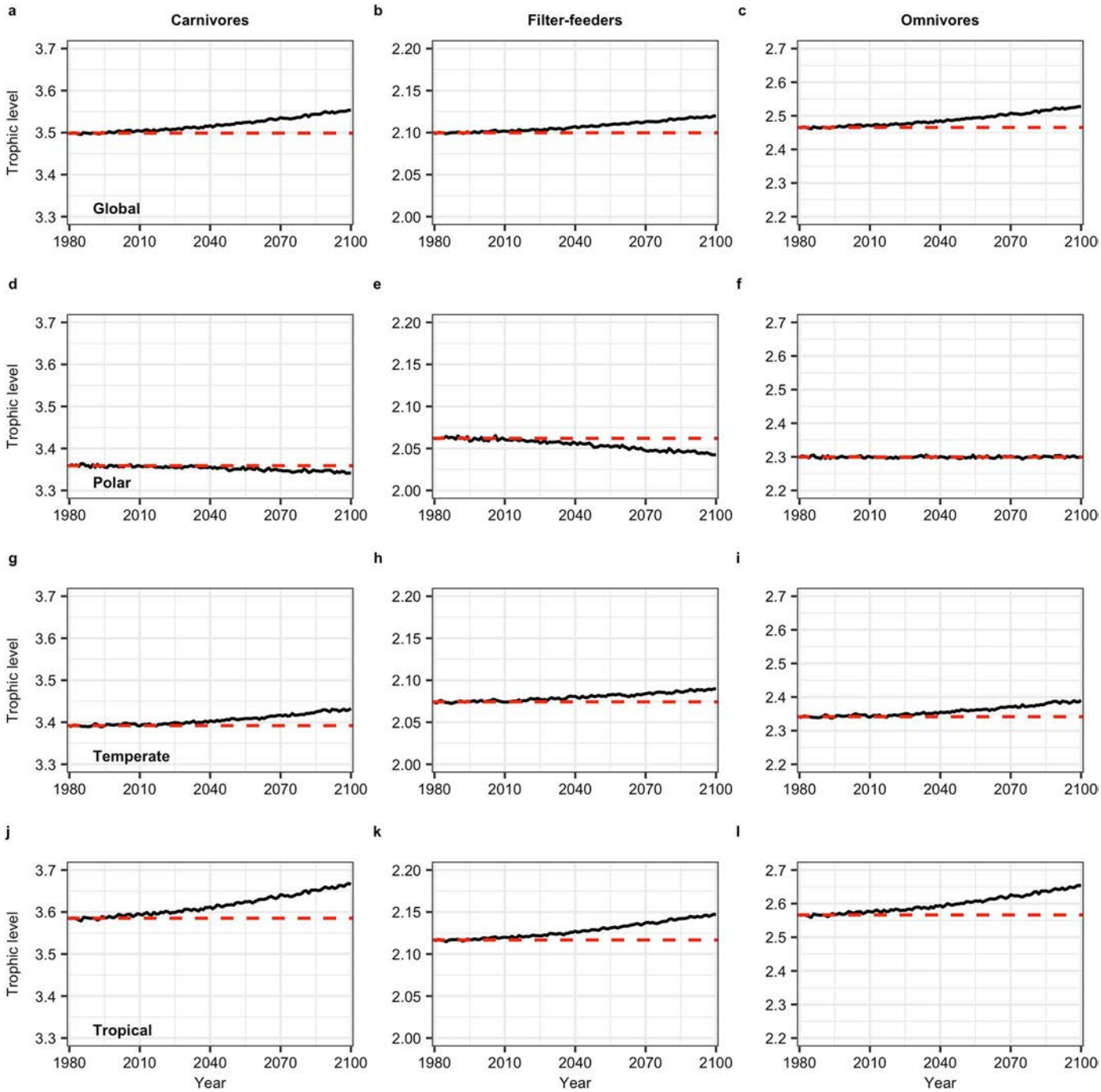
https://doi.org/10.1038/s41558-023-01630-7



Extended Data Fig. 5 | Impacts of climate change on the plankton. Mean change (%) in (**a, d, g, j**) zooplankton (Zoo.) community composition; (**b, e, h, k**) phytoplankton (Phy.) biomass and (**c, f, i, l**) zooplankton community carbon content (Zoo. carbon), relative to 1980–2000 under SSP 5–8.5, in (**a**–**c**) Global; (**d**–**f**) Polar; (**g**–**i**) Temperate and (**j**–**l**) Tropical waters, across the five Earth-system models used to force ZooMSS in this study. Carnivores include chaetognaths, jellyfish and carnivorous copepods, Filter-feeders include salps and larvaceans, and Omnivores include euphausiids and omnivorous copepods. Note here that Temperate and Tropical respectively correspond to Westerlies and Trades Longhurst biomes, and Global results exclude the Coastal biome, see Extended Data Figure 10 for a map of the biomes.

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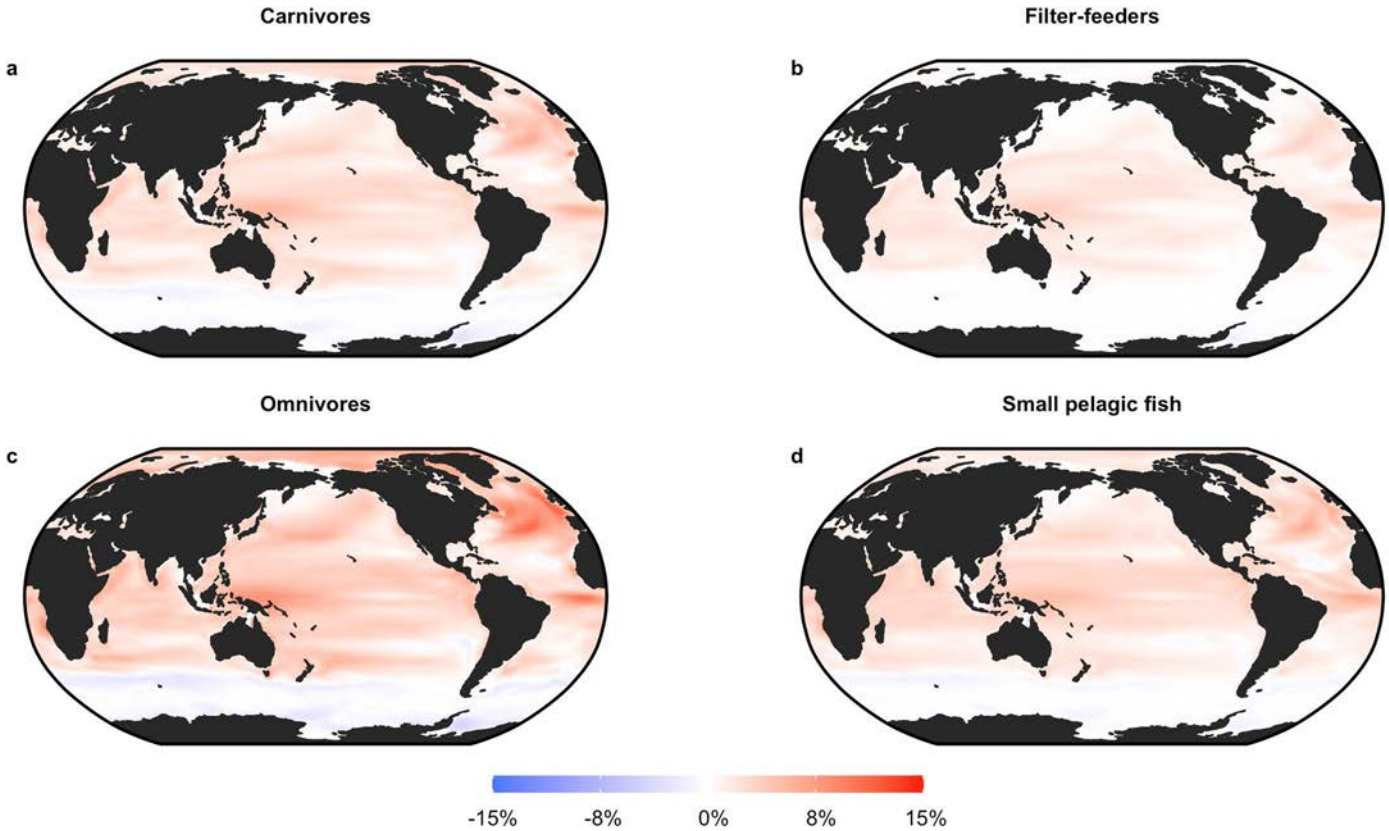
https://doi.org/10.1038/s41558-023-01630-7



Extended Data Fig. 6 | Impacts of climate change on zooplankton trophic levels. Mean trophic level of carnivores (carnivorous copepods, chaetognaths and jellyfish; **a, d, g, j**), filter-feeders (salps and larvaceans; **b, e, h, k**) and omnivores (omnivorous copeopods and euphausiids; **c, f, i, l**) from 1980–2100 under SSP 5–8.5 in (**a**–**c**) Global; (**d**–**f**) Polar; (**g**–**i**) Temperate and (**j**–**l**) Tropical waters, across the five Earth-system models used to force ZooMSS in this study. Note here that Temperate and Tropical respectively correspond to Westerlies and Trades Longhurst biomes, and Global results exclude the Coastal biome, see Extended Data Figure 10 for a map of the biomes. The red dashed line in each figure indicates the mean trophic level from 1980–2000.

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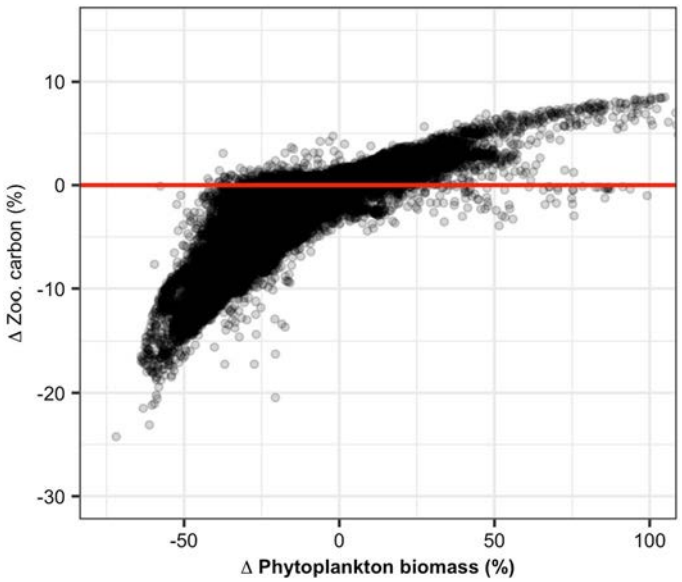
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Extended Data Fig. 7 | Climate-induced shifts in trophic levels. Maps of the mean change (%) in trophic level of **a**, Carnivores; **b**, Filter-feeders; **c**, Omnivores; and **d**, Small (Pelagic) fish in 2080–2100 relative to 1980–2000 under emission scenarios SSP 5–8.5, across the five Earth-system models used to force ZooMSS.

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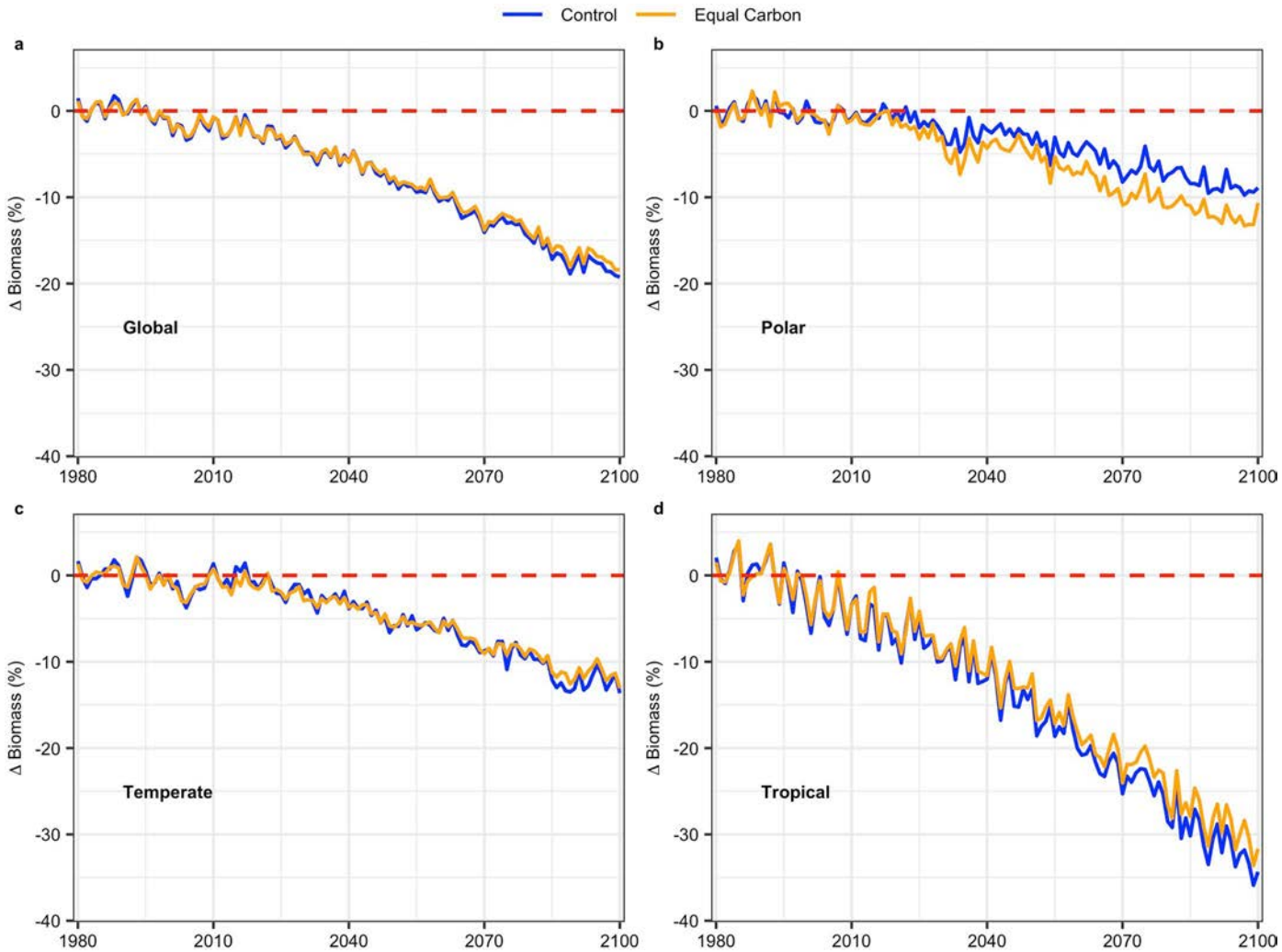
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Extended Data Fig. 8 | Impacts of changing phytoplankton biomass on zooplankton community carbon content. Percentage change in zooplankton community carbon content against the percentage change in phytoplankton biomass, for individual 1° grid squares from 1980–2000 to 2080–2100 under the SSP 5–8.5 emissions scenario. The red solid horizontal line indicates where the percentage change in zooplankton community carbon content is zero.

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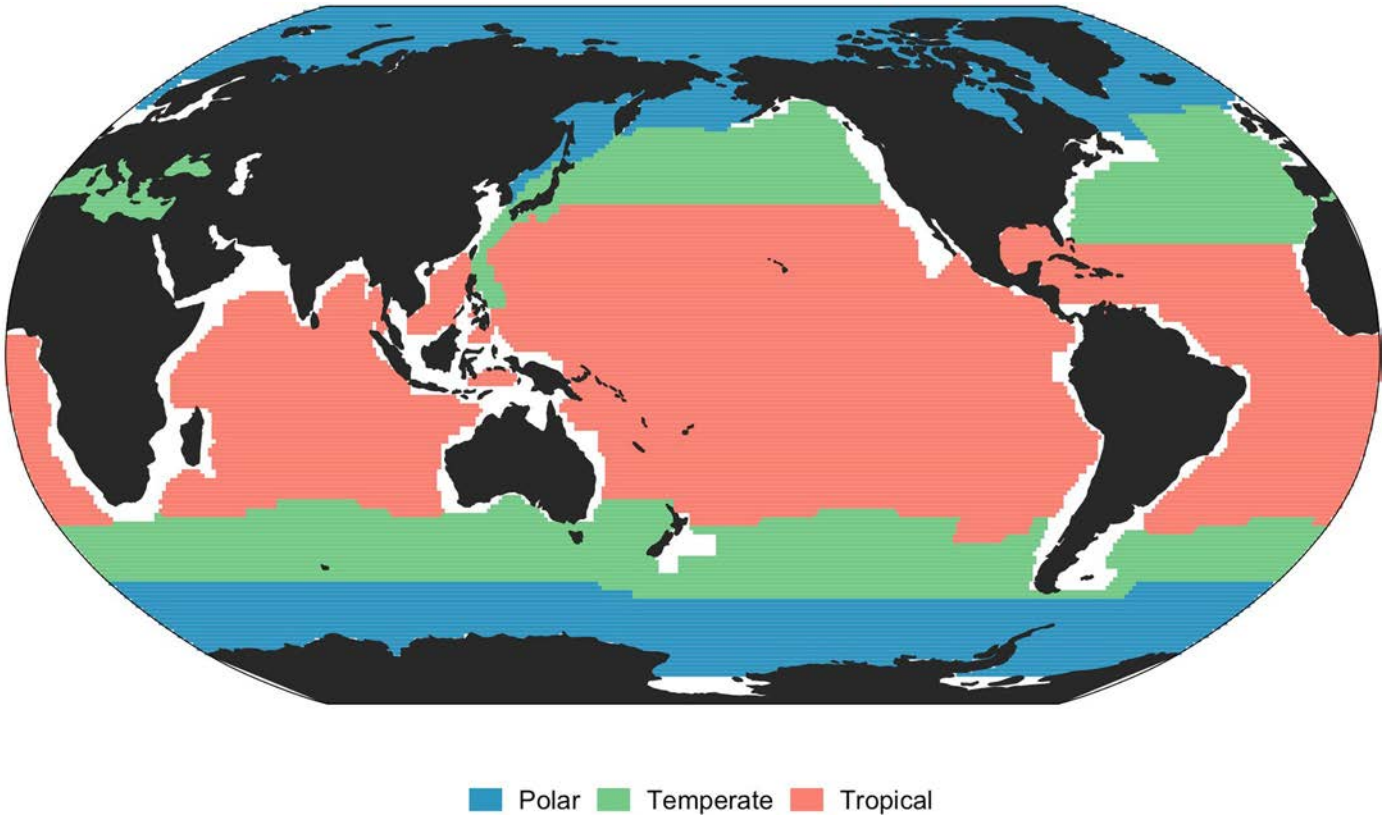
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Extended Data Fig. 9 | Impacts of zooplankton carbon content on SPF biomass. Mean percentage change in the biomass of SPF under SSP 5–8.5, from 1980–2100 across **a**, Global (excluding the coastal biome); **b**, Polar; **c**, Temperate; **d**, Tropical waters. The blue line in each plot is the change in small pelagic biomass under the standard model run, where the carbon content of each zooplankton group is given in Table S1, while the orange line is the change in SPF biomass when the carbon content of all zooplankton groups is fixed at 10%. The red dashed line indicates where there is no biomass change against mean levels in 1980–2000.

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Extended Data Fig. 10 | Map of the three Longhurst ocean biomes used in this study. The Coastal biome has been excluded from our analysis. Note that in this study, the Westerlies and Trades biomes have been renamed to Temperate and Tropical, respectively. See Assessing climate impacts on zooplankton in the Methods for more information.

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Data was collected using the Zooplankton Model of Size Spectra (ZooMSS). Code to run ZooMSS is available here: https://github.com/MathMarEcol/ZoopModelSizeSpectra. ZooMSS model outputs analysed in this study are available at https://doi.org/10.5281/zenodo.7619220. All other inputs to force ZooMSS came from existing sources (see 'Assessing climate impacts on zooplankton' in Methods section).
Data analysis	We used CDO (climate data operators) and R 4.2.2 to analyse the data in this study. All code and data used to generate results in this study are available at Zenodo: https://doi.org/10.5281/zenodo.7619220

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- Accession codes, unique identifiers, or web links for publicly available datasets
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ZooMSS environmental inputs were sourced from five climate models from CMIP6 (see Methods for more information; climate model data are available here: https://esgf-node.llnl.gov/search/cmip6/). ZooMSS model outputs analysed in this study are available at https://doi.org/10.5281/zenodo.7619220

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	N/A
Population characteristics	N/A
Recruitment	N/A
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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Ecological, evolutionary & environmental sciences study design

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Study description	We used a global marine size-spectrum model (ZooMSS) to assess the impacts of climate change on the composition of zooplankton across the world's oceans. We also assessed potential implications for fish communities of projected changes in zooplankton composition.
Research sample	We used data on: Climate models: 5 earth-system models from the Coupled Model Intercomparison Project Phase 6 (https://esgf-node.llnl.gov/search/cmip6/) provided environmental forcings to force ZooMSS, from 1980-2100 under three climate change scenarios (SSP1-2.6, SSP3-7.0 and SSP5-8.5). The five models were CESM2, GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, UKESM1-0-LL. All models provided sea surface temperature and chlorophyll concentration. GFDL and CESM2 provided depth-resolved, size-fractionated phytoplankton carbon as well. Marine provinces: Longhurst biomes from Marine Regions (www.marineregions.org). This dataset has been provided in the Zenodo respository for this study).
Sampling strategy	Environmental drivers required to run the model over the historical and three future SSP scenarios were sourced from five Coupled Model Intercomparison Project Phase 620 (CMIP6) earth-system models: CESM2, GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, UKESM1-0-LL. We chose these five models because they had been previously selected from the larger CMIP6 model cohort to force ecosystem models in the Fisheries and marine ecosystem Model Intercomparison Project (FishMIP), of which ZooMSS is a participating model (https://www.isimip.org/protocol/3/).
Data collection	Data was generated by ZooMSS, or obtained from online repositories. All data presented in this study can be found at: https://doi.org/10.5281/zenodo.7619220
Timing and spatial scale	Global spatial scale, exploring 1980-2100 under three climate change scenarios (SSP1-2.6, SS3-7.0 and SSP5-8.5).
Data exclusions	No data were excluded from our study
Reproducibility	N/A - No experiments were performed

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Randomization	N/A - No experiments were performed
Blinding	N/A - No experiments were performed

Did the study involve field work? ☐ Yes ☒ No

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☒	☐ Dual use research of concern

Methods

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☒	☐ MRI-based neuroimaging

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Conservation Biology

Review

A Framework for Developing Objective and Measurable Recovery Criteria for Threatened and Endangered Species

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Abstract: *For species listed under the U.S. Endangered Species Act (ESA), the U.S. Fish and Wildlife Service and National Marine Fisheries Service are tasked with writing recovery plans that include "objective, measurable criteria" that define when a species is no longer at risk of extinction, but neither the act itself nor agency guidelines provide an explicit definition of objective, measurable criteria. Past reviews of recovery plans, including one published in 2012, show that many criteria lack quantitative metrics with clear biological rationale and are not meeting the measureable and objective mandate. I reviewed how objective, measureable criteria have been defined implicitly and explicitly in peer-reviewed literature, the ESA, other U.S. statutes, and legal decisions. Based on a synthesis of these sources, I propose the following 6 standards be used as minimum requirements for objective, measurable criteria: contain a quantitative threshold with calculable units, stipulate a timeframe over which they must be met, explicitly define the spatial extent or population to which they apply, specify a sampling procedure that includes sample size, specify a statistical significance level, and include justification by providing scientific evidence that the criteria define a species whose extinction risk has been reduced to the desired level. To meet these 6 standards, I suggest that recovery plans be explicitly guided by and organized around a population viability modeling framework even if data or agency resources are too limited to complete a viability model. When data and resources are available, recovery criteria can be developed from the population viability model results, but when data and resources are insufficient for model implementation, extinction risk thresholds can be used as criteria. A recovery-planning approach centered on viability modeling will also yield appropriately focused data-acquisition and monitoring plans and will facilitate a seamless transition from recovery planning to delisting.*

Keywords: Endangered Species Act, environmental laws, environmental policy, extinction risk assessment, population modeling, population viability analysis, recovery plans, threatened species

Un Marco de Referencia para Desarrollar Criterios de Recuperación Objetivos y Medibles para Especies Amenazadas y en Peligro

Resumen: *Para las especies enlistadas bajo el Acta de Especies en Peligro de los EUA, el Servicio Estadunidense de Pesca y Vida Silvestre y el Servicio Nacional de Pesquerías Marinas tienen la labor de establecer planes de recuperación que incluyan "criterios objetivos y medibles" que definan cuando una especie ya no está en riesgo de extinción, pero ni el acta ni las guías de trabajo de las agencias proporcionan una definición explícita de criterios objetivos y medibles. Resúmenes anteriores de planes de recuperación, incluyendo uno que se publicó en 2012, muestran que muchos criterios carecen de métricas cuantitativas con un razonamiento biológico claro y no están cumpliendo el mandato medible y objetivo. Revisé cómo los criterios objetivos y medibles han sido definidos implícita y explícitamente en literatura revisada por pares, el Acta de Especies en Peligro, otros estatutos de los EUA y decisiones legales. Basado en una síntesis de estas fuentes, propongo que los siguientes seis estándares se usen como requerimientos mínimos para criterios objetivos y medibles: que contengan un umbral cuantitativo con unidades calculables, que estipulen un marco de tiempo dentro del cual deben cumplirse, que explícitamente definan la extensión espacial o la población a la que aplican, que especifiquen*

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un procedimiento de muestreo que incluya tamaño de muestra, que especifiquen un nivel de significancia estadística y que incluyan una justificación proporcionando evidencia científica de que los criterios definen una especie cuyo riesgo de extinción se ha reducido al nivel deseado. Para que cumplan estos seis estándares, sugiero que los planes de recuperación sean guiados explícitamente por y organizados alrededor de un marco de trabajo de modelación de viabilidad poblacional aunque los datos o los recursos de las agencias sean muy limitados para completar el modelo de viabilidad. Cuando los datos y los recursos estén disponibles, los criterios de recuperación pueden desarrollarse a partir de los resultados del modelo de viabilidad poblacional, pero cuando los datos y los recursos son insuficientes para implementar un modelo, se pueden usar los umbrales de riesgo de extinción como criterios. Un método de planificación de recuperación centrado en el modelo de viabilidad también proporcionará datos y planes de monitoreo enfocados apropiadamente y facilitará una transición sencilla de la planificación de la recuperación al retiro de las especies de la lista.

Palabras Clave: Acta de Especies en Peligro, análisis de viabilidad poblacional, estudio de riesgo de extinción, especies amenazadas, leyes ambientales, modelación de poblaciones, planes de recuperación, políticas ambientales

Introduction

When a species is listed as threatened or endangered under the U.S. Endangered Species Act (ESA), the act requires that a recovery plan "for the conservation and survival" of the species be developed. Following amendments to the ESA in 1988, recovery plans are required to include "objective, measurable criteria which, when met, would result in a determination . . . that the species be removed from the list." Despite the pivotal role of recovery criteria in defining recovery for a species and indicating when delisting should be initiated, the ESA provides no clear guidance concerning the substance or structure of criteria beyond the objective, measurable language. Neither does the ESA define *endangered* or *recovered* in unequivocal terms that could dictate criteria content (Vucetich et al. 2006; Robbins 2009).

Scientific reviews of recovery plans and recovery criteria conducted in the third decade of the ESA found them effective in promoting and guiding recovery in some respects but lacking in others, and reviewers made the following recommendations for improvement: make recovery criteria more quantitative and consistent (Tear et al. 1993; Gerber & Hatch 2002), create clearer and more consistent links between criteria and a species' biological status and threats (Tear et al. 1993; Schemske et al. 1994; Gerber & Hatch 2002), increase the use of quantitative models for assessing extinction risk (e.g., population viability analysis [PVA]), and more thoroughly integrate such models into the recovery-planning process (National Research Council 1995; Morris et al. 2002). Some of these reviews (e.g., Gerber & Hatch 2002; Morris et al. 2002) were conducted collaboratively with the U.S. Fish and Wildlife Service (USFWS) and led directly to changes in the Recovery Plan Guidance Document (NMFS & USFWS 2010). The Guidance Document is an ESA-mandated how-to manual for the recovery-planning process written by and for the federal agencies responsible for implementing the ESA (USFWS and National Marine Fisheries Service [NMFS]; hereafter, the Services). The updated Guidance Document explicitly discussed the recommendations and suggested that recovery plans should "provide clearer and more consistent linkage between the biology of the species and the recovery criteria" should "outline and *justify* a strategy to achieve recovery" (emphasis added), and should be "specific," "technically feasible," "grounded in good science," and "time-referenced."

Despite the direction provided in the Guidance Document and previous recommendations, a recent assessment of recovery criteria and delisting thresholds showed that recovery plans and recovery criteria, although improved in some ways, have not improved with respect to many of the critical deficiencies previously identified. For example, 90% of species with potential for delisting (as defined by the Services) have at least one quantitative demographic recovery criterion listed in their recovery plan (an increase from past reviews), but justification for those numbers through quantification of decline in abundance, habitat, or range is rare, and "probabilistic assessments of persistence over time are nearly nonexistent" (Neel et al. 2012). The majority of recovery plans (93%) require higher total abundance than existed at recovery plan writing, but the percentage of species that would rank as secure (>10 populations) under International Union for Conservation of Nature (IUCN) standards at delisting has decreased in recent plans compared with older plans (Neel et al. 2012). Recent plans are also just as likely as older plans to allow delisting to occur with the same or fewer populations than existed at the time of listing or recovery plan writing (Neel et al. 2012).

Given these patterns, it bears asking why recovery criteria have not improved more over time. This question is complex and involves many factors, including sociopolitical ones, but one factor may be the lack of explicit, detailed protocols for developing objective, measurable criteria. The qualitative language of the ESA and lack of specificity in the Guidance Document has long been blamed for inefficiency and ineffectiveness in implementing the law (Easter-Pilcher 1996; Shelden et al. 2001; Vucetich et al. 2006). Although previous reviews and the updated Guidance Document provide more directed guidance than the ESA, they too lack clear and

explicit guidelines on how to develop truly objective, measurable recovery criteria with clear biological justification. I sought to address this absence of an explicit set of best practices for recovery criteria and recovery plans. After synthesizing previous recommendations, the content of the ESA and Guidance Document, and other relevant statutes, policies, and court decisions, I devised a concrete working definition of *objective, measurable criteria* on the basis of 6 unequivocal standards. I also formulated a specific approach to the recovery-planning process that I suggest will result in comprehensive recovery plans that are quantitative and thoroughly justified, complete with recovery criteria that meet the 6 proposed standards. I designed the approach to be feasible under the different circumstances faced by writers of recovery plans, including those with time, budget, and informational constraints.

Definition of Objective and Measurable

The Oxford English Dictionary defines *objective* as "not influenced by personal feelings or opinions in considering and representing facts" (OED Online 2012). *Measurable* is synonymous with *quantifiable*, *determinate*, and *estimable* (i.e., that which can be determined without ambiguity). These definitions suggest that an objective, measurable criterion contains an unambiguous target that leaves no room for interpretation as to whether it has been achieved. In other words, "they minimize interpretation and judgment so that, at least in principle, anyone who applies the same criteria to the same data will get the same results" (Sagoff 1987), and those results will provide a definitive yes or no answer as to whether the criterion has been met.

Objective and *measureable* should, however, be defined not only from dictionary definitions, but within the broader context of the ESA and the policies, documents, and scholarly work that pertain to the statute and accepted scientific practices. For example, in multiple rulings regarding ESA implementation, courts have faulted the Services for their lack of specificity and for providing inadequate justification for decisions and actions (e.g., Middle Rio Grande Conservancy District v. Norton 2002; National Wildlife Federation v. NMFS 2011). Additionally, the Administrative Procedures Act, the Information Quality Act, and the Policy on Information Standards under the ESA require that federal decisions be objective, justified, and transparent (i.e., not be "arbitrary and capricious") (Murphy & Weiland 2011) and that justification be documented (APA 1946; USFWS 1994; IQA 2001). These sources in addition to previously published recommendations and the Guidance Document emphasize quantification, justification, clarity, consistency, specificity, and biological relevance (e.g., Schemske et al. 1994; Easter-Pilcher 1996; Tear et al. 2005).

To meet the measureable mandate as defined by all of these sources, I suggest that a recovery criterion must be quantitative and descriptively and statistically complete. To be objective it must be explicitly justified in the context of a species' ecology, and that justification must be documented and transparent. Specifically, I suggest that the following 6 standards define an objective and measurable criterion: (1) contains a quantitative threshold with specified quantifiable units, (2) stipulates a time frame over which it must be met, (3) explicitly defines the spatial extent or population to which it applies, (4) specifies a statistical significance level, (5) specifies a sampling procedure including sample size, and (6) is justified by providing scientific evidence that the threshold defines a species with the desired risk of extinction.

Quantification

The quantitative standard has 3 components: a numeric threshold, specified units of measure, and units technically measurable under standard scientific protocol. The value of using numeric metrics in recovery criteria and other natural resource management situations has long been recognized (Easter-Pilcher 1996; Tear et al. 2005; Robbins 2009). Although most recent plans include at least one numeric demographic criterion, other types of criteria pertaining to threat abatement or habitat conservation, for example, are rarely quantitative (Neel et al. 2012). Although demographic criteria should be the primary numerical criteria defining when the actual population is no longer at risk of extinction, management- or threat-focused criteria should also be written quantitatively. For example, a requirement to establish a cooperative agreement between 2 (or more) specific entities qualifies as quantitative in that it specifies that one agreement be established between a specific number and set of entities. In contrast, a criterion indicating, for example, that cooperation should be established with affected state agencies is qualitative and provides no definitive threshold to judge whether it has been met. To ensure measurability, clarity, and transparency, and to eliminate ambiguity and subjectivity, an actual numeric value is necessary in all criteria.

A quantitative threshold is useless, however, if units are not specified or if the units specified are not defined. For example, if a criterion requires a population to have 5 viable subpopulations, the units are stated (viable subpopulations); but unless *subpopulation* and *viable* are defined in explicit and numerical terms (e.g., the population occurring above 10,000 feet in the Green Mountains has <5% probability of extinction within 100 years), the quantitative nature of the criterion is lost. Similarly, if a criterion requires a specific amount of habitat, but *habitat* is not defined in explicit terms (e.g., what are the necessary components and in what quantity), determining whether that criterion has been met will necessarily

be based on subjective judgment (Carroll et al. 2010). The same standard applies to management-related criteria. For the cooperative-agreement example above, the criterion should explicitly state what the agreement is to address and how it will be enforced.

Finally, if the specified units are not technically quantifiable or logistically possible to measure, the criterion is rendered unachievable. For example, the requirement that a population attain a specified size is a commonly used criterion. However, for most populations it will be impossible to know with certainty when a population reaches a specific level; rather, it is only possible to know when the estimated population size reaches the threshold. In most cases, each member of a population cannot be counted individually, so the size of a population is estimated through sampling and statistical estimation. Such approaches inherently involve uncertainty; thus, knowing when the true population size has reached the specified threshold will be equivocal. Although this may sound overly pedantic, unless the uncertainty in population sampling and population size estimation is considered and explicitly acknowledged, the criterion loses both scientific credibility and true attainability. If, however, a criterion states that the estimated population size or the field counts, for example, reach a specified threshold, the units are stated and technically measurable. Again, management- or threat-based criteria must meet this same standard. A criterion requiring a cooperative agreement, for example, must specify how the agreement is to be finalized and officially adopted to avoid uncertainty about completion of the criteria. Thus, to meet the quantitative standard of measurability, a criterion (regardless of content or focus) must include a numerical value defining a threshold, must have defined units, and those units must be realistically measurable or estimable under standard scientific practices.

Temporal and Spatial Specificity

To ensure the quantitative metric can be met without ambiguity or alternate interpretation, temporal and spatial references must be included (Mattson & Craighead 1994). A temporal reference indicates over how many years, seasons, or generations a metric must be met to satisfy the criterion. For example, the estimated population size or specific threat may be required to meet or exceed a specified threshold for 10 years before the criterion is met. Without a temporal requirement, the criterion is open to interpretation, and it will be unclear whether delisting should be initiated as soon as the threshold is crossed or whether that level must be sustained over some period. Threat levels and population parameters (e.g., size, growth rate, range) vary over time as a result of intrinsic and extrinsic factors; thus, a population or threat that meets a threshold at a single point in time is usually insufficient evidence of threat neutralization or population viability. The actual length of time specified in a criterion will be a function of the species' biology and policy determinations based on the level of extinction risk acceptable for the particular decision (downlisting or delisting). Non-demographic criteria should also contain temporal specificity. For example, a criteria requiring the development of a management plan should specify how long the plan should be in place prior to delisting and how frequently it should be updated once in place.

Spatial specificity means stipulating either the geographic area or specific populations or subpopulations to which the criterion applies. As noted above, if a criterion fails to indicate to which population or to what portion of the species' range it applies, it is neither technically measurable nor unequivocal and thus does not meet the objective and measurable standard. For example, habitat protection criteria must describe not only the extent of protected habitat, but also the spatial distribution of protected habitat to adequately protect necessary habitat components (e.g., protected patches should be within 20 km of one another to allow for dispersal [Carroll et al. 2010]). Spatial specificity is also necessary because a species' abundance can be increasing at a broad scale (e.g., over its entire range) and declining or remaining static at smaller scales (e.g., among localized populations). Threats and habitat decline can be similarly discordant at different scales. Recognizing the importance of scale and specifying the scale at which recovery will be measured and particular criteria will be applied are necessary to provide a clear unequivocal metric that will be less subject to alternate interpretations. As with temporal specification, the spatial object of the criterion should not be an arbitrary decision; rather, it should be based on the species biology and on policy decisions regarding acceptable losses and relevant scales.

Statistical and Sampling Specificity

If the quantitative criterion involves data collection and parameter estimation, as most demographic and habitat criteria do (e.g., population size, quantity of habitat occupied), it must include statistical specifications, including statistical significance level, sampling procedure, and sample size or some equivalent measure of statistical resolution. Inclusion of a significance level (e.g., 95% confidence that the estimated value meets the specified threshold) or a statement of probability (in a Bayesian context) is an acknowledgement that, as discussed above, the true value of a population metric cannot be known with certainty but only estimated, and that an estimate will inherently contain uncertainty. Such specification is critical to safeguard against falsely concluding that a species has met the criteria when it actually has not (type II error) (McGarvey 2007). For example, a point estimate of population growth rate may exceed the specified threshold,

but considerable uncertainty may surround that estimate such that the confidence limits or credible interval spans zero, indicating the population may be declining rather than growing at the requisite rate (Taylor et al. 2002; Martin et al. 2007). Including a significance level or statement of probability sets a maximum tolerance for making an incorrect decision.

Specifying a sampling procedure, or referencing documentation that describes a sampling protocol to be followed, is also necessary. Such specification will require forethought about what kind of sampling protocols are reasonable given the species' biology and life history as well as agency budget and time constraints (Legg & Nagy 2006; Martin et al. 2007; Lindenmayer & Likens 2010). The sampling protocols meeting these criteria will in turn dictate what kind of population metrics are likely to result from such sampling and therefore what kind of quantitative metrics and error tolerances should be included in the recovery criteria. An illustrative example of the importance of considering biologically reasonable sampling protocols when identifying demographic recovery criteria can be seen in the case of the West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). The population metrics measured for this species over many years of monitoring (representing the most feasible metric to monitor) did not match the population metrics required under the recovery criteria (Friends of Blackwater v. Salazar 2012).

The sampling procedure specified should also take detectability into account and should adequately spread sampling over time and space to ensure that heterogeneity is measured (Martin et al. 2007). As part of this, the sample size required to make such a determination is essential and should be specified in the criterion. Sample size is an indication of statistical power and, as such, is as important to full statistical specification as the statistical significance level (Ellison 1996; Legg & Nagy 2006). Statistical power, to use a population abundance trend example, is the ability of an analysis to detect a trend in abundance (positive or negative) if one exists. Thus, including within each criterion the sampling procedure and sample size necessary to adequately measure the metric of interest will ensure that the appropriate type, quality, and quantity of data will be collected for estimating whether the parameters of interest have met the specified criteria thresholds.

Scientific Justification

Of the 6 standards, the requirement for formal scientific justification is arguably the most important. If a criterion is quantitative and descriptively and statistically complete (thus measurable) but no justification is provided for the numeric value stipulated, the criterion may not define a truly recovered state by objective biological standards. Federal courts have indicated that agencies must articulate "a rational connection between the facts found and the choice made" (Baltimore Gas & Elec. v. Natural Resource Defense Council 1983) and, more specifically, that criteria must address the threats identified as the source of the species decline (Fund for Animals v. Babbitt 1995). These requirements for justification are not only legal requirements, but they serve the intent of the ESA; species with clear links between recovery plan criteria and their biology are more likely to have improving status than those with no link between their biology and criteria (Gerber & Hatch 2002).

Justification of criteria solely through the use of logical argument, however, is insufficient to meet this justification requirement. Although the logic behind some recovery criteria may appear self-evident and not in need of formal justification, many of the cause-and-effect arguments to justify recovery thresholds do not stand up under closer scrutiny (Taylor et al. 2002). For example, a population-size or growth-rate criterion might be set at some arbitrary level higher than the current depressed value based on the logic that a larger or increasing population size is sufficient evidence to demonstrate that threats have been addressed. Although such a line of reasoning may seem logical, both empirical and theoretical evidence suggests that large population sizes and short-term positive growth trajectories are neither assurance against extinction nor guarantors of a species' future success (Goodman 1987; Mangel & Tier 1994). Similarly, if a population's decline appears clearly linked to a specific threat, it cannot be assumed that removal of that threat will inevitably lead to species recovery (Peterman 1977; Suding et al. 2004; Metzger et al. 2010). The Cook Inlet beluga whale (*Delphinapterus leucas*) population is a prime example. Overharvest appeared to be the obvious reason for the species' decline, but a moratorium on harvest did not result in the expected population rebound (Goodman 2009). Although straightforward logic may provide guidance regarding recovery actions, it does not provide adequate scientific justification for criteria—the metrics used to measure whether recovery has actually occurred.

As an alternative to qualitative reasoning and logical argument, use of formalized demographic modeling can lead to biologically based recovery criteria and provide the scientific rationale to justify the defined criteria thresholds. PVA, an approach that uses quantitative methods to provide a probabilistic estimate of a population's viability (Table 1), is the most widely used and studied type of model available for these purposes (e.g., Beissinger & McCullough 2002; Morris & Doak 2002). Its utility in ESA implementation and recovery criteria development has been widely recognized in both agency documents (Angliss et al. 2002; DeMaster et al. 2004; U.S. Marine Mammal Commission 2008) and peer-reviewed literature (Carroll et al. 1996; Morris et al. 2002; Murphy & Weiland 2011).

Table 1. Definition of population viability analysis (PVA) and descriptions of PVA-related techniques.

Concept	*Description*	*Examples and background reading*
Population viability analysis (PVA)	Population viability analysis (PVA) comprises a broad set of analytical and modeling approaches used to assess a species' risk of falling below some specified threshold (extinction, quasi extinction, or other management goal). Such approaches can integrate a species' life history, demography, and sometimes genetics, with environmental variability, measurement uncertainty, and assumptions and uncertainties about future management, threats, and ecological conditions to project the future status of a species. The output of a PVA usually includes a probabilistic statement about a species' risk within a set time horizon, e.g., species X has 8.6% probability of falling below 250 individuals within 100 years.	Beissinger and McCullough (2002), Morris and Doak (2002), Beissinger et al. (2006)
Types of PVA and PVA-related techniques		
Count-based PVA	A probabilistic estimate of extinction risk based only on population count data over a number of years (not necessarily consecutive). From the count data, the population growth rate mean and variance are estimated and the probability of extinction calculated or simulated under the assumption of static mean growth and variance. This is the simplest type of PVA with the lowest data requirements.	Dennis et al. (1991), Shelden et al. (2001), NMFS (2008)
Demographic PVA, stage-structured PVA, demographically structured PVA	A probabilistic estimate of extinction risk based on survival, growth, and reproduction data for each life stage of a population (e.g., pre-breeders, seedlings, adults, senescent individuals). This type of PVA requires significantly more data than count-based PVA, but can yield more information relevant to managers, such as which vital rates are unnaturally low and most limiting to population growth or stability.	Holmes (2001), Bakker et al. (2009)
Metapopulation PVA	A PVA that incorporates multiple populations (of the same species) and dispersal rates among them to project a risk of extinction for the individual populations and the metapopulation as a whole. In addition to the data necessary to conduct PVAs on the individual populations, information about dispersal rates is also required for this type of PVA.	Beissinger and McCullough (2002), Schultz and Hammond (2003), USFWS (2010)
Sensitivity analysis	Any number of analytical approaches that estimate how sensitive one variable in a demographic PVA model is to changes in another variable. The sensitivity is usually measured in a population's growth rate or risk of extinction. Sensitivity analyses can be used to assess the likely effectiveness of different management strategies.	Mills and Lindberg (2002), Morris and Doak (2002)
Bayesian PVA	An approach that applies Bayesian statistical techniques to the estimation of PVA input parameters and extinction risk. Specifically, a Bayesian PVA incorporates parameter uncertainty into the model through the use of probability distributions rather than point estimates for the various input parameters (e.g., survival rate, frequency of catastrophic events). The result of a Bayesian PVA is a posterior probability of extinction that incorporates both parameter uncertainty and environmental stochasticity and can include model structure uncertainty (e.g., the level of density dependence).	Goodman (2002*a*), Wade (2002), NMFS (2008)
Quantitative threats analysis, risk assessment, and effects analysis	Represent a variety of analytical approaches to identifying or quantifying how threats will affect a species. Some threats analyses are a form of sensitivity analyses, wherein threat levels within a model are systematically varied to assess their effect on demographic parameters and extinction risk. A similar approach formally compares output from multiple PVAs under varying future threat or management scenarios. Risk assessment is a formal process of gathering information on specific threats to inform decision-making and to develop risk-management strategies to minimize those threats.	USFWS (1992), Runge et al. (2007), Murphy and Weiland (2011)
Population viability management	An approach that combines adaptive management and population viability assessment into a single comprehensive framework. It uses iterative PVA modeling to assess extinction risk and management efficacy, which then can be used to update species monitoring approaches and management actions.	Bakker and Doak (2009), Ralls et al. (2002), Burgman (2006)

Population viability analyses vary from simple count-based models to highly complex metapopulation analyses. The type of model and the degree of complexity needed depend on the species of interest and the available data. In their various forms, PVA models can provide a structured method for exploring how threats might have affected a species and how the species might respond to reductions in those threats in the future (Beissinger & McCullough 2002; Burgman 2006). They can also be used to assess what population parameters (e.g., survival) are most crucial in maintaining or increasing population size and to suggest different combinations of population size and other parameter levels that define a population that is no longer readily susceptible to extinction (Mills & Lindberg 2002; Morris & Doak 2002). When integrated with adaptive management approaches PVA can also yield directed management and monitoring recommendations focused on achieving specified population targets (Ralls et al. 2002; Burgman 2006; Bakker and Doak 2009). Given the uncertainty inherent in the estimation of population parameters and in modeling both past and future scenarios, a good viability model will also incorporate this uncertainty and yield quantitative estimates of the uncertainty as output (Goodman 2002*a*; Burgman 2006; Bakker et al. 2009).

Much of the data and assumptions used in a PVA would likely be gathered as part of the typical recovery-planning process, but the biologically based mathematical modeling involved in PVA provides a formalized way to synthesize the information and distill the results into a common unit of measurement (i.e., extinction risk). It is this formalized synthesis that renders PVA more scientifically robust and transparent than cause-and-effect logic, historical patterns, educated guesses, expert opinion, or any other approaches used to set recovery thresholds (Burgman 2006). Through the formalized modeling process, a PVA can point to appropriate criteria thresholds that meet management limitations and goals, provide robust justification for those thresholds in the context of the species biology and its threats, make explicit any assumptions that are used in the model, suggest management and monitoring schemes to meet specified goals, and describe the degree of certainty (or uncertainty) that specified thresholds truly define a recovered state. It may not be possible to incorporate every threat or aspect of management into a PVA, but the majority of recovery criteria, whether focused on demography, threats, or management actions, can and should be linked to the species biology through a formalized modeling process. Criteria developed from such an approach will be scientifically justified, biologically based, and transparent. PVA also allows for new data and changes in assumptions to be readily incorporated into the synthesis and can serve as a unifying framework beyond recovery planning, including the 5-year review process and the threat assessments necessary for delisting.

An objective, measurable criterion that meets the letter and intent of the ESA, relevant statutes, policy statements, previous recommendations, and current scientific standards is one that is quantitative, temporally, spatially, and statistically specific, specifies a sampling protocol, and is justified on the basis of current population viability modeling methods that incorporate demographics, limiting factors, threats, future management actions, and uncertainty. Adherence to a subset of these recommendations will result in improved recovery criteria, but I suggest that unless all 6 standards are applied, recovery criteria will continue to fall short of the ESA's objective, measurable mandate.

Implementing the Standards

Although the 6 standards are scientifically and legally justified, the reality of limited time and resources makes it imperative to also address how the Services can feasibly meet these standards. In this section, I outline an approach to recovery planning that I believe can make achievement of all 6 standards realistically attainable even when data and resources are limited. The approach uses PVA as an organizing framework, but in cases of limited data and resources, it does not require actual development of a PVA model.

PVA-Framed Recovery Planning with Model Implementation

When expertise and data are available to conduct a PVA as part of the recovery-planning process, the development of the PVA model should be done simultaneously and in conjunction with the information-gathering and writing phases of the recovery plan. The PVA can be used to direct and focus the entire recovery-planning process, an approach that will yield a cohesive recovery plan centered on the factors most important for recovering a species and for developing recovery criteria that define a species with an explicit level of extinction risk. All the components necessary for developing a scientifically credible PVA are the same elements of a comprehensive recovery plan (Ralls et al. 2002; NMFS & USFWS 2010):

- assemble available data about a species (e.g., current status, biology, population dynamics, habitat requirements, spatial structure, etc.),
- document what data are not yet available and need to be gathered,
- identify the types and level of current and historical threats affecting the species (i.e., threats assessment),
- specify the level of various population, habitat, management, and threat parameters that define the desired level of extinction risk or population stability (recovery criteria), and

- outline the recovery strategy and the management actions necessary to reduce threats and improve the status of the species to reach the recovery criteria thresholds.

Approaching these steps with the goal of not only writing a recovery plan, but developing a PVA model will improve efficiency of the process and result in recovery plans and models of higher quality.

For example, in the threats assessment step, both the writing of the recovery plan and the development of a PVA should include an accounting of the data and uncertainty related to the mechanisms and intensities of threats and the projected effect of those threats in the future. Using the requirements of a PVA to focus information-gathering will necessitate defining quantitative metrics rather than the qualitative assessments that might otherwise be deemed sufficient for writing the recovery plan (e.g., Neel et al. 2012). In turn, the thorough accounting of threats for the recovery plan may clarify the structure and scope of the PVA model. Melding the 2 processes of writing the recovery plan and conducting a PVA will yield a more focused and quantitative recovery plan and a more comprehensive viability analysis, ensuring that synthesis of the available data and justification of recovery criteria will be an integral part of the recovery-planning process. In addition, the natural results of the melded processes should be targeted management actions (which are required under the ESA), appropriately directed data-acquisition and monitoring plans (Bakker & Doak 2009), and a more seamless transition from recovery planning to Section 7 consultation (Murphy & Weiland 2011), 5-year reviews, and the threat assessment necessary for delisting.

PVA-Framed Recovery Planning without Model Implementation

In cases when the necessary data or resources are not available to fully complete a PVA as part of the recovery-planning process, the structure and data requirements of a viability analysis can still be used as the organizing theme around which a recovery plan is focused. Although such an approach does not require implementation of a model, it will require the participation of a person knowledgeable in viability-analysis modeling to help guide the process. Using this approach, each step of the recovery-planning process, as described above, will focus on gathering the specific data that can be used in a viability model in the future and on identifying the information that is unavailable but necessary for a future model. Identification and quantification of missing data can be used to develop specific management actions for collection of appropriate data in the future or can be incorporated as quantified uncertainty in the future model. In this approach, the recovery-planning process itself serves as the early stage of PVA model development and informs the structure and scope of the future model. Combining the recovery planning and PVA development processes in this way reduces redundancy in effort, results in a more coherent and quantitative plan, informs monitoring needs and management actions (Bakker & Doak 2009), and can lead to development of a PVA for the delisting threat-assessment process.

When a PVA is not conducted as part of the recovery-planning process, however, the quantitative rationale for defining specific recovery criteria will be lacking. To address this, extinction risk thresholds (e.g., <1% risk of extinction in 100 years) can be used as recovery criteria. Extinction-risk criteria are by definition quantitative and descriptively and statistically specified, thus meeting the quantification and temporal, spatial, and statistical specificity standards outlined above. In addition, if the PVA structure is used to direct the recovery-planning process as recommended, the recovery plan should yield management actions in the form of data-collection protocols (including sample size and sample design) to conduct a future PVA and assess extinction risk. These data-collection protocols should be included with the extinction risk criteria to satisfy the sampling protocol standard. Because the level of extinction risk that defines a recovered (or threatened or endangered) species is a policy question rather than a scientific question, extinction-risk thresholds do not need a scientific rationale, only an explicit policy decision (Goodman 2002*b*; Robbins 2009). Nonetheless, use of an extinction-risk threshold as a criterion presumptively leads to implementation of a PVA in the future, which will ultimately provide the biological rationale for the demographic metrics deemed necessary to achieve the extinction risk specified in the criterion. If threats are included in the PVA, as recommended above, it can be used directly in the threat-assessment process necessary for delisting. In this way, recovery criteria adhering to all 6 proposed standards can be developed even when data and resource limitations preclude implementation of a PVA as part of the recovery-planning process.

Discussion

Although the standards and protocol outlined above are unlikely to raise objections on the basis of biological or scientific questions, several arguments could be made on the basis of more practical grounds that these standards are either unreasonable or unwarranted. Some argue, for example, that PVAs require too much data or provide answers that are too imprecise; therefore, their use as tools for assessing and managing threatened and endangered species is impractical or unconstructive (e.g., Coulson et al. 2001). The ESA requires the development of recovery criteria regardless of the quantity or quality of the existing information, and the uncertainty of a species'

future prospects are present whether a PVA is used or not. As others have demonstrated, PVA is not perfect, but it is the best tool currently available and is valuable even when data are limited (Beissinger & McCullough 2002; Brook et al. 2002; Burgman 2006). In addition, the explicit quantification of uncertainty is one of its primary benefits rather than one of its drawbacks (Goodman 2002*a*; Taylor et al. 2002; Murphy & Weiland 2011).

In a recent court ruling concerning the delisting of the West Virginia Northern Flying Squirrel (Friends of Blackwater v. Salazar 2012) a circuit court of appeals ruled that recovery criteria are not legally binding and that recovery plans are not contractual documents. Some might argue that this ruling alleviates the need for the specificity and quantitative rigor specified in the 6 proposed standards. Regardless of whether criteria themselves are legally binding, many recovery plans are failing to meet either the letter or intent of the ESA in conserving and recovering species such that they will be self-sustaining and no longer in need of special management under the law (Neel et al. 2012). The recovery-planning approach and 6 standards I advocate here will yield comprehensive and quantitatively focused recovery plans and scientifically justified recovery criteria that define truly recovered species and thus will increase the effectiveness and efficiency of the ESA and the delisting process.

Some might argue that too much specificity in recovery criteria will impede future management flexibility. Although my approach requires explicit and transparent documentation of criteria and management and policy intentions, maintaining policy- and management-related flexibility is no more or less achievable under the framework outlined here than under any less well-defined approach. Provisions in the ESA allow recovery plans to be modified as new information becomes available, and the court decision in the flying squirrel case allows for further agency flexibility (Friends of Blackwater v. Salazar 2012). Use of PVA can significantly streamline incorporation of new data and new policy directives; thus, it is easier to change criteria or management direction while maintaining transparency and scientific justification for those decisions when PVA is used. When a PVA cannot be developed, use of extinction-risk thresholds as recovery criteria provides maximal flexibility in future management direction while maintaining scientific rigor, adhering to the 6 criteria standards, and making policy decisions explicit and transparent.

Recovery planning and development of recovery criteria are difficult endeavors, made more difficult in the all-too-common situation when data are limited and budgets are tight. My recommendations are made in the spirit of providing a framework that might be useful to the Services even under these difficult limitations, and are not meant to trivialize the task of recovery planning or the constraints under which the Services operate in implementing the ESA. Strictly adhering to the approach recommended here may, in some cases, make recovery-plan development more time-consuming initially, but I argue that, in the long run, it will aid the Services and threatened and endangered species by integrating recovery planning, species monitoring, status review, and the threat-assessment delisting process into a unified framework defined by the application of PVA. The framework is also designed to increase transparency, thus potentially decreasing legal challenges related to recovery planning and delisting. However, it is unlikely that the Services could meet the rigorous standards set out herein without assistance. If academics and other scientists with expertise in conservation biology and PVA development are willing to contribute to the process, significant progress could be made toward making recovery criteria fully justified and truly objective and measurable.

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ARTICLE

Marine Mammal Science

Traditional summer habitat use by Southern Resident killer whales in the Salish Sea is linked to Fraser River Chinook salmon returns

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Abstract

Southern Resident killer whales (SRKW, *Orcinus orca*) are a small, endangered population of fish-eating killer whales that inhabit coastal and inland waters of the western United States and British Columbia. SRKW have been in decline since 1995, with food availability, vessel disturbance, and pollutants proposed as drivers of their decline. We used 17 years of sightings data from the SRKW core summer habitat in the Salish Sea to examine trends in presence of SRKW, and how these trends may be related to the availability of a key food source, Fraser River-origin Chinook salmon. We found that SRKW occupancy has declined by more than 75%, in step with reduced average catch per unit effort (CPUE) of Fraser River Chinook salmon. J pod was present in the core summer habitat most often, followed by K and L pods. All three pods demonstrated declines in visitation to the core summer habitat from 2004 to 2020, and presence of SRKW was significantly related to annual average Fraser Chinook CPUE. Our findings suggest that declining Fraser River Chinook returns may be reaching a point where SRKW cannot reliably meet their energetic needs, driving them to forage in areas outside of their traditional core summer habitat.

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KEYWORDS
food limitation, generalized additive models, killer whale, *Orcinus orca*, predator–prey dynamics

1 | INTRODUCTION

Southern Resident killer whales (SRKW, *Orcinus orca*) are a small population of fish-eating killer whales that inhabit coastal and inland waters of the western United States and British Columbia (Ford et al., 1998). The SRKW population is comprised of three matrilineal pods, referred to as J, K, and L pods. K and L pods range widely, particularly in winter and spring, with observations as far north as southeast Alaska and as far south as central California. J pod, in contrast, is more commonly encountered in the Salish Sea, and all three pods are routinely encountered in the Salish Sea during summer months (Hanson et al., 2017; National Marine Fisheries Service, 2019). The SRKW population has been in decline since 1995 and is listed as endangered under both the U.S. Endangered Species Act and the Canadian Species at Risk Act (Fisheries and Oceans Canada, 2008; National Marine Fisheries Service, 2019). Three main stressors have been proposed as possible drivers of the SRKW population decline: (1) high levels of persistent organic pollutants and other toxicants in their core habitat range (and in their tissues) that could impact survivorship and fecundity (Krahn et al., 2009); (2) disturbance by vessels in the heavily-trafficked Salish Sea, which could impact their foraging efficiency (Holt et al., 2021; Lusseau et al., 2009); and (3) declining availability and energetic content of their primary prey, Chinook salmon (*Oncorhynchus tshawytscha*), which may be leading directly to poor condition of SRKW and decreased survival probability (Ford et al., 2010; Ohlberger et al., 2018; Stewart et al., 2021).

SRKW feed exclusively on fishes, with Chinook salmon making up the majority of their diet, and smaller contributions from other salmon species, flatfish, and groundfish (Ford et al., 2016; Hanson et al., 2010). The summer and fall diets of SRKW, in particular, appear to be composed largely of Chinook salmon returning to tributaries in the Salish Sea, including the Fraser River and Puget Sound (Hanson et al., 2021). Similarly, analyses of body condition (Stewart et al., 2021), demographic rates (Vélez-Espino et al., 2014), and the timing of SRKW visitation to the Salish Sea (Ettinger et al., 2022) all suggest that SRKW health, population dynamics, and movement patterns may be influenced by Fraser River and Puget Sound Chinook returns. Traditionally, all three matrilineal family units have been found regularly in the central Salish Sea between April and October (Olson et al., 2018), in what has been designated as their core summer habitat (National Marine Fisheries Service, 2008; Figure 1). Accessing high densities of returning Chinook salmon in the Salish Sea during this summer foraging period appears to be important for building up blubber stores prior to the winter and early spring period when prey may be lower quality and more dispersed along the outer coast of the U.S. and Canada (Hanson et al., 2021). This potential importance is reflected in the interannual seasonal decline in SRKW body condition (Fearnbach et al., 2020).

Understanding how SRKW foraging behavior is influenced by prey availability in their traditional core summer habitat is important in developing strategies to support the recovery of this endangered species. The abundance of returning Fraser River Chinook may be a key driver of SRKW foraging behavior and habitat use from April through September, as Fraser River Chinook generally have larger individual body sizes (and therefore higher energetic value as prey) than other Salish Sea Chinook stocks (O'Neill et al., 2014), and make up an estimated 40%–50% of Chinook salmon that are present in the Salish Sea during the summer months (Stewart et al., 2021). Here, we explore how traditional core summer habitat use by SRKW is related to the abundance of returning Fraser River Chinook salmon. We use nearly two decades of compiled observations of the daily presence of each pod, and a higher resolution 7-year data set on the daily abundance of SRKW to evaluate seasonal trends in SRKW use of core summer habitat, and pod-level relationships to Fraser River Chinook returns.

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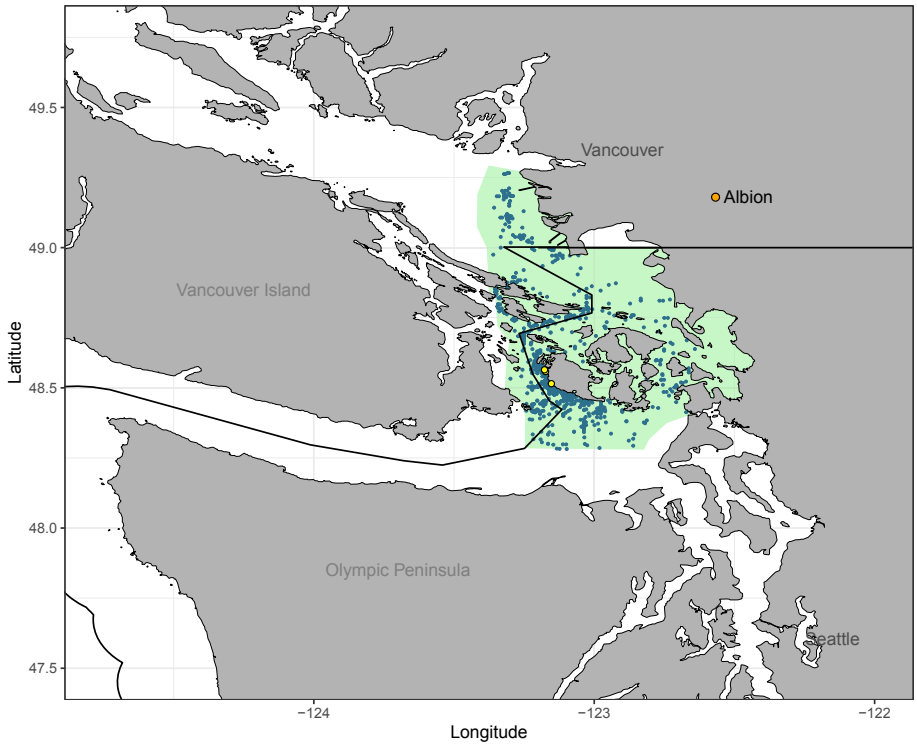


FIGURE 1 Traditional core summer habitat for Southern Resident killer whales. Green shading indicates the traditional core summer habitat area, spanning both United States and Canadian waters. Blue points indicate sighting locations of SRKW 2014–2020. The black line indicates the United States Exclusive Economic Zone and the border between the U.S. and Canada. The orange point indicates the location of the Albion test fishery, in Albion, British Columbia on the Fraser River. The yellow points indicate locations of hydrophones used to detect SRKW and supplement sightings reports.

2 | METHODS

2.1 | Sighting data collection

Sightings data were compiled from April 1 to October 31 for each year, from different sources throughout the core summer habitat range. From 2004 to 2013, sightings data were collected with resolution to the pod level, whereas from 2014 to 2020 sightings data were resolved to the individual whale level. Data sources included:

(1) Center for Whale Research encounter data (individual level 2004–2020): photographs collected during field research activities as well as photos contributed by members of the public and verified by CWR researchers (Center for Whale Research, 2020).

(2) Photo-identification data (individual level 2008–2020) collected by authors JWD and HF during aerial photogrammetry field efforts (Fearnbach et al., 2020; Stewart et al., 2021).

(3) First-hand reports from the public provided to Orca Network (https://www.orcanetwork.org) with accompanying photographic and video confirmation (pod and individual level 2004–2020).

(4) First-hand reports from naturalists, field researchers, and individual sighting data contributors provided directly to J.C. with accompanying photographic confirmation (pod level 2004–2020; individual level 2014–2020).

(5) Hydrophone detections from the west side of San Juan Island (2014–2020). Although sightings data were based primarily on visual reports, live hydrophone streams and hydrophone recordings from Lime Kiln State Park

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(https://www.smruconsulting.com/lime-kiln-live-hydrophone), Haro Strait (https://www.orcasound.net), and a privately owned hydrophone on San Juan Island were used to supplement visual sightings data and fill detection gaps. For example, hydrophone recordings were frequently used to pinpoint the time at which a pod arrived or departed from the region after visual sightings were reported from another source listed above. Detections were identified to the pod level using pod-specific call types (Ford, 1987).

(6) For 2004–2011 and 2014, supplemental sightings reports (pod level) were extracted from the 2012 NOAA/Whale Museum Orca Master database (Olson et al., 2018).

Sightings from all of the above sources were summarized into a single daily record for each pod; either presence/absence for 2004–2020, or number of whales for 2014–2020. For the count data from 2014 to 2020, if the same pod or whales were sighted by multiple sources in a given day, the total number of individual whales confirmed by photo identification across all sources was considered the count for that day.

Quantifying effort from six disparate sightings sources is extremely challenging. To develop metrics of relative survey effort, we compiled sightings of a suite of cetaceans that were recorded by JC from sightings reports (and hydrophone detections of killer whales), using the same sighting sources as SRKW. We recorded the number of days with reports of gray (*Eschrichtius robustus*), humpback (*Megaptera novaeangliae*), minke (*Balaenoptera acutorostrata*), and transient (Bigg's) killer whales in the SRKW traditional core summer habitat as a proxy for the number of days with survey effort in the region throughout the study period. In addition, we compiled sightings reports from the same sources for SRKW both inside and outside the core summer habitat, to determine the number of days that SRKW were accounted for in total as an indicator of detection probability and whether days with no SRKW sightings in the core habitat reflect true absences. These cetacean sightings data were only available for 2014–2019 from gray, humpback, and minke whales, and 2014–2020 for transient killer whales.

SRKW social structure is complex, with dynamic associations between individuals changing through time to form different numbers of social clusters both at the pod level and the population level (Parsons et al., 2009). In addition, while the population is conventionally split into three matrilineal pods, individuals that are natal members of a pod do not always remain associated with that pod permanently. Although uncommon, a small number of whales in our sightings data set have routinely associated with pods outside their family groupings throughout the study period. For example, whale L87, a natal member of L pod, began associating with K pod in 2006 after his mother died. Starting in 2010, L87 associated with J pod for almost a decade until he returned to L pod in late 2019. Whales L7, L53, and L57 all similarly associated with J pod during some years in the core summer habitat. In order to remain consistent with the pod-level designations used in the majority of previous studies focused on SRKW and examine pod-level differences in presence and abundance of SRKW in the core summer habitat, we excluded records of these four whales from our data set to avoid situations where their presence while associating with J pod would inflate the reported presence or abundance of L pod whales in cases where the rest of L pod was absent. We note that because all of these whales were from L pod, their exclusion could lead to a slight positive bias in the mean number of L pod whales sighted in the core summer habitat (by eliminating cases where only one of the above whales is present), and a slight negative bias in the mean occurrence of L pod for the same reason.

2.2 | Salmon data

We used daily gill net catch per unit effort (CPUE) data on Chinook salmon returning to Fraser River tributaries that are collected by the Albion test fishery at the mouth of the Fraser River (https://www.pac.dfo-mpo.gc.ca/fm-gp/fraser/docs/commercial/albionchinook-quinnat-eng.html). We chose this metric of returning Fraser River Chinook relative abundance as it is most likely to closely represent the availability of Chinook salmon to SRKW in the core summer habitat area, and has finer temporal resolution for evaluating seasonal trends than available estimates of at-sea total Chinook abundance (e.g., Fishery Regulation Assessment Model, FRAM; Pacific Fishery Management Council, 2008). The Albion test fishery does not collect Chinook CPUE data every day of the year. For each year, we

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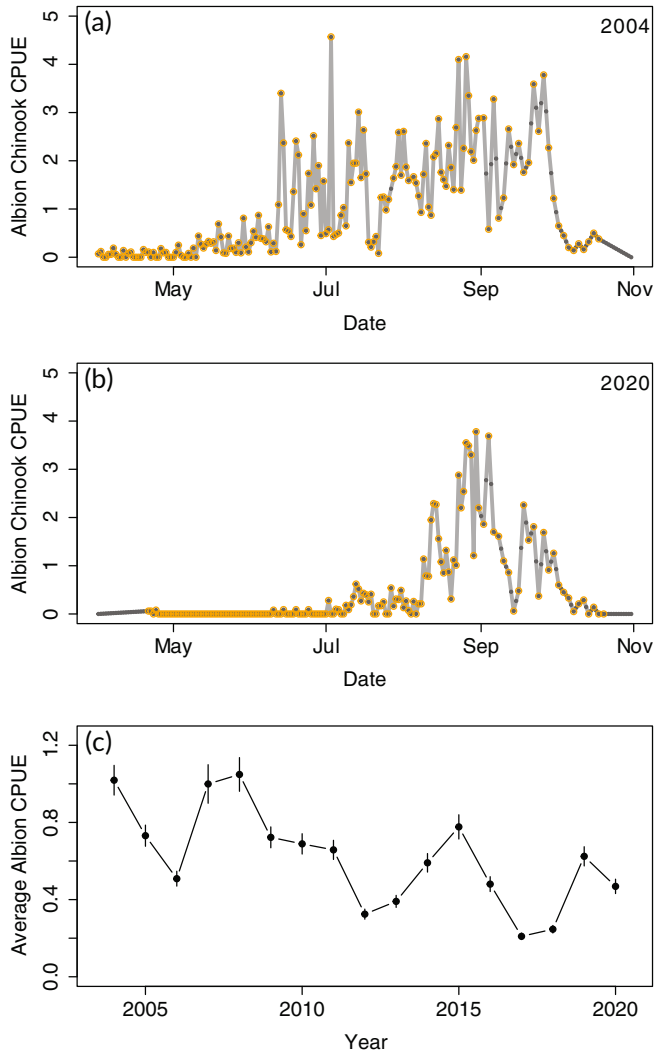


FIGURE 2 Albion test fishery Chinook catch per unit effort. Panels (a) and (b) show daily CPUE in the Albion test fishery in 2004 and 2020, respectively. The dark gray points indicate daily CPUE values used as inputs in the generalized additive model analyses. The orange circles indicate days with recorded CPUE data, whereas points without orange circles indicate interpolated values. Annual mean CPUE values (not including interpolated CPUE) are shown from 2004 to 2020 in (c). Vertical bars in (c) indicate the standard error of mean CPUE values.

set the CPUE values for April 1 and October 31 to zero, unless a sample was collected on that day, as these dates are close to the beginning and end of the expected migration timing of the combined spring, summer and fall Fraser Chinook runs. We then estimated missing values using a simple linear interpolation (Figure 2, Table S1). Finally, we moved the observed and interpolated CPUE values forward by 10 days to account for the approximate time it would take a Chinook salmon to migrate from the central San Juan Islands to the mouth of the Fraser River (Ayres et al., 2012; Ettinger et al., 2022). In addition to daily CPUE values, we calculated the average daily CPUE in the Albion test fishery from April 1 to October 31 for each year from 2003 to 2020, excluding interpolated values. Our final salmon metrics for inclusion in the following analyses were (1) the daily interpolated Albion CPUE, with a 10-day lead; (2) the mean daily CPUE for the contemporary year; and (3) the mean daily CPUE from the previous year.

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2.3 | Data analysis

For coarse inference and visualization purposes we used simple linear regressions to examine relationships of year and mean annual CPUE with the number of days each pod was present in the core summer habitat (2004–2020), and the number of whales from each pod on days when that pod was present (i.e., excluding zeros; 2014–2020). We calculated the occupancy proportion as the number of days each pod was observed within the core summer habitat divided by 215 (the number of days between April 1 and October 31).

Next, to account for a variety of potential drivers of SRKW occupancy in the Salish Sea, we used generalized additive models (GAMs) to examine relationships between SRKW attendance and pod membership, day of the year, daily Chinook salmon CPUE, and annual mean CPUE (contemporary and lagged). We chose to use GAMs as we hypothesized that some relationships with SRKW attendance (e.g., day of year) may exhibit nonlinear responses. We conducted two separate GAM analyses for the two different levels of resolution in the sightings data. First, we conducted an analysis of the full 2004–2020 data set at the pod resolution level, using a binomial response model for presence/absence of each pod. The input data were structured such that the response variable was presence (1) or absence (0) within the traditional core summer habitat area (Figure 1), and each record was associated with a pod (J, K, or L), and the corresponding covariates for that observation (day of the year, daily Chinook CPUE, and annual mean CPUE). We included fixed effects for pod and year, and smooth terms for day of the year, mean contemporary CPUE, mean lagged CPUE, and contemporary daily CPUE. For all smooth terms, we estimated an independent smooth for each pod. We fit the model using the R package *mgcv*, where the model was defined as:

$$\begin{aligned}\text{Presence} \sim\ & s(\text{Day of Year}, \text{by} = \text{Pod}) + s(\text{Mean CPUE}, \text{by} = \text{Pod}) + s(\text{Lagged Mean CPUE}, \text{by} = \text{Pod}) \\ & + s(\text{Daily CPUE}, \text{by} = \text{Pod}) + \text{Pod} + \text{Year}\end{aligned}$$

where s() indicates a smoothed spline fit, Day of Year and CPUE covariates were fit independently for each pod (by = Pod), and the final two terms are the fixed effects of Pod and Year.

Next, we analyzed the higher resolution individual-level data set from 2014 to 2020. The explanatory variables included in the high-resolution analysis were identical to the terms described above for the binomial model. However, these sightings data included the number of individual members of each pod recorded in the core summer habitat on a given day, making them effectively count data. As such, we evaluated three possible formulations of the above model using (1) a standard Poisson distribution; (2) a zero-inflated Poisson distribution, and (3) a negative binomial distribution. The zero-inflated Poisson distribution estimates the frequency of zeros accounted for by included covariates, as well as "excess" zeros (the zero-inflation component), whereas the negative binomial distribution accounts for overdispersion in the response data including the possibility of many zero counts. These two distribution families potentially better account for overdispersed sightings data that could result from variable survey effort and reporting from the many data sources included in this study. We compared these three model formulations using Akaike's information criterion (AIC; Burnham & Anderson, 2004), and for all models (binomial and count) we examined diagnostic plots of residual distribution and quantiles (Q-Q plots). We evaluated concurvity (the nonlinear analog of multicollinearity) in the estimated effects of covariates in the GAMs using the concurvity() function in *mgcv* and evaluating the pairwise concurvity estimates. Concurvity values are bounded by 0 and 1, where 0 indicates no concurvity and 1 indicates a lack of identifiability between predictor variables. There are no established criteria for identifying unacceptable levels of concurvity, however, we followed (Carvalho et al., 2021; Johnston et al., 2019) in removing one covariate if the pairwise concurvity between two covariates exceeded 0.3. For the final models (binomial and count), we evaluated fit by rerunning the models five times using a different randomly selected subset of 80% of the data each time, predicting the remaining 20% of the data using the fitted model, and comparing the model predictions to the observed values using Pearson's correlation tests and two-sided Wilcoxon rank sum tests. For all models, we used the restricted maximum likelihood to estimate model coefficients. This smoothing method estimates the adjustment and smoothing parameters on the covariate relationships

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depending on the type and number of basis functions used to create the smoothing term. Each basis function is multiplied by an overfit penalty value and then summed, resulting in the smoothing function for each parameter. This method penalizes for overfitting in each smoothing function and is recommended when modeling ecological data with GAMs to prevent overfitting (Pedersen et al., 2019).

3 | RESULTS

3.1 | Sighting trends

The number of days that each pod was observed in the core summer habitat between April 1 and October 31 declined steadily between 2004 and 2020 for all pods ($p < .001$; Figure 3). J pod was generally present on more days than K and L pods. The highest years of presence were 2005 for J pod (164 days), 2009 for K pod (124 days), and 2004 for L pod (103 days). The lowest years of presence were 2016 for J pod (36 days), 2017 for K pod (10 days), and 2019 for L pod (10 days). On days when whales were present, there was not a clear pattern in the mean number of whales observed over time ($p > .05$; Figure 3). The mean number of whales present per day ranged from 20.4 to 24.1 each year for J pod, 8.2 to 16.5 for K pod, and 14.9 to 21.4 for L pod. Similarly, whales from all pods were present on more days in years with higher average CPUE in the Albion test fishery ($p < .001$), but there was not a clear relationship between the number of whales present and average annual CPUE ($p > .05$; Figure 3).

From 2014 to 2019, the number of days with sightings of non-SRKW cetaceans—our proxy for relative survey effort—exceeded 85% of the April–October study period, and in 2019 approached 100% coverage (Table 1). Over the same period, SRKW were accounted for both inside and outside the core summer habitat for 37%–76% of the survey period, with 52%–90% of those sighting days inside the core habitat (Table 1). Spatial coverage of sighting reports spanned the Salish Sea from Puget Sound to the Strait of Georgia and the Strait of Juan de Fuca, with few additional sightings on the outer coast of Washington and British Columbia (Figure S1).

3.2 | Generalized additive models

Pairwise concurvity values for all covariates included in the GAM analyses of presence/absence and count data were <0.3, with the exception of contemporary mean Albion CPUE and lagged mean Albion CPUE (pairwise concurvity 0.446 in binomial model and 1 in count models). We therefore removed the lagged mean CPUE from the analyses and reran the GAMs retaining all other covariates.

The GAM analysis of presence/absence data from 2004 to 2020 found significant effects of pod, year, day of year, and mean annual Albion CPUE on the probability of whales being present in the core summer habitat ($p < .01$ in all cases; Figures 4 and 5). The binomial GAM explained 32.3% of the deviance in the data. J pod was most likely to be present between roughly June 1 and October 1, with two peaks in presence around mid-July and mid-September. K pod probability of presence increased steadily until mid-July and plateaued before declining in mid-September. L pod presence peaked in mid-June and plateaued before declining starting in late September. J pod had the highest probability of presence, followed by K pod, and then L pod. The partial effect of year (taking into account all of the other included covariates) fluctuated between 2004 and 2018, with notably negative partial effects in 2019 and 2020. The model estimated a significant smooth term ($p < .001$) for J pod's relationship to daily Albion CPUE (with a 10-day lead). There was an increasing probability of presence with increasing daily CPUE from roughly 0 to 1 CPUE, after which the relationship plateaus and becomes increasingly uncertain (Figure 5). We found no significant relationship between daily CPUE and the probability of whales being present for either K or L pods.

Of the three candidate count models, the standard Poisson GAM performed the poorest, both in terms of AIC score (43,703.08) and diagnostics of residuals and overdispersion (Figure S2), and explained 39.3% of the deviance

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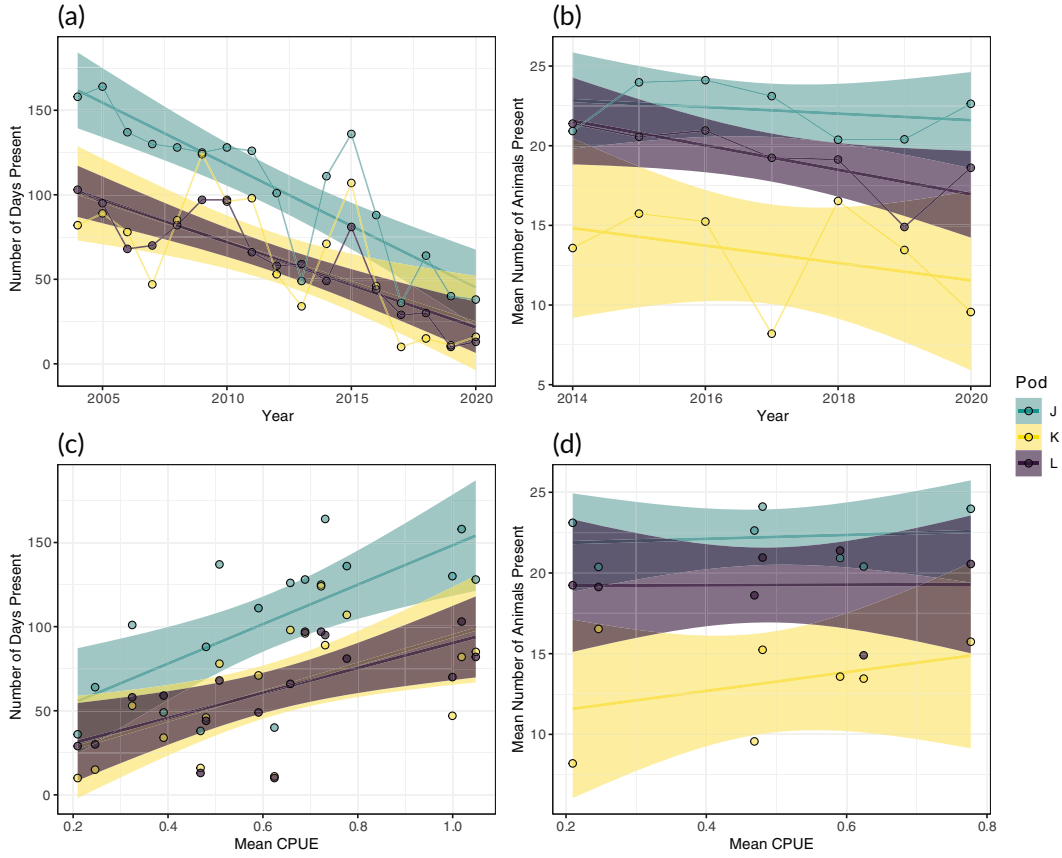


FIGURE 3 Changes in Southern Resident killer whale core summer habitat occupancy. (a) The number of days that any member of J pod (teal), K pod (yellow), or L pod (purple) was recorded in the core summer habitat between April 1 and October 31 each year. (b) The mean number of whales observed on days when each pod was present, by year. (c) The relationship between the number of days each pod was present in core summer habitat and the contemporary annual mean Albion test fishery CPUE. (d) The relationship between the mean number of whales observed on days when each pod was present and contemporary annual mean CPUE. In all panels, the linear model fits are plotted with the standard error of the fit (polygons).

in the count data. We report the effective degrees of freedom for each smooth term for all models in Table S2. The zero-inflated Poisson model (34.8% deviance explained) had a lower AIC score (11,459.97) than the negative binomial model (32.8% deviance explained; AIC 13,553.09), but diagnostics suggested that the negative binomial model better accounted for overdispersion in the data set. The residuals in the negative binomial model were slightly negatively biased, but were far less dispersed than the residuals from either the Poisson or zero-inflated Poisson models, both of which had bimodal residual distributions and were more likely to underpredict observations on the left side of the distribution (Figure S2). Consequently, we selected the negative binomial model as our preferred model for inference.

In our model validations, we found a significant correlation between the observed presence/absence records and the binomial model-predicted presence/absence, and between the observed counts and the negative binomial model-predicted counts using 80% of the data to train the model and 20% of the data to validate the model (Pearson's correlation $p < .001$ in all five validations for both models). For the binomial model, the Wilcoxon rank sum test was significant ($p < .001$) in two of five validations. For the negative binomial count model, the Wilcoxon

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TABLE 1 Cetacean sightings as proxies for survey effort 2014–2020. Number of days that each of four cetacean species were reported to JC from any of the sightings sources in the Southern Resident killer whale traditional core summer habitat between April 1 and October 31. The proportion of days with whales is the number of days with any cetacean reported (excluding SRKW) divided by 215. Proportion of days that SRKW were accounted for refers to the number of days SRKW were reported to JC from any sightings sources in any location (not restricted to the core habitat) divided by 215. The proportion of SRKW days in the core habitat refers to the number of days SRKW were reported in the core habitat divided by the number of total days SRKW were accounted for.

Year	Gray whale	Humpback whale	Minke whale	Transient killer whale	Any cetacean (excluding SRKW)	Proportion of days with whales	Days SRKW reported in core habitat	Days SRKW reported anywhere	Proportion of days SRKW accounted for	Proportion of SRKW days in core habitat
2014	3	80	102	97	183	0.85	119	146	0.68	0.82
2015	4	154	119	103	197	0.92	146	163	0.76	0.90
2016	15	139	102	112	201	0.93	97	130	0.60	0.75
2017	11	146	68	140	201	0.93	53	85	0.40	0.62
2018	9	145	104	146	203	0.94	69	108	0.50	0.64
2019	123	168	130	140	208	0.97	45	86	0.40	0.52
2020	—	—	—	118	—	—	46	80	0.37	0.58

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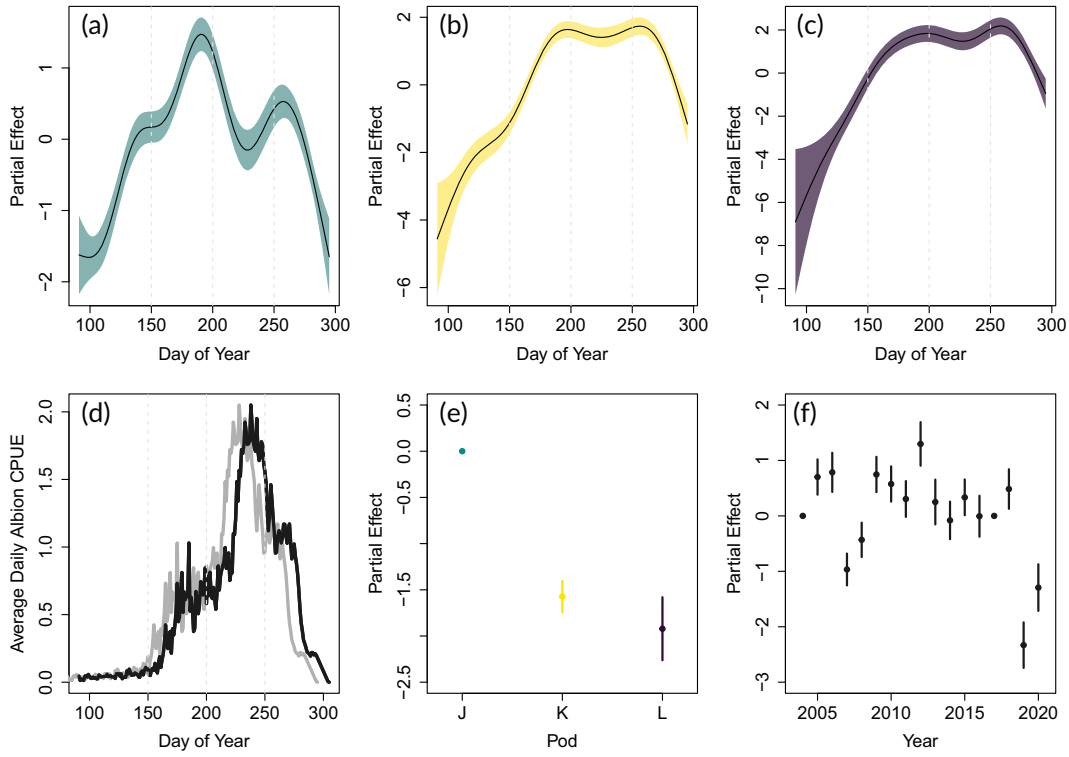


FIGURE 4 Generalized additive model results for the presence of Southern Resident killer whale pods in the core summer habitat (binomial model). The day-of-year partial effect smooth for (a) J pod, (b) K pod, and (c) L pod. (d) The mean daily Albion test fishery Chinook CPUE, averaged across 2004–2020 (black line) and shifted forward by 10 days (gray line) for inclusion in the GAM. The partial effect of pod (e) and year (f) on the probability of presence in the core summer habitat. Shading in a–c and error bars in e–f represents the standard error of the partial effect.

rank sum test was significant ($p < .001$ in all five validations), indicating that while the binomial and negative binomial models are capable of estimating mean trends, the observed data were still overdispersed relative to the modeled distributions.

The negative binomial count model (hereafter simply "count model") found similar patterns from 2014 to 2020 as the binomial model did for the full 2004–2020 study period. There were significant estimated effects of pod, year, day of year, and mean contemporary Albion CPUE for all pods ($p < .01$ in all cases) (Figures 6 and 7). Daily Albion CPUE appears to have had no significant effect for any of the pods (Figure 7). As with the binomial model, the count model estimated J pod to have the highest mean attendance in the traditional core summer habitat, followed by K pod and then L pod. We found no significant difference in the estimated year effect from 2014 to 2018, but 2019 and 2020 both had significantly lower estimated mean attendance ($p < .001$). Attendance of J and K pods peaked from mid-July to late September, whereas attendance of L pod was generally very low until early June, at which point it plateaued for the remainder of the summer season. Mean contemporary Albion CPUE was positively related to the attendance of all three pods.

4 | DISCUSSION

This study adds to a substantial body of work showing that the movements, habitat use, health, and demographic trends of the Southern Resident killer whale population are closely linked to Fraser River Chinook salmon

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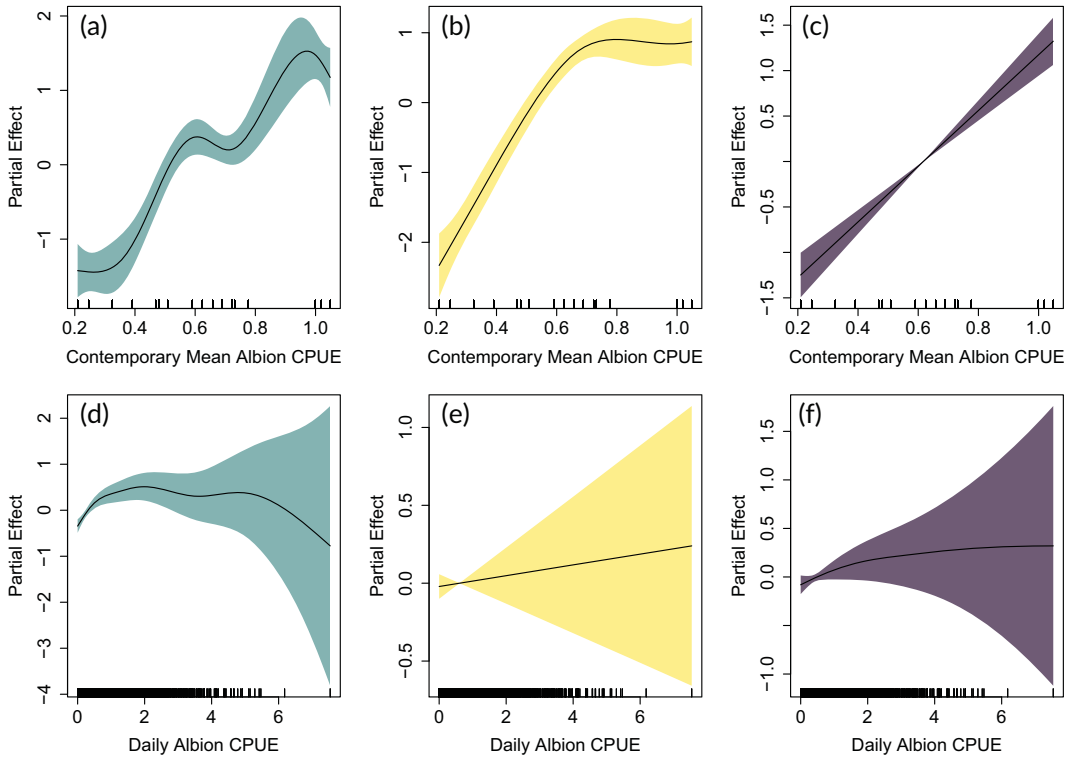


FIGURE 5 Relationships between the probability of Southern Resident killer whale presence in the traditional core summer habitat and Albion test fishery Chinook CPUE (binomial model). The partial effect smooths are shown for the contemporary year mean Albion CPUE and (a) J pod, (b) K pod, and (c) L pod, and for the daily Albion CPUE and (d) J pod, (e) K pod, and (f) L pod. Shading in all panels represents the standard error of the partial effect. Smooth terms in a–d were significant, whereas smooth terms in e–f were not significant (see Results).

abundance. We show that the probability of all three SRKW pods being present in their traditional core summer habitat is related to the average annual Fraser River Chinook returns in the current year. We demonstrate a striking decline in the core summer habitat use by all three SRKW pods, which had an observed occupancy rate of roughly 50%–75% from April 1 to October 31 in the early 2000s, down to an occupancy rate of roughly 5%–15% in recent years, with J pod seen more frequently than K or L pods. Over the same period, average daily Fraser River Chinook CPUE has declined by more than half. While the abundance of the SRKW population also declined from 2004 to 2020, the relative magnitude of that decline is far smaller than the decline in core summer habitat occupancy both overall and at the pod level (Table 2), suggesting that the decline in occupancy is not driven by patterns in SRKW abundance. Our findings corroborate a recent study showing that the phenology of SRKW visitation to the San Juan Islands (within the traditional core summer habitat area) is linked to the timing of Fraser River Chinook returns, and has shifted later in the summer season as spring returns have declined dramatically (Ettinger et al., 2022). The potential impact of declining prey availability on SRKW foraging strategies was highlighted in 2019 and 2020, when despite a modest increase in mean Fraser River Chinook CPUE, SRKW presence in the core summer habitat remained near its minimum level for the study period. This suggests that declining trends in Fraser River Chinook returns may be driving SRKW to forage in other areas outside of the core summer habitat (e.g., in their typical winter range; Hanson et al., 2021) rather than risk encountering low prey densities that they experienced in prior years.

Accounting for survey effort when using many different types of opportunistic and community-contributed survey data is extremely challenging. Our metrics of non-SRKW cetacean sighting days suggest that between 2014 and

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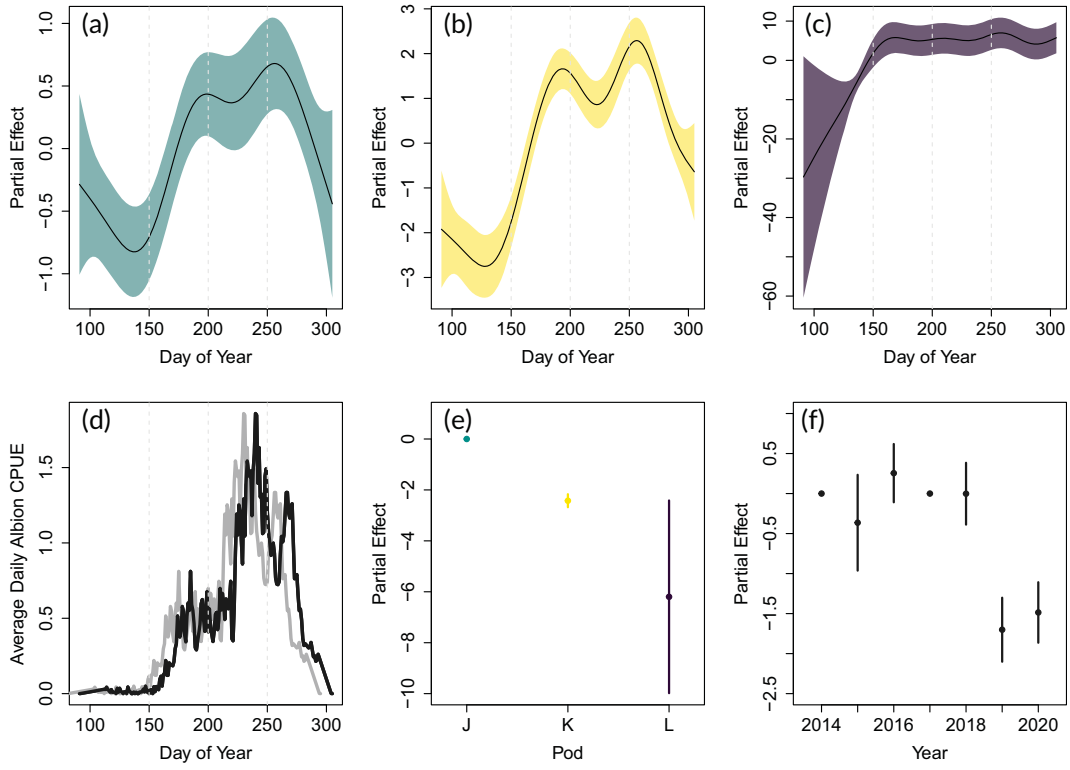


FIGURE 6 Generalized additive model results for the number of Southern Resident killer whales from each pod observed in the traditional core summer habitat (count model). The day-of-year partial effect smooth for (a) J pod, (b) K pod, and (c) L pod. (d) The mean daily Albion test fishery Chinook CPUE, averaged across 2014–2020 (black line) and shifted forward by 10 days (gray line) for inclusion in the GAM. The partial effect of pod (e) and year (f) on the number of whales observed per day in the core summer habitat. Shading in a–c and error bars in e–f represents the standard error of the partial effect.

2020, the same sources that provided SRKW sightings reports, both from shore, research vessels, and commercial whale watching operations, were active and submitting cetacean sightings on average more than 90% of the April–October study period. In addition, our SRKW sightings from outside of the core summer habitat indicate that SRKW whereabouts were known for, in some cases, almost twice as many days as their reported presence in the core habitat. This suggests that for the 2014–2020 period, our sightings data approach true presence/absence of SRKW in the core summer habitat, rather than days without sightings simply reflecting a lack of survey effort. For the 2004–2013 study period, we do not have similar non-SRKW cetacean sightings to quantify relative survey effort. Survey effort during this early period may have been lower than the 2014–2020 period as there were fewer whale watching operations and researchers compared to recent years, although we note that in 2004 and 2005 we have SRKW sighting reports from more than 75% of the days in the April–October study period. If survey effort was lower in early years and increased over time, with more false SRKW absences in early years than in later years, the decline in core habitat occupancy that we report would in fact be underestimated. In addition, the negative binomial distribution we used in our count model should account for overdispersion in the sightings data, which could be caused in part by false absences.

With very few exceptions, J pod spent the most time in the traditional core summer habitat each year, and more J pod whales were present on average in the core habitat than any other pod, despite L pod being about 50% larger numerically than J pod. From 2014 to 2020 when individual-level data were available for each pod, virtually all of J

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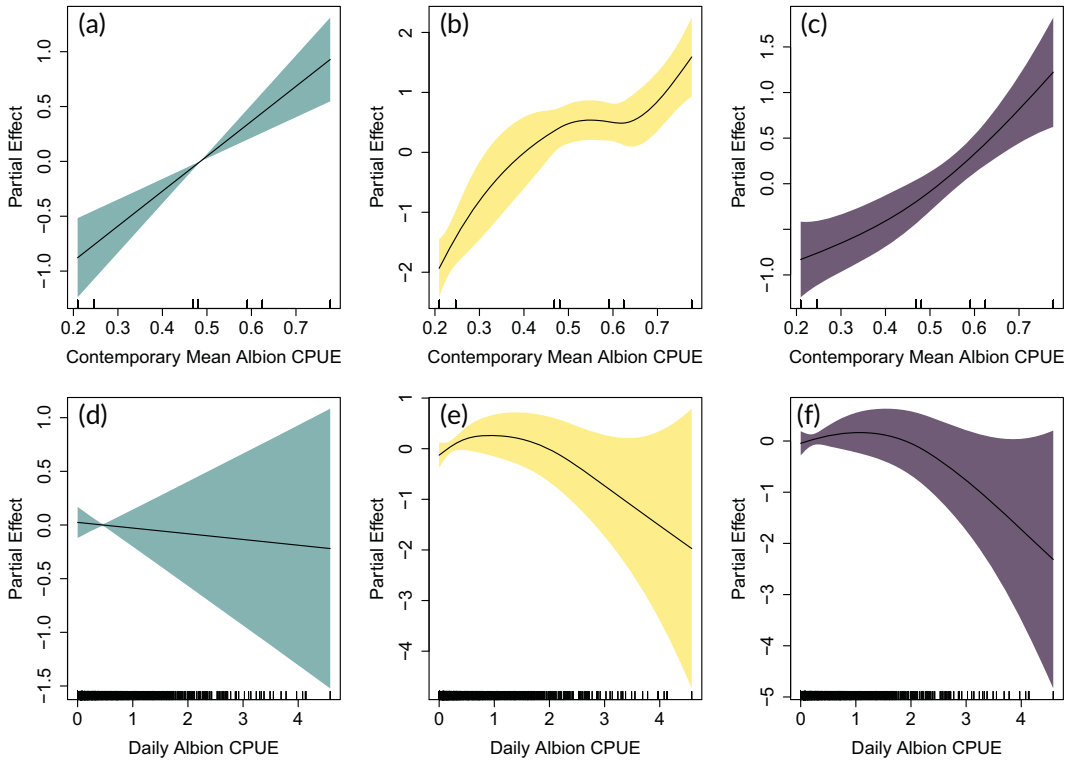


FIGURE 7 Relationships between the number of Southern Resident killer whales observed in the traditional core summer habitat and mean annual Albion test fishery Chinook CPUE (count model). The partial effect smooths are shown for the contemporary year mean Albion CPUE and (a) J pod, (b) K pod, and (c) L pod, and for the daily Albion CPUE and (d) J pod, (e) K pod, and (f) L pod. Shading in all panels represents the standard error of the partial effect. Smooth terms in a–c were significant, whereas smooth terms in d–f were not significant (see Results).

pod was present on days when the pod was observed, whereas roughly two-thirds of K and L pods were typically present on average when those pods were observed. These findings align with previous studies indicating that K and L pods use the outer coast of Washington, Oregon, and California more extensively than J pod (Hanson et al., 2013, 2017), and a recent study showing that J pod body condition was closely related to Fraser River Chinook at-sea abundance (Stewart et al., 2021), whereas L pod body condition was best explained by Puget Sound Chinook salmon and K pod body condition had no clear relationship to the abundance of a specific Chinook stock. Collectively these studies suggest that the three SRKW pods may target somewhat distinct but overlapping prey sources throughout the year, resulting in pod-specific spatiotemporal distributions throughout their range. However, we note that although K and L pods spent fewer days in the core summer habitat than J pod on average, all three pods showed relationships between presence in the region and mean Fraser River Chinook returns. J pod has also exhibited the greatest shift in peak occurrence in the San Juan Islands in step with the shifting peak daily returns of Fraser River Chinook (Ettinger et al., 2022), further suggesting that J pod's use of the SRKW core summer habitat may be most closely related to this Chinook stock. This suggests that while Fraser River Chinook may be an important diet item for all three pods, J pod may be impacted most by declining Fraser returns.

While we did not explicitly examine changes in the timing of SRKW visitation throughout the study period, the modest differences in the seasonal (day of year) smooths in the GAM analyses between the presence/absence GAM for 2004–2020 (Figure 4a–c) and the count-based GAM for 2014–2020 (Figure 6a–c) mirror the phenological shifts described in Ettinger et al. (2022). J pod peak attendance shifted slightly later in the summer in the 2014–2020

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TABLE 2 Sighting rates of Southern Resident killer whales in the traditional core summer habitat 2004–2020. The July census is the total abundance of each pod as of July 1 in each year. Note that the mean number of whales present can be higher than census abundance due to births and/or deaths prior to/after the census. Occupancy proportion is the number of days each pod was present divided by 215 (the number of days between April 1 and October 31).

	J pod					K pod					L pod					
				Animals present					Animals present					Animals present		
Year	July census	Days present	Occupancy proportion	*Mean*	*SD*	July census	Days present	Occupancy proportion	*Mean*	*SD*	July census	Days present	Occupancy proportion	*Mean*	*SD*	Days any SRKW present
2004	22	158	0.73	—	—	20	82	0.38	—	—	41	103	0.48	—	—	162
2005	23	164	0.76	—	—	21	89	0.41	—	—	44	95	0.44	—	—	168
2006	24	137	0.64	—	—	21	78	0.36	—	—	44	68	0.32	—	—	140
2007	25	130	0.60	—	—	19	47	0.22	—	—	42	70	0.33	—	—	136
2008	25	128	0.60	—	—	19	85	0.40	—	—	41	82	0.38	—	—	142
2009	26	125	0.58	—	—	19	124	0.58	—	—	40	97	0.45	—	—	143
2010	28	128	0.60	—	—	19	96	0.45	—	—	39	97	0.45	—	—	132
2011	26	126	0.59	—	—	19	98	0.46	—	—	42	66	0.31	—	—	133
2012	25	101	0.47	—	—	19	53	0.25	—	—	40	58	0.27	—	—	103
2013	26	49	0.23	—	—	19	34	0.16	—	—	37	59	0.27	—	—	78
2014	25	111	0.52	20.92	5.95	19	71	0.33	13.58	6.96	34	49	0.23	21.39	5.64	116
2015	27	136	0.63	23.98	6.66	19	107	0.50	15.74	5.09	35	81	0.38	20.56	9.40	145
2016	29	88	0.41	24.11	7.88	19	46	0.21	15.24	4.93	35	44	0.20	20.95	9.07	96
2017	24	36	0.17	23.11	2.97	18	10	0.05	8.20	6.76	35	29	0.13	19.24	8.71	51
2018	23	64	0.30	20.38	5.20	18	15	0.07	16.53	4.16	34	30	0.14	19.13	4.51	68
2019	22	40	0.19	20.40	4.11	17	11	0.05	13.45	4.74	34	10	0.05	14.90	8.01	44
2020	22	38	0.18	22.63	0.82	17	16	0.07	9.56	5.74	33	13	0.06	18.62	5.91	46

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analysis compared to the 2004–2020 analysis, K pod attendance remained largely the same, and L pod attendance peaked (and plateaued) slightly earlier in the season.

We found no clear relationships between the daily CPUE reported in the Albion test fishery (moved forward by 10 days) and SRKW presence or abundance in the traditional core summer habitat. It is possible that our selection of a 10-day lead period was inadequate to capture the migratory period of a salmon between the SRKW core summer habitat and the Albion test fishery, although we did explore a range of leads from 0 to 21 days, all of which had similarly nonsignificant relationships between SRKW attendance and daily Albion CPUE. We suggest that a more likely explanation is that SRKW are not responding to prey availability at such fine (i.e., daily) timescales, but are instead responding to seasonal patterns in Chinook returns, as suggested by Ettinger et al. (2022). Further, if daily Chinook returns are generally high but have periods of low abundance between pulses, this overall prey availability may be sufficient for SRKW to remain within the core summer habitat but may obscure estimated relationships with daily returns and be better reflected in average returns, as indicated by our model results. Our GAM analyses showed similar patterns, regardless of whether the data were binomial presence/absence records or counts of individual whales. Given the relative consistency in the mean number of whales typically observed in the core summer habitat (Figure 3), most of the information content in our analyses is contained in the presence or absence of whales rather than the recorded daily abundance. It would be reasonable to predict that not only the probability of visitation in the core summer habitat, but also the number of whales present on a given day, would decline with decreasing prey availability. However, given the strong social foraging behaviors exhibited by SRKW pods and matrilines, it is perhaps unsurprising that we did not find any clear decline in the average number of whales recorded on days that they accessed the core summer habitat.

Several recent studies have suggested that prey availability during the winter foraging period may be most relevant to SRKW population health and dynamics, given that their preferred Chinook prey are more dispersed and make up a smaller portion of their diet (Ford et al., 2016; Hanson et al., 2010, 2021; Wasser et al., 2017). Consequently, perturbations to their food supply in winter months could have greater consequences for fitness, survival, and fecundity than similar perturbations to summer prey stocks. However, given the reported seasonal decline in SRKW body condition when comparing late summer (September) to late spring (May) (Fearnbach et al., 2020), the availability and abundance of summer prey may be critical to building blubber stores that facilitate survival through the winter period when prey availability is low. Our findings suggest that SRKW are facing increasing challenges to finding and capturing adequate prey in the core summer habitat during this important feeding period, and may be foraging in other locations instead. Furthermore, given the comparatively high energetic content of Fraser River Chinook (O'Neill et al., 2014), it may be difficult for SRKW to compensate for the decline in Fraser Chinook availability by foraging in other locations and on other salmon stocks and species during the summer months. Increasing Fraser River Chinook abundance is not necessarily straightforward, as climate change (Crozier et al., 2008) and upstream habitat degradation (Greene & Beechie, 2004) are thought to be major threats to Fraser Chinook stocks, both of which are challenging to address with short-term management interventions. In addition, hatchery supplementation of wild stocks in the Fraser River tributaries is minimal compared to other tributaries (Hanson et al., 2021). Reductions in the take of Fraser River Chinook stocks could increase their availability to SRKW during this important summer feeding period. Given the decline in traditional core summer habitat use over the past two decades that we report here, it will be important for future studies to evaluate if and how the summer diets of SRKW have changed over this period, and if the population is able to meet its energetic demands by supplementing its summer diet with other prey species or Chinook salmon stocks found outside of the central Salish Sea. Given the major decline in Fraser River Chinook returns, reducing disturbance of the SRKW population within their traditional summer foraging grounds may be critical in order to maximize foraging efficiency during the truncated period that they now occupy the Salish Sea.

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Many individual contributors and organizations provided sighting reports for this study, including Orca Network and the Pacific Whale Watch Association. Additional sighting reports have come from regional, shore-based sighting

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groups including the SGI Whale Sightings Network, Whale Watch - Pender Island, and Salish Sea Orca Squad. The authors appreciate having access to the 2012 edition of the Whale Museum Orca Master sighting data base. Although this study focused on the traditional core summer habitat of Southern Resident killer whales, sightings from surrounding areas played a role in establishing where the whales were located. Sighting reports for other regions have come from individual contributors, Orca Network, the Pacific Whale Watch Association, Jared Towers, The Whale Centre of Tofino as well as regional shore-based sighting groups including Sooke Whale Spotting, Whale Spotters of Otter Point & Sooke, Nanoose Whale Watch, Gabriola Island Whale Sightings, Field Naturalists of Vancouver Island, Comox Valley Wildlife Sightings, Howe Sound/Atl'ka7tsem Cetacean Sightings Group, Sunshine Coast Whale and Dolphin Sightings, Whale Spotting Powell River/Qathet, Puget Sound Orcas, and Puget Sound Whale Sightings.

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AUTHOR CONTRIBUTIONS

Joshua D. Stewart: Conceptualization; formal analysis; investigation; methodology; supervision; visualization; writing – original draft; writing – review and editing. **Jane Cogan:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – review and editing. **John W. Durban:** Conceptualization; funding acquisition; investigation; project administration; writing – review and editing. **Holly Fearnbach:** Conceptualization; funding acquisition; investigation; project administration; writing – review and editing. **David K. Ellifrit:** Investigation; methodology; resources; writing – review and editing. **Mark Malleson:** Investigation; methodology; resources; writing – review and editing. **Melisa Pinnow:** Data curation; investigation; methodology; resources; writing – review and editing. **Kenneth C. Balcomb:** Conceptualization; data curation; funding acquisition; investigation; methodology; resources; writing – review and editing.

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CLIMATE CHANGE

Sustained climate warming drives declining marine biological productivity

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Climate change projections to the year 2100 may miss physical-biogeochemical feedbacks that emerge later from the cumulative effects of climate warming. In a coupled climate simulation to the year 2300, the westerly winds strengthen and shift poleward, surface waters warm, and sea ice disappears, leading to intense nutrient trapping in the Southern Ocean. The trapping drives a global-scale nutrient redistribution, with net transfer to the deep ocean. Ensuing surface nutrient reductions north of 30°S drive steady declines in primary production and carbon export (decreases of 24 and 41%, respectively, by 2300). Potential fishery yields, constrained by lower–trophic-level productivity, decrease by more than 20% globally and by nearly 60% in the North Atlantic. Continued high levels of greenhouse gas emissions could suppress marine biological productivity for a millennium.

The Southern Ocean strongly influences Earth's climate and biogeochemistry (*1*, *2*). Deep ocean waters upwell to the surface at the Antarctic Divergence. Subantarctic Mode and Antarctic Intermediate waters form as northward-drifting surface waters sink and continue northward at mid-depths, transporting nutrients into the low-latitude thermocline. The Southern Ocean increasingly dominates ocean uptake of heat and CO_2 with strong climate warming because of a poleward shift and intensification of the mid-latitude westerly winds (*3*–*5*). Earth system models (ESMs) in the fifth phase of the Coupled Model Intercomparison Project (CMIP5) show consistent declines in global marine net primary production (NPP) during the 21st century in scenarios with high fossil fuel emissions, often with increasing Southern Ocean NPP (*4*, *6*–*8*).

Biological export of organic matter transfers nutrients vertically as sinking particles decompose, releasing nutrients. Where surface currents diverge (and subsurface currents converge), nutrients are transported upward, but some of the nutrients subsequently rain down as a result of biological export, instead of being advected away laterally at the surface. If the time scale for downward transfer by sinking particles is fast relative to the flushing time, nutrients become trapped, increasing concentrations locally and reducing lateral transport of nutrients out of the area. Idealized model studies, with imposed increases in Southern Ocean productivity, can develop nutrient trapping that boosts Southern Ocean nutrient concentrations and decreases northward lateral nutrient transport, reducing subsurface nutrient concentrations and decreasing biological productivity at low latitudes (*9*–*16*). Southern Ocean nutrient trapping, modulated by circulation, can potentially transfer nutrients from the upper ocean to the deep ocean (*12*, *15*).

We found intense Southern Ocean nutrient trapping as a result of climate warming in a fully coupled simulation to the year 2300, with the Community Earth System Model forced with representative concentration pathway 8.5 (RCP8.5) and extended concentration pathway 8.5 scenarios. The prescribed atmospheric CO_2 concentrations increase to 1960 parts per million by 2250, before leveling off (*17*, *18*). We previously used this ESM to examine marine biogeochemistry to the year 2100 (*19*–*21*) and century-by-century changes in the climate-carbon feedback to 2300 (*22*). Southern Ocean nutrient trapping has not been simulated previously without imposed NPP increases (arbitrarily modifying biological or physical forcings). In our simulation, nutrient trapping develops naturally after centuries of climate warming. This nutrient trapping drives a global reorganization of nutrient distributions, with a net transfer to the deep ocean, leading to a steady decline in global-scale marine biological productivity. This climate-biogeochemistry interaction amplifies the declines in productivity due to increasing stratification projected previously for the 21st century, and its negative effects on productivity eventually exceed those of increasing stratification (*6*–*8*).

The Southern Hemisphere westerly winds strengthen and shift poleward with climate warming, approaching Antarctica by 2300 (Fig. 1 and fig. S1). The Antarctic Divergence upwelling zone also strengthens and shifts poleward (*1*), ultimately initiating coastal upwelling along Antarctica, in areas with downwelling today (Fig. 1 and figs. S1 and S2). Ocean heat content and stratification increase globally, and deep mixing in the North Atlantic collapses, reducing North Atlantic Deep Water (NADW) formation from 30 to 5 sverdrups by 2200 (1 sverdrup = 10^6 m^3 s^{-1}) (*21*, *22*). Global sea surface temperature and stratification (0 to 500 m) peak by 2200 (*22*). Deeper down, the ocean is still warming in 2300, increasing stratification between intermediate depths and the deep ocean. Density differences between 500 and 1500 m and between 1000 and 2000 m more than double preindustrial differences by 2300, with most (>80%) of the change occurring after 2100 (table S1). Vertical exchange with cold, deep waters contributes to a slower warming trend in the Southern Ocean at depth, though surface waters warm considerably (Fig. 1 and fig. S4).

Biological export in the Southern Ocean increases by 2100 but declines at lower latitudes and in the high-latitude North Atlantic (table S1). Both patterns intensify after 2100, leading to nutrient trapping, with subsurface nutrient concentrations near Antarctica increasing substantially by 2300 (Fig. 2, fig. S3, and table S2). Concentrations of macronutrients (phosphate, nitrate, and silicic acid) decrease in the northward-subducting waters, decreasing thermocline concentrations and depressing low-latitude NPP and export (Fig. 2, figs. S3 and S4, and tables S1 to S3). Low-latitude productivity steadily drops as stratification increases and both surface and subsurface nutrient concentrations decline (Fig. 2, fig. S3, and tables S1 and S3). The equatorial upwelling flux of phosphate declines sharply (41%), even though the mean equatorial upwelling rate declines modestly (3%). The sharp drop in nutrient flux is due to the decrease in subsurface nutrients after 2100, driven by reduced lateral transport from the Southern Ocean (Fig. 3, fig. S3, and tables S1 and S3).

The nutrients stripped out of surface waters by enhanced productivity in the Southern Ocean are redistributed through the deep ocean by large-scale circulation (Fig. 4). Nutrient concentrations steadily increase in the Southern Ocean and the global deep ocean after 2100, while declining everywhere to the north, from the surface down to the depth of Antarctic Intermediate Water (~1500 m) (Fig. 4). We found similar global redistribution patterns for nitrate and silicic acid but not for iron (figs. S5 to S7), because iron is removed on time scales too short to permit long-range transport (*23*, *24*) (supplementary materials).

Three distinct processes drive the transfer of nutrients to the deep ocean. First, Southern Ocean nutrient trapping lowers the nutrient flux from the deep ocean to the upper ocean within the northward-subducting Antarctic Intermediate and Subantarctic Mode waters. This is the primary pathway for nutrients to return to the upper ocean (*12*, *15*). Second, increasing stratification globally decreases vertical mixing and exchange between the upper and deep ocean (table S1). Third, reduced vertical mixing and reduced NADW formation (*21*, *22*) decrease the main

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source of lower-nutrient waters to the deep ocean (*12*), driving nutrient declines that are larger in the Atlantic basin and high northern latitudes than in other regions (Fig. 4, figs. S5 to S7, and supplementary materials).

Increasing NPP in the Southern Ocean (south of 60°S) is driven by the poleward shift of the westerlies, warming surface waters, and vanishing sea ice, all of which enhance phytoplankton growth. Initially, the rise in NPP is driven by the shifting westerlies, with upwelling rates increasing to the year 2150 before leveling off (Fig. 3A). Surface stratification intensifies to the year 2300, driven by strong surface warming and decreases in surface salinity (Fig. 3, fig. S3, and table S2). The 6°C warming of polar surface waters increases maximum phytoplankton growth rates by 52% (table S2 and supplementary materials). The mean surface mixed-layer depth shoals with increasing stratification, declining from 75 m in 1850 to 40 m by 2300 (table S2). Sea ice cover reduces radiation to the contemporary Southern Ocean, but this shielding is weakened considerably by 2300 because the ice-covered area declines by 96% (fig. S9 and tables S1 and S2). Mean light levels in the surface mixed layer increase 245% by 2300 as a consequence of near-complete sea ice loss and shoaling mixed-layer depths (table S2 and supplementary materials).

Iron availability modulates phytoplankton capacity to take advantage of improving light and temperature growth conditions. Subsurface iron concentrations increase by 34% south of 60°S by 2300, with particularly high subsurface concentrations near Antarctica (table S2 and figs. S7 and S10). Volumetric upwelling rates remain ~25% above preindustrial levels after 2150, and the upwelling phosphate flux follows this temporal pattern, boosted modestly by the nutrient trapping effect (table S2 and supplementary materials). In contrast, the iron upwelling flux continues to rise to the year 2300, increasing 276% relative to preindustrial levels (Fig. 3 and table S2). This large increase is due to the southward shift in the upwelling zone, which entrains more margin-influenced, high-iron waters, further boosting productivity (Fig. 2; figs. S2, S3, and S9 to S12; and supplementary materials).

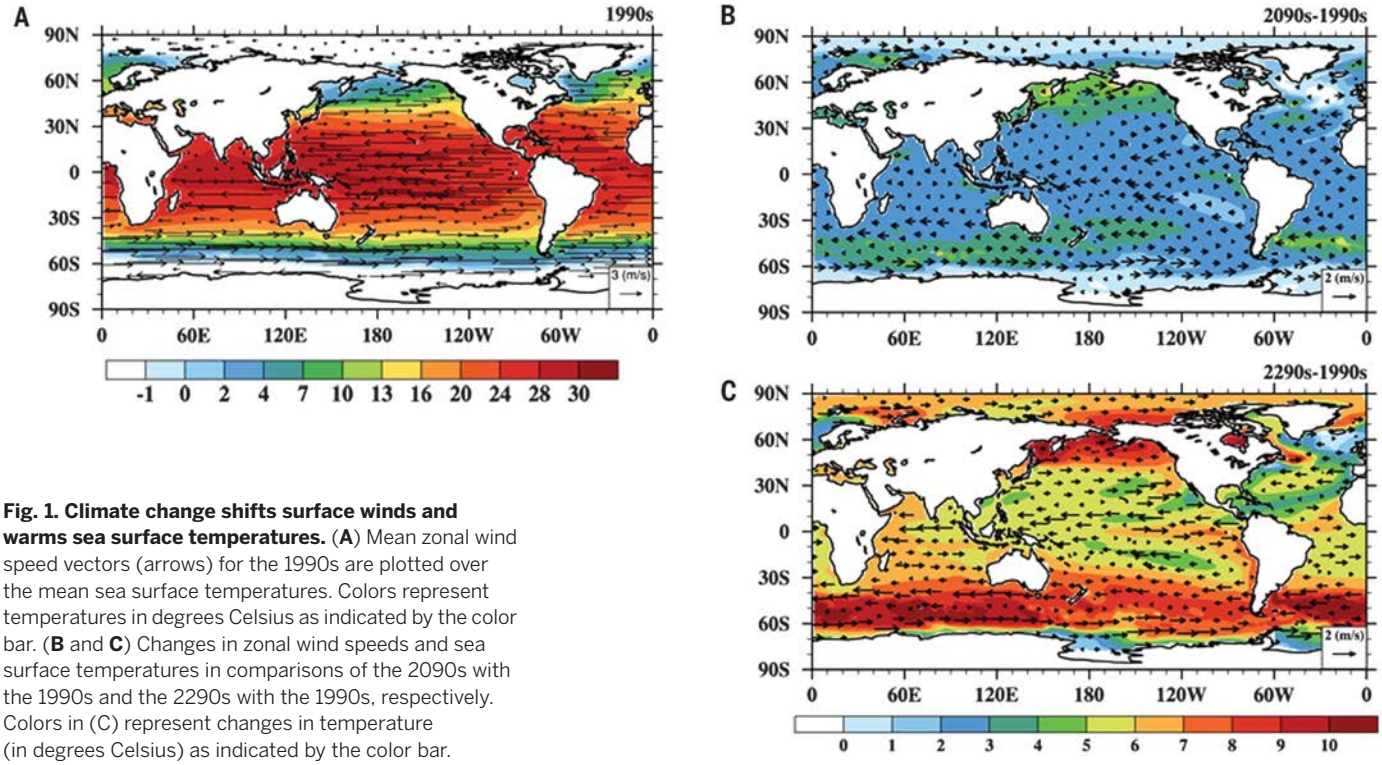


Fig. 1. Climate change shifts surface winds and warms sea surface temperatures. (**A**) Mean zonal wind speed vectors (arrows) for the 1990s are plotted over the mean sea surface temperatures. Colors represent temperatures in degrees Celsius as indicated by the color bar. (**B** and **C**) Changes in zonal wind speeds and sea surface temperatures in comparisons of the 2090s with the 1990s and the 2290s with the 1990s, respectively. Colors in (C) represent changes in temperature (in degrees Celsius) as indicated by the color bar.

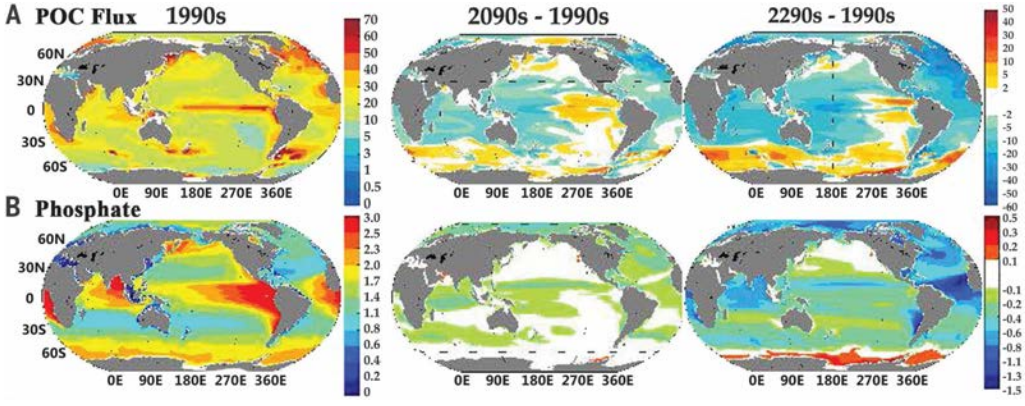


Fig. 2. Climate change effects on biological export and nutrient distributions. Global maps of (**A**) particulate organic carbon (POC) flux at a depth of 100 m (expressed in grams of carbon per square meter per year) and (**B**) mean phosphate concentrations at depths of 200 to 1000 m (expressed as micromolar concentrations). The left column shows 1990s means, the middle column shows the difference between the 2090s and the 1990s, and the right column shows the difference between the 2290s and the 1990s. Phosphate concentrations increase around the Antarctic by 2300 because of nutrient trapping.

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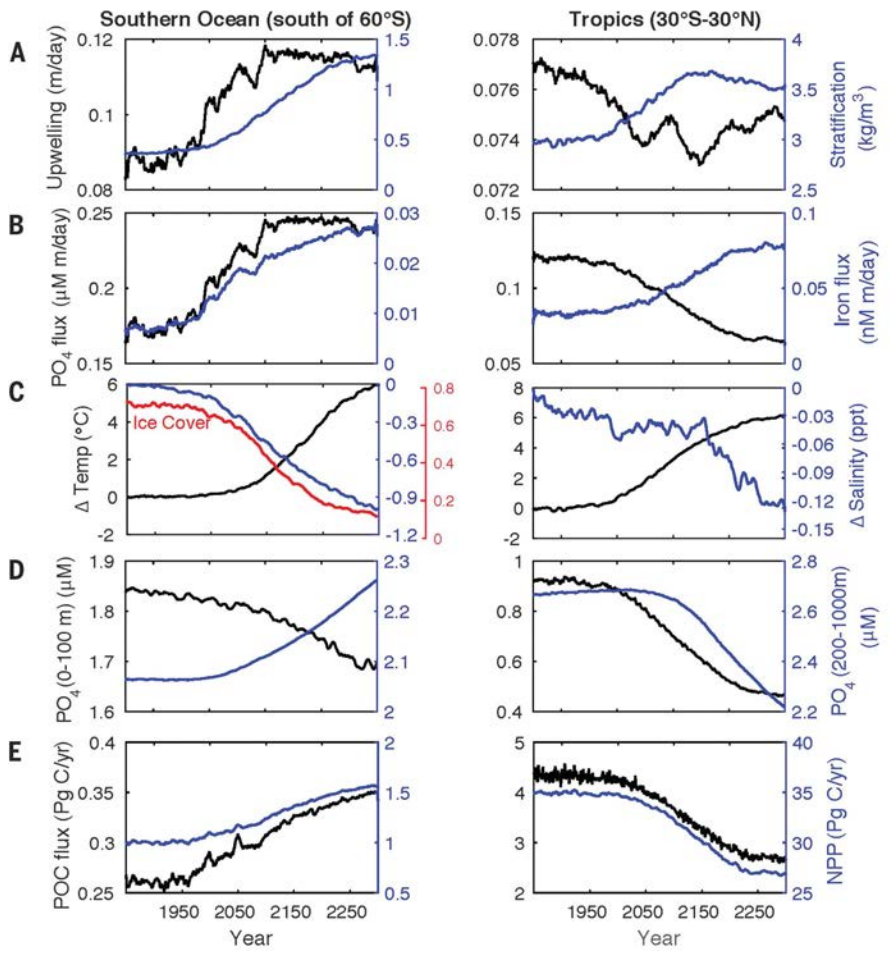


Fig. 3. Regional time series of ocean physical forcing and biogeochemical response. (**A**) Evolution of biogeochemical and physical variables over time (1850 to 2300) for the Southern Ocean and the tropics. The mean upwelling rate increases in the Southern Ocean but slows in the tropics, as surface stratification increases in both regions. (**B**) Upwelling rates for phosphate (expressed as the micromolar concentration per meter of upwelled water per day) and dissolved iron (expressed as the nanomolar concentration per meter of upwelled water per day), (**C**) changes in temperature and salinity [in parts per thousand (ppt)], (**D**) surface (0 to 100 m) and intermediate-depth (200 to 1000 m) phosphate concentrations, and (**E**) sinking POC flux and NPP [both in petagrams of carbon per year (Pg C/yr)]. The fractional sea ice cover is overlain in (C) (left column). Upwelling flux was averaged for 10°S to 10°N for the tropical time series, and stratification was estimated from the density difference between the surface and 200 m for both regions.

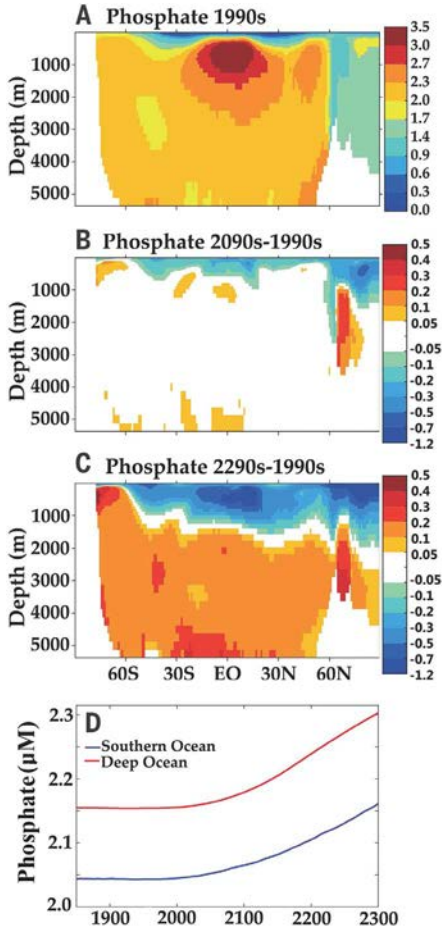


Fig. 4. Southern Ocean nutrient trapping transfers phosphate to the deep ocean. Zonal mean phosphate concentrations (micromolar) are shown for the 1990s (**A**), along with the differences in zonal phosphate concentrations in comparisons of the 1990s with the 2090s (**B**) and the 1990s with the 2290s (**C**). Phosphate concentrations increase over time in the high-latitude Southern Ocean (at all depths south of 60°S) and in the global deep ocean (below 2000 m and north of 60°S) (**D**).

Phytoplankton biomass and community composition do not change greatly, but growth rates increase and the growing season is longer, leading to a doubling of the annual biological surface phosphate drawdown by 2300 (table S2). Additional productivity increases are possible with additional iron input, because surface phosphate concentrations are far from depleted. One possible iron source (not included in our simulation) is from Antarctic glaciers (*25*). The strong climate warming would greatly increase glacial discharge (*26*), increasing iron inputs, allowing for even more efficient nutrient trapping, and modifying freshwater dynamic forcing of the oceans.

Marine food webs will shift with increasing nutrient stress outside the Southern Ocean. Relative changes in biological export are larger than those in NPP (table S1); because NPP can include substantial recycled production, changes in export more directly reflect the decreased flux of nutrients to surface waters (*8*) (tables S1 to S3 and supplementary materials). The smallest phytoplankton benefit most from increasing temperatures and nutrient depletion in surface waters (*27*), outcompeting larger phytoplankton and reducing the efficiency of biological export (*8*, *28*). Loss of the sea ice biome at both poles will considerably modify biological communities, with reduced competitiveness and, potentially, extinction of some polar-adapted, ice-dependent organisms, including the Antarctic krill central to Southern Ocean food webs (*29*) (supplementary materials).

Decreasing NPP and biological export north of 30°S more than offset productivity increases in the Southern Ocean, driving global-scale declines in NPP (−15%) and export (−30%) by 2300 (figs. S12 and S13 and table S1). The declines above 30°S are 24% for NPP and 41% for particulate organic carbon export (tables S1 to S3). The largest reductions occur in the North Atlantic, western Pacific, and southern Indian oceans, with zooplankton productivity closely tracking phytoplankton (figs. S12 and S13 and tables S1 to S4). Production at higher trophic levels (including potential fishery yield) is limited by lower–trophic-level production and trophic transfer efficiency (*30*–*32*). To estimate how changing zooplankton productivity influences higher trophic levels and maximum potential fishery yields, we used an empirical model with optimized transfer efficiencies, constrained by fishery data sets (*32*) (supplementary materials). We found that for higher trophic levels, production declines by more than

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20% globally and by nearly 60% in the North Atlantic (fig. S14 and table S5). Spatial patterns are similar to zooplankton production shifts but are modified by decreasing transfer efficiency where the warm-water biome expands (*32*) (figs. S13 to S15).

The processes leading to the climate-driven transfer of nutrients to the deep ocean are scarcely apparent by 2100 but dominate ocean biogeochemistry by 2300. Little macronutrient accumulation occurs in the upper ocean around Antarctica by 2100 (Fig. 2 and figs. S3, S5, and S6). This trend is consistent with the finding of only a modest increase in biological carbon storage in the Southern Ocean across multiple CMIP5 models in 2100, driven by a slowdown of the deep circulation rather than by nutrient trapping (*4*). In 2300, tropical subsurface phosphate concentration is still declining and the deep ocean phosphate level is still increasing linearly (Figs. 3 and 4). Thus, the transfer of nutrients to the deep ocean will continue well past 2300, further depressing upper-ocean nutrient concentrations and global-scale productivity. ESM simulations must extend well past 2100 to capture key ocean physical and biogeochemical responses to multicentury climate warming.

Southern Ocean nutrient trapping appears to be a robust response to multicentury warming. All CMIP5 models project southward shift and intensification of the westerlies over the 21st century under the RCP8.5 scenario, despite considerable differences in the structure and performance of atmospheric models (*5*). Most CMIP5 models predict increasing Southern Ocean export by 2100, despite large differences in plankton and biogeochemical models (*4*, *6*–*8*, *24*, *28*). We found that the same climate-driven nutrient redistribution occurs in two other ESMs [the Hadley Centre Global Environmental Model, version 2 (HadGEM2) (*33*), and the Max-Planck-Institute Earth System Model (MPI-ESM) (*34*)] that conducted RCP8.5 simulations to the year 2300 (fig. S16). Both models show nutrient increases in the Southern Ocean and in the deep ocean, accompanied by nutrient reductions in the upper ocean. Thus, our results are not dependent on the model details of atmosphere-ocean circulation, plankton dynamics, or biogeochemistry, but rather seem to represent a robust Earth system response to multicentury climate warming.

Relatively modest increases in export are sufficient to induce nutrient trapping if they occur in the critical location above the Antarctic Divergence. Currently, heavy sea ice cover, cold temperatures, and iron limitation depress biological production in this region. Warming of surface waters and removal of sea ice greatly improve phytoplankton growth conditions, inducing strong regional nutrient trapping that further boosts productivity. If the climate warms enough to remove Southern Ocean sea ice, the nutrient redistribution and depression of global-scale productivity outlined here seem inevitable. Thus, the loss of Southern Ocean sea ice marks a critical biogeochemical tipping point in the Earth system. More research is needed on the physical forcings and the degree of warming necessary for removal of southern sea ice cover and the initiation of Southern Ocean nutrient trapping, including simulations with more moderate future trajectories of fossil fuel emissions. Rapid southern sea ice decline begins in about the year 2050 in our simulation, when mean surface air temperature has risen by ~2.5°C, with near-complete removal of sea ice by 2200 (Fig. 3 and fig. S9). This sea ice trend and the biogeochemical responses documented here support emission reduction targets that keep climate warming below 2°C (*26*).

The ongoing depletion of upper-ocean nutrients in 2300 will not reverse until the climate cools and sea ice returns to the Southern Ocean, depressing high-latitude productivity and enhancing northward lateral nutrient transfer. Southern Ocean dynamics will dominate this climate-cooling time scale, because the Southern Ocean will dominate ocean uptake of CO_2 by 2300 (figs. S17 and S18 and supplementary materials). The long time scales associated with ocean uptake and storage of anthropogenic CO_2 (*35*) and the subsequent time necessary for the circulation to return depleted nutrients to the upper ocean (*12*) ensure that NPP will be depressed for a thousand years or more. This puts the climate change impacts on marine biogeochemistry and productivity on the same time scale as continental ice sheets, with cumulative, catastrophic effects that will be increasingly difficult to avoid with delayed reductions in greenhouse gas emissions (*26*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
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References (*36*–*47*)

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Science

Sustained climate warming drives declining marine biological productivity

J. Keith Moore, Weiwei Fu, Francois Primeau, Gregory L. Britten, Keith Lindsay, Matthew Long, Scott C. Doney, Natalie Mahowald, Forrest Hoffman and James T. Randerson

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Starving ocean productivity

Projected increases in greenhouse gas emissions could suppress marine biological productivity for a thousand years or more. As the climate warms, westerly winds in the Southern Hemisphere will strengthen and shift poleward, surface waters will warm, and sea ice will disappear. Moore *et al.* suggest that one effect of these changes will be a dramatic decrease in marine biological productivity (see the Perspective by Laufkötter and Gruber). This decrease will result from a global-scale redistribution of nutrients, with a net transfer to the deep ocean. By 2300, this could drive declines in fisheries yields by more than 20% globally and by nearly 60% in the North Atlantic.

Science, this issue p. 1139; see also p. 1103

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A cumulative effects model for population trajectories of resident killer whales in the Northeast Pacific

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ABSTRACT

Like numerous species at risk, the resident killer whale populations of the Northeast Pacific are vulnerable to the cumulative effects of anthropogenic threats. A Pathways of Effects conceptual model summarised the current understanding of each threat (prey availability, acoustic and physical disturbance, and contaminants), threat interactions, and potential impacts to fecundity and mortality. A Population Viability Analysis utilised the most recent available data to quantify impacts of threats on population parameters. The impacts of individual and cumulative threat scenarios on modelled Southern and Northern Resident Killer Whale populations were compared to the observed population demographics to define a model that best captured the real world dynamics. Of the individual and combined threat models tested, the cumulative model incorporating all threats predicted demographic rates closest to those observed for both populations. Recent low Chinook salmon abundance and its interactions with vessel disturbance and contamination strongly influenced modelled killer whale population dynamics. The cumulative effects population viability analysis model projected a mean increase in the modelled Northern Resident Killer Whale population to the carrying capacity within 25 years. In contrast, the mean modelled Southern Resident Killer Whale population trajectory was projected to decline under current conditions, with a 26% probability of population extinction, and in those projections, extinction was estimated to occur after 86 (± 11) years. Our results highlight the importance of considering the collective impact of multiple threats to imperilled species and the necessity of testing management and mitigation measures aimed at recovery using a holistic, validated model.

1. Introduction

Effective conservation of species at risk now requires an understanding of the cumulative effects of multiple activities in the ecosystem. The impact of a single threat on a species through time and across its geographical range will always have a degree of associated uncertainty and these uncertainties are compounded when multiple threats co-occur and potentially interact. Uncertainties and interactions among threats make recovery efforts fraught with confusion as decision-makers must consider all evidence to assess potential recovery actions. This balance is demonstrated by killer whale populations around the world that are under threat from several anthropogenic pressures (Desforges et al., 2018; NASEM, 2017). The Southern Resident Killer Whale (SRKW) population is listed as Endangered under the Canadian Species at Risk Act (SARA) and the US Endangered Species Act, and the more northerly but sympatric Northern Resident Killer Whale (NRKW) population is listed as Threatened under the SARA. All populations of Resident Killer Whales are piscivorous, feeding primarily on Chinook (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*), but despite the similarities in diet and a substantial overlap in range (from southeastern Alaska to Washington State), SRKW and NRKW do not interact with one another socially and are distinct in terms of their culture, acoustics, and genetics (Ford et al., 1998, 2000; DFO, 2017a, 2017b). A comparison of their population dynamics can thus provide insights into the different ways they are affected by human threats (NASEM, 2017).

Long-term photo-identification census surveys for SRKW and NRKW, which were initiated in the 1970s and continue to the present day, show contrasting trends in the two populations (DFO Cetacean Research

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Program; Center for Whale Research, CWR). Population trends based on these census data indicate that the SRKW population has experienced an overall negative population growth rate (−0.002; 1979–2017), with a particularly sharp decline between 1995 and 2001 (Fig. 1). Since then, the SRKW population has shown little recovery, having 73 members as of July 2019. In contrast, the NRKW population has experienced a steady increase over the census period (population growth rate = 0.02; 1979–2017), except for a decline between 1997 and 2001 (Fig. 1). The NRKW population has since increased from 219 members in 2004, to 310 members in 2019 (Olesiuk et al., 2005; DFO, 2020).

The three primary threats to SRKW and NRKW are reduced prey availability, acoustic and physical disturbance, and environmental contaminants (COSEWIC, 2008; Ford et al., 2010; DFO, 2011, 2017a; NMFS, 2008). There is strong evidence that survival and fecundity of these populations are affected by prey availability (Ford et al., 2010; Ward et al., 2009) but limited quantitative evidence on the impacts of disturbance and contaminants. These threats may act on the populations at multiple life history stages and throughout their range. Thus, there is potential for cumulative effects on these populations through repeated exposures to a single threat, exposures at multiple life stages to a threat, and/or exposures to multiple threats. Additionally, threat interactions are known to be common when multiple stressors act within a system (Crain et al., 2008; Darling and Côté, 2008) and non-linear relationships make the effects at a population level difficult to determine. Understanding the effects of cumulative as well as individual threats is therefore necessary to inform the development of effective population conservation strategies (NASEM, 2017).

Several approaches have been used for consideration of cumulative effects on cetaceans. Previous cumulative effects assessments (CEAs) fall into three categories: risk assessment, statistical analysis, and population viability analysis (PVA) (Lacy et al., 2017; Lawson and Lesage, 2012; O et al., 2015). Risk assessment has been used to rank threats and activities of interest occurring in cetacean habitat (Lawson and Lesage, 2012; O et al., 2015). Statistical models have been used to evaluate the impact of single threats on mortality and fecundity of resident killer whales (Vélez-Espino et al., 2015; Ward et al., 2009). A PVA model was developed to evaluate cumulative effects of anthropogenic threats on the SRKW population (Lacy et al., 2017).

The aim of the current assessment is to define and apply a cumulative effects model to evaluate and compare the individual and cumulative effects of anthropogenic threats on both the SRKW and NRKW populations of resident killer whales (after Lacy et al., 2017; Clarke Murray et al., 2019). The study is limited to considering the primary threats identified in the SARA action plan for NRKW and SRKW (COSEWIC, 2008; Ford et al., 2010; DFO, 2011, 2017a, 2018; NMFS, 2008). The definition and testing of an acceptable cumulative effects model will support evaluation of future changes in anthropogenic activities and potential mitigation measures and management actions.

2. Methods

2.1. Cumulative effects assessment

The cumulative effects assessment consisted of two phases: a Pathways of Effects (PoE) conceptual model and a Population Viability Analysis (PVA) quantitative simulation model. The PoE conceptual model described the impacts of threats (or stressors) on killer whale vital rates (mortality and fecundity). As the interaction of threats over space and time can alter their respective intensities and consequent effects on individuals and populations, potential interactions between threats were also assessed to more accurately represent the natural system. The PoE conceptual model consisted of a visual representation of the threat linkage pathways, with supporting justification text (Stephenson and Hartwig, 2009; Government of Canada, 2012) and was developed through literature review and elicitation of expert opinion through consultation with colleagues in relevant fields of expertise.

The outputs of the PoE conceptual model were used to design and refine the structure and parameterisation of the PVA model, building upon the methods and results of previous work (DFO, 2018; Lacy et al., 2017; Taylor and Plater, 2000; Vélez-Espino et al., 2015; Ward et al., 2009; Williams et al., 2017). Existing literature and data were used to parameterise the impact of each threat on killer whale vital rates, and previously published relationships were updated with recent data and re-analysed (detailed in Supplementary Material). The quantitative values and relationships specific to each population (SRKW and NRKW) were used to define the inputs to the population model describing the combined impact on population persistence through time. The model structure builds upon an existing PVA model developed for the SRKW population by Lacy et al. (2017). To capture the unique population structure and threat exposure, a PVA model was developed for each population (SRKW and NRKW) using Vortex 10.3.1, an open access modelling software (Lacy and Pollak, 2014).

2.2. Killer whale population model

Population models were constructed using census data obtained from DFO's Cetacean Research Program encompassing the years 1979–2017 (DFO, 2020; DFO CRP, unpublished data). Annual population surveys have occurred without interruption since 1973 for the NRKW population and 1976 for the SRKW population (DFO Cetacean Research Program; Center for Whale Research, CWR). The SRKW census is considered to be more precise than the NRKW census, as not all members of the Northern

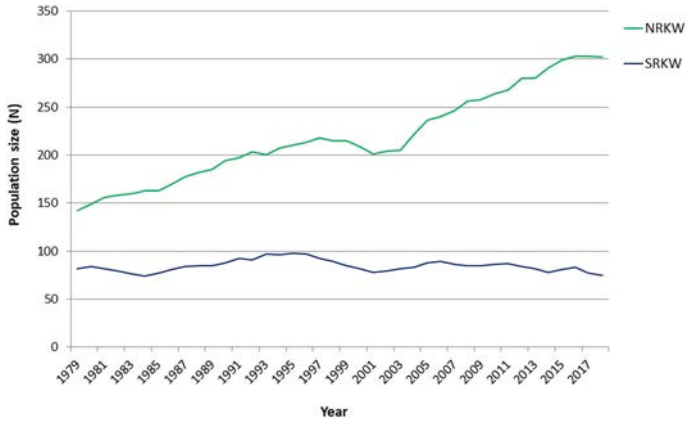


Fig. 1. Resident killer whale population time series, 1979–2018. Source data: long-term photo-identification census surveys for Southern and Northern Resident Killer Whales (SRKW and NRKW), which were initiated in the 1970s and continue to the present day (Fisheries and Oceans Canada Cetacean Research Program; Center for Whale Research).

population have been seen each year (DFO, 2018, 2020). By using demographic rates starting in 1979 for both populations, the time series is composed mostly of data from direct observations rather than reconstructed data (Olesiuk et al., 2005). The killer whale reproductive system was defined as polygynous and sexually dimorphic with observed population parameters (Table A1; Olesiuk et al., 2005; Vélez-Espino et al., 2014; Ward et al., 2009). Details can be found in Appendix A. The SRKW range extends from southeastern Alaska to central California and the NRKW range from the coastal waters of Glacier Bay (Alaska, USA) to Gray's Harbor (Washington State, USA) (Ford, 2006; Ford et al., 2000).

The neighboring Southern Alaska Resident Killer Whale (SARKW) population has a similar life history strategy but is relatively removed from the threats to which the SRKW and NRKW populations are exposed. The SARKW population has over 700 individuals and has an annual rate of increase considered to be at its maximum, 3.5%, attributed to rebounding salmon stocks (Matkin et al., 2014). The SARKW census data, which began in 1984, were used to define the reference mortality and fecundity rates for the population models, assuming the rates represent those expected from a population in unrestrained growth. The SARKW population is not considered to be pristine as it is exposed to anthropogenic impacts; contaminants and oil spills are the main threats (Matkin et al., 1998, 2014). Notably, a major oil spill (*Exxon Valdez*) occurred in 1989 and resulted in a 33% loss of the resident AB matriline (Matkin et al., 1998, 2008), which has not recovered. However, these anomalous deaths were excluded from the data analysis of Matkin et al. (2008) and do not affect the estimates of vital rates for SARKW used in the present analysis (Table 1). The rates and age/sex structure of the SARKW population were found to be similar to NRKW in their period of unrestrained growth, except that the age of maturity was one year younger for SARKW (Matkin et al., 2008; Olesiuk et al., 2005).

The SARKW vital rates (Table 1) were used in the SRKW and NRKW population models to represent the reference vital rates that determine the growth of each population in the absence of anthropogenic threats. This is an important change from the SRKW model developed by Lacy et al. (2017), where the "baseline" was defined using the mean demographic rates that were observed from recent decades and would therefore include current threat levels. Model scenarios were developed and tested for individual and cumulative threats where threats (described in further detail in later sections) were included in the model as modifiers of the SARKW reference vital rates.

Table 1
Age-specific mortality and fecundity rate for each Resident Killer Whale population: Southern Resident Killer Whales (SRKW), Northern Resident Killer Whales (NRKW) and Southern Alaska Resident Killer Whales (SARKW). SRKW and NRKW data were sourced from Vélez-Espino et al. (2014) for years 1987–2011. SARKW data were sourced from Matkin et al. (2014) for years 1984–2010.

	SRKW	NRKW	SARKW
Age class (y) (male and female combined)	Age-specific mortality rate		
0–1	0.215 (SD = 0.284)	0.078 (SD = 0.082)	0.054 (SD = 0.244)
1–2	0.019 (SD = 0.047)	0.028 (SD = 0.019)	0.003 (SD = 0.040)
2–5	0.019 (SD = 0.047)	0.028 (SD = 0.019)	0.010 (SD = 0.054)
6–10	0.019 (SD = 0.047)	0.028 (SD = 0.019)	0.012 (SD = 0.064)
10–16	0.015 (SD = 0.033)	0.011 (SD = 0.012)	0.008 (SD = 0.032)
17–51	0.033 (SD = 0.054)	0.011 (SD = 0.025)	0.023 (SD = 0.066)
51+	0.072 (SD = 0.108)	0.117 (SD = 0.114)	0.217 (SD = 0.292)
Age class (y) (female only)	Age-specific fecundity rate		
10–30	0.116 (SD = 0.077)	0.142 (SD = 0.046)	0.233 (SD = 0.118)
31–50	0.069 (SD = 0.074)	0.101 (SD = 0.051)	0.154 (SD = 0.118)

2.3. Population viability analysis modelling

The population genealogical and demographic data were partitioned to allow model validation and verification; the complete set of living animals in the year 2000, with their known dams, calving histories, and genealogies, were used as the starting population for each of the population models (SRKW and NRKW). This allowed a comparison of the modelled and observed populations as an evaluation of the ability of the model scenario output data to represent observed data.

Data and knowledge for each of the primary threats were reviewed and statistical analyses updated (see details in following sections). The results of the review and analyses were used to develop single and cumulative threat scenario models.

Model simulations were run on each scenario 10,000 times and summary statistics were recorded for population growth rate (r), population size at each time step (N_t), and probability of extinction (defined as only a single sex remaining). The population size at each year (mean and standard deviation) was compared to the observed (realised) population size for each population from the census survey data. Population growth rate (r) was quantified as the exponential rate of increase, according to the following equation:

$$r = ln\left[\frac{N_{t+1}}{N_t}\right]$$

In long-term simulations that reached an arbitrarily set maximum population size ("carrying capacity", K), the annual growth rate was calculated each year before the truncation of the population size to K, so that the r represented the intrinsic growth that would occur if a ceiling was not imposed on the population size. The model results (the predicted population size resulting from threat-modified reference vital rates) were then compared to the observed (realised) population dynamics from the census data over the same time period (2000–2017). The assumption of this approach is that if a model scenario replicates the realised dynamics for both the SRKW and NRKW populations then the model is appropriate for the system. The inspection approach method was used to validate the models (Law and Kelton, 1991); for the threat-modified model scenarios that most closely approached the observed population parameters, a simulation scenario with historical input data in place of the parameter randomly chosen from a distribution was also evaluated. In this case the yearly Chinook salmon index data was included in the historical scenario. A valid model should closely resemble the observed killer whale survey data when the historical data are used, including population size, age structure and sex ratio.

A sensitivity analysis was conducted on the prey, noise and contaminant parameters in the model to test the impact of uncertainty in these parameters on the results of the study. The sensitivity analysis was conducted in Vortex 10.3 using the Sensitivity Testing operations.

Once a model with acceptable performance was defined, model scenarios were projected into the future to examine the long-term population growth rate and future of the populations. The projection of the cumulative effects model from the 2017 population assumed that the current levels of threats continued into the future, with no changes in threats and no mitigation actions.

2.4. Threats

2.4.1. Prey availability

Field observation and statistical evidence support the relationship between the availability of Chinook salmon and mortality and fecundity rates for these populations (Ford et al., 2010; Ford et al., 1998; Vélez-Espino et al., 2015; Ward et al., 2009). Analysis of prey remains indicates that Chinook salmon can comprise up to 90% of the summer diet of SRKW (Ford and Ellis, 2006; Ford et al., 1998; Hanson et al., 2010).

Ford et al. (2010) reported that SRKW and NRKW survival rates were related to the modelled abundance of Chinook stocks available to six fisheries (Alaska Troll, BC North Troll, BC Central Troll, West Coast Vancouver Island Troll, Georgia Strait Sport, and Washington/Oregon Troll).

The statistical relationship between SRKW/NRKW mortality rates and Chinook salmon ocean abundance index values was updated using the entire time series of SRKW/NRKW and Chinook salmon data (1979–2017). The Chinook salmon stock index that best explains the mortality patterns seen in both populations was tested using model selection (Akaike Information Criterion, AIC). Linear regression was performed between SRKW/NRKW mortality with a one-year time lag and either the Coastwide Index (excluding Southeast Alaska (SEAK) stock, as done in Ford et al. (2000)), or the Chinook salmon runs deemed most relevant to each population (SRKW-stocks and NRKW-stocks). For SRKW-stocks, the WCVI + FL + OC runs were used (West Coast Vancouver Island, Fraser Late, and Oregon Coastal) and for NRKW-stocks the FE + PS + URB were used (Fraser, Puget Sound, and Upper Columbia River Brights) (Table A3) (Stredulinsky, 2016; Vélez-Espino et al., 2015).

To represent prey abundance in the models, Chinook salmon ocean abundance data were obtained from the DFO Salmon Program (A. Vélez-Espino, DFO, Pacific Biological Station) (1979–2017) from the 2018 Pacific Salmon Commission's (PSC) Chinook model calibration. Ocean abundance is an adequate representation of fish available for consumption by killer whales, given that the full time series of terminal run reconstruction data was unavailable, and ocean abundance has statistical support in previous analyses (Stredulinsky, 2016; Vélez-Espino et al., 2015). Yearly modelled ocean abundance was converted to an index of abundance by standardising the value by the mean for the full time series. The Chinook index value was randomly assigned in each model year using a normal distribution as defined by the median value (for a skewed distribution) and standard deviation from the entire time series. Selecting a value from a distribution in each year allowed the model to represent the fine temporal structure and variation in Chinook salmon abundance, and its impacts on killer whale vital rates. The distribution can then be used to project model scenarios over time periods not covered by the historical abundance data.

The availability of prey can also have significant effects on SRKW/NRKW reproductive success and the probability of calving. Ward et al. (2009) assessed calving probability (fecundity) of combined NRKW and SRKW females using a logistic regression model and found that fecundity was highly correlated with the PSC index of Chinook salmon abundance for the WCVI troll and recreational fishery in the prior year (one year lag). The model that best supported the data included age-structured effects on reproduction and a region effect to represent the lower calving rates in SRKW compared to NRKW. The logistic regression analysis was repeated with the additional 10 years of data for calving probabilities and PSC Chinook model ocean abundance salmon indices, following the statistical methods of Ward et al. (2009); additional details can be found in Appendix A. R code for the statistical analyses for prey abundance effects on mortality and fecundity can be found in Appendix B.

2.4.2. Vessel disturbance

Acoustic disturbance (noise) may come from a range of anthropogenic activities but this study focuses on the impacts of vessel-associated disturbance on killer whales. There is limited field evidence on the effects of vessel disturbance. Lusseau et al. (2009) observed a 25% reduction in SRKW feeding activity when boats were present. A noise exposure model combined with a Population Consequences of Disturbance (PCoD) model (National Research Council, 2005; Tollit et al., 2017) estimated that the lost foraging time for SRKW in the Salish Sea from a combination of behavioural responses and acoustic masking due to vessel presence was 20–23% of each whale-day (Tollit et al., 2017). Lacy et al. (2017) assumed that the effect on demographic rates of reduced feeding activity was the same as a comparable reduction in prey (i.e., no behavioural compensation by killer whales). In the PVA model, Lacy et al. (2017) estimated that vessels are present 85% of the daytime and killer whales are foraging in the presence of vessels 78% of the time. This represents a 16.6% reduction in Chinook salmon availability in the model (25% x 85% x 78%).

A time series of vessel activity for the study region that is comparable to the data available for killer whale population dynamics and Chinook salmon was not available. In order to estimate the relative presence of vessels in each population's range, data on the magnitude of vessel presence (commercial, recreational, and whale watching vessels) in the range of SRKW and NRKW were compiled (Appendix A). This estimate was used to set the vessel presence parameter for acoustic disturbance in the model. Acoustic disturbance was modelled as a reduction in feeding efficiency, and was directly linked to the variation in Chinook salmon abundance. The noise parameter was set to 0.85 for SRKW (equivalent to a 16.6% reduction in prey availability) and 1 for NRKW (no effect on prey availability).

2.4.3. Vessel strike

Fatal vessel strikes remove individuals completely from the population, affecting small populations disproportionately. Attributing cause of death in killer whales is difficult in many cases as carcasses often sink and are lost, meaning only a small proportion are recovered for necropsy examination (DFO, 2018; Ford et al., 1998; National Marine Fisheries Service, 2008). Limited data on cause of mortality suggest that SRKW have a slightly higher risk of strike than NRKW, 9.5% and 7.1% respectively between 1979 and 2017 (Appendix A; Baird, 2002; Ford et al., 2000; Williams and O'Hara, 2010). Changes in the frequency of vessel transits and the characteristics of ships (quieter or faster ships may increase strike risk) could affect this probability in the future. The vessel strike threat was modelled as an animal being removed randomly from the modelled adult population once every ten years. The probability was shared equally between males and females of the population.

2.4.4. Polychlorinated biphenyls contamination

The impact of environmental contaminants on killer whale vital rates was investigated using polychlorinated biphenyls (PCBs) as a representative class of contaminants due to a lack of available information on the impacts of other toxins. Hall et al. (2006, 2018) developed a PCB accumulation/depuration model to link PCB levels to calf mortality in cetaceans. The PCB model simulates the accumulation of PCBs in individuals over time, based on a set accumulation rate. Females offload an estimated 77% of their PCB loads to each calf during gestation and nursing (Hall et al., 2006, 2018). This PCB model has been used in cumulative effects assessment for SRKW (Lacy et al., 2017) and in estimating risk to global killer whale populations (Desforges et al., 2018). The dose-response logistic regression model curve used in these studies (Hall et al., 2018) was applied in the PVA scenario models to predict calf survival based on maternal PCB level. Contaminant model scenarios were run using either initial PCB levels from tissue samples summarised by Ross et al. (2000) (1993–1996) or the grand mean for the entire time series of tissue samples (Guy, 2018; Pearce and Gobas, 2018) (Appendix A; Table A10), with three different accumulation rates (1, 2, and 6 mg per year). The modelled PCB concentrations were then compared to the measured PCB levels in tissue samples.

3. Results

3.1. Pathways of Effects conceptual model

The overall PoE conceptual model (Fig. 2a) identified the important conceptual connections between threats (prey availability, acoustic and physical disturbance, and contaminants) and SRKW/NRKW population vital rates (fecundity, mortality), based on literature review and expert opinion. Prey availability appeared to be a central node, with six linkage

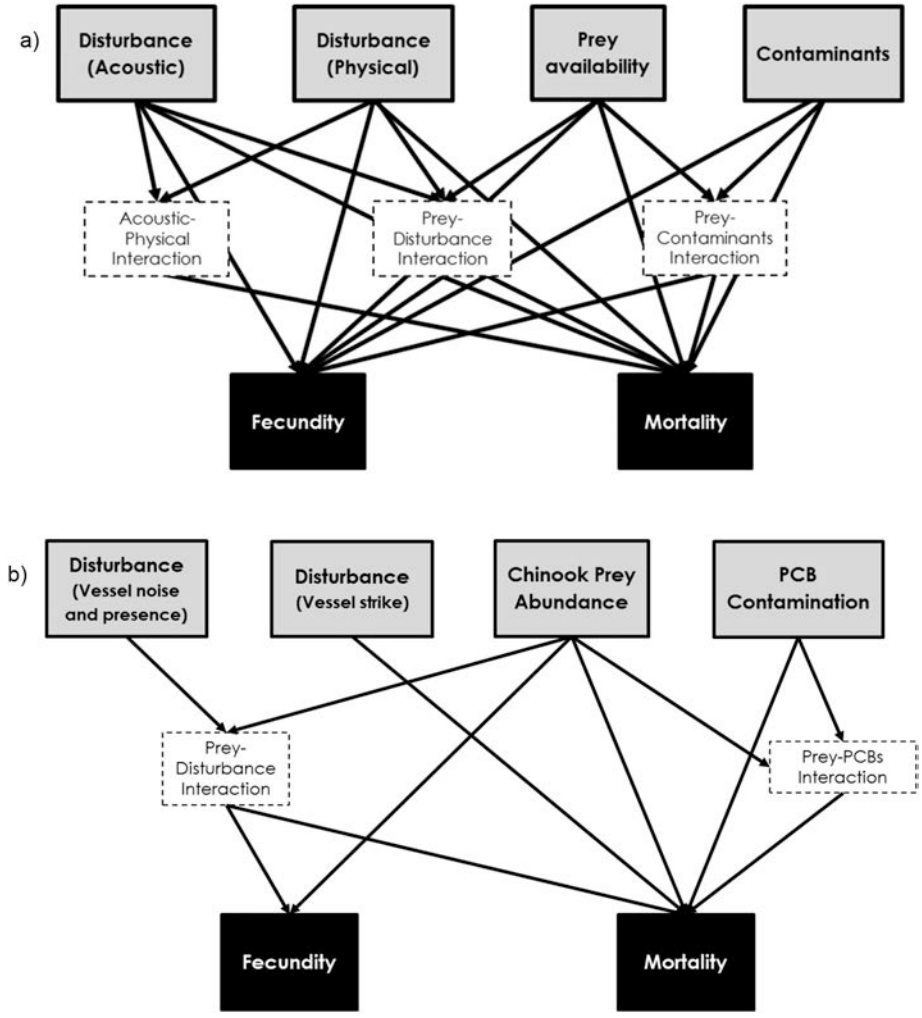


Fig. 2. a) Overall Resident Killer Whale Pathways of Effects conceptual model, including threats, interactions, and impacts on Resident Killer Whale fecundity and mortality and b) Population Viability Analysis model reduced to only the quantifiable threats and interactions.

pathways to fecundity and mortality, including two interactions with other threats (acoustic disturbance, physical disturbance) (Fig. 2a). Interactions make the assessment of impacts more difficult, as they imply that impacts may not be additive and instead may have non-linear or threshold effects. For example, the ability of killer whales to successfully catch and consume prey (access to prey) may be affected by disturbance. The impacts of disturbance could be exacerbated when prey abundance is low, and conversely, disturbance may have little or no effect on overall feeding efficiency when prey abundance is high (Prey-Disturbance Interaction). It has been hypothesised that killer whales might have a higher risk of vessel strike when exposed to loud sounds, which could impair the whales' ability to detect vessels and result in an acoustic-physical interaction effect (Erbe et al., 2018). The effects of PCBs on killer whales may be mediated by nutritional stress and the amount of blubber stores, as observed in seals, resulting in a prey availability-contaminants interaction (Robinson et al., 2018). Blubber-bound toxin levels are higher in Bigg's (transient) killer whales but their population is increasing rapidly (Ford et al., 2007) and therefore may not experience the same toxic effects as in prey-limited populations that are mobilising the toxins during periods of nutritional stress (Mongillo et al., 2016).

Based on the review of the available literature and data, only a subset of the linkages in the PoE conceptual model could be parameterised with empirical data and statistical relationships in the Population Viability Analysis (Fig. 2b). The Disturbance (acoustic) threat was represented by the combined effects of vessel noise and vessel presence as there was no way, with current knowledge, to separate impacts of vessel presence from those of vessel noise. The Disturbance (physical) threat was represented by the effects from vessel strikes. Prey availability was represented by Chinook salmon abundance in the PVA model, even though it is acknowledged that other types of salmon are also consumed. For the Contaminants threat, despite the evidence that other contaminants are present in killer whales, only PCBs could be included.

3.2. Population viability analysis

3.2.1. Threat scenarios

Scenarios for each of the individual threats were constructed and tested using the available knowledge and data (Appendix A). The baseline model using SARKW rates is shown in Fig. 3a. The best fitting statistical relationship between killer whale mortality and Chinook salmon abundance (1979–2017) included the relevant stocks for each killer whale population ($y = 1.6773–0.673\times$; $r^2 = 0.0889$, $p = 0.012$). The previous Ford et al. (2010) analysis used data up to 2003 and the addition of fourteen years of data reduced the explanatory power of the prey-mortality relationship. The best model to explain calving probability (lowest relative AIC value) included the relevant Chinook salmon stocks and an SRKW/NRKW age structure (Appendix A). The percentage of adult females breeding (Br) was defined as a logistic function with age structure, using separate parameters for younger (< 31 years of age; Br_1) and older females (> 30 years of age; Br_2). These coefficients were re-

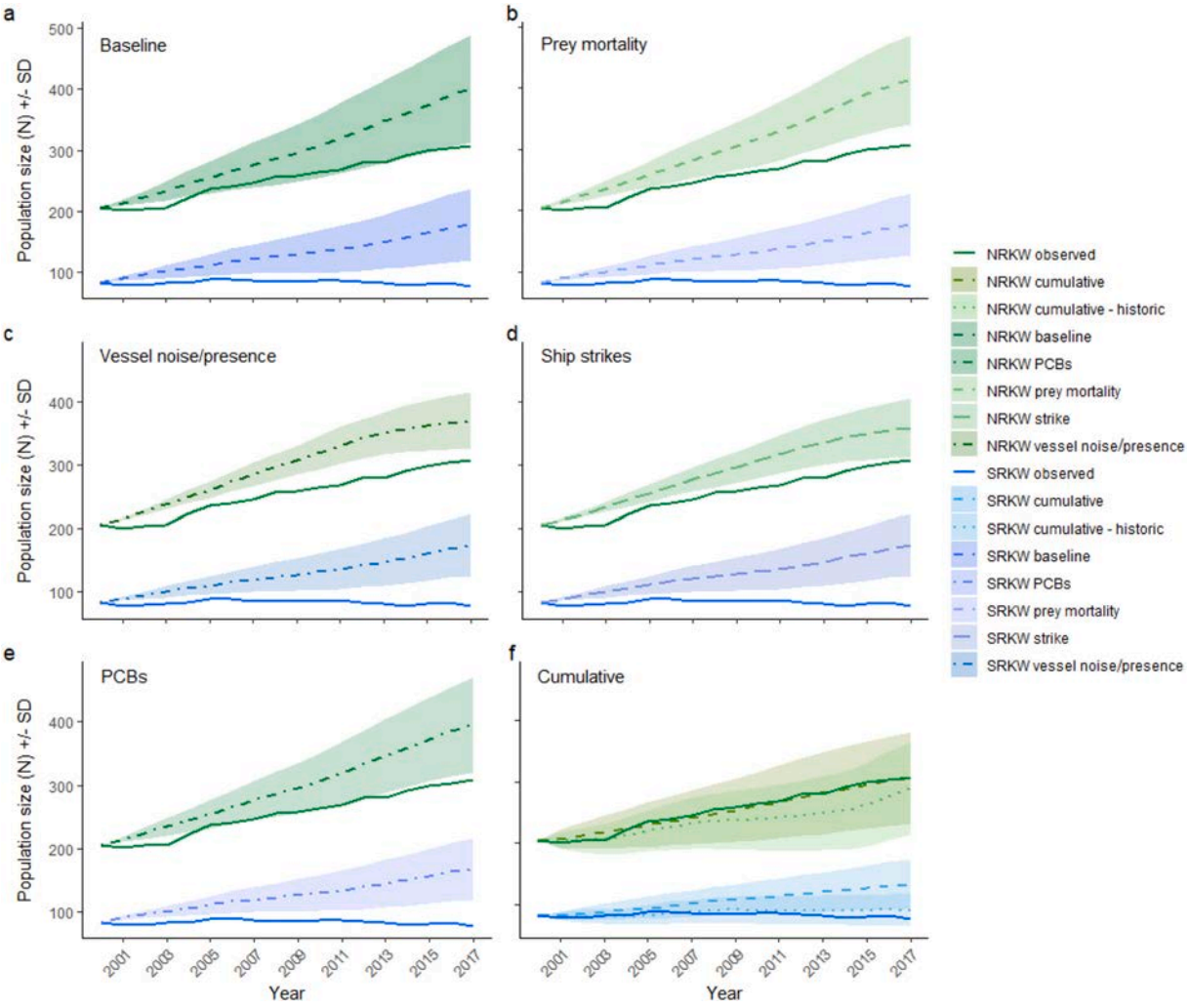


Fig. 3. Mean model simulations of population size (± standard deviation) for single threat scenarios a) baseline, b) prey mortality, c) vessel noise/presence, d) vessel strikes e) PCB contamination, and f) the cumulative effects and historic scenarios (all four threats) on NRKW (green dashed lines) and SRKW (blue dashed lines), with observed population size (solid lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

scaled for use in the model scenarios as a reduction to the reference fecundity rate.

In PVA scenario testing, prey abundance effects on mortality alone did not explain the realised population growth (Fig. 3b). The most realistic model for NRKW included the effects of prey abundance on both mortality and fecundity and approached the observed population trend, especially in the first 12 years of the simulation. For SRKW, the model scenario that incorporated impacts on both mortality and fecundity did not match the observed population trend, as it predicted slow population growth, rather than the observed decline. Additional combinations of Chinook stocks and distribution shape scenarios were tested but did not approach the observed population trends (details in Appendix A).

Vessel noise/presence scenarios tested the effect of noise as a reduction in prey abundance, with additional scenarios testing the model for the possibility of a threshold effect where noise affected feeding efficiency only when prey abundance was below the long-term average (Appendix A). None of the vessel noise/presence scenarios approached the observed population dynamics (Fig. 3c). The vessel strike threat scenarios did not match the observed population trends (Fig. 3d). These results suggest that the relatively rare vessel strike threat does not control the dynamics of these populations.

The PCB threat scenario simulations generated a range of mean PCB tissue concentrations in adults across different initial PCB levels and accumulation rates (Table A10). The model scenarios that most closely approached the range of measured PCB levels in recent SRKW/NRKW samples were those with initial PCB levels set to the grand means (SRKW: females = 17.5; NRKW: females = 4.9 mg kg-1 lw), with accumulation rates slightly higher in SRKW than NRKW (2 mg yr^{-1} and 1 mg yr^{-1}, respectively). However, the impact of PCBs alone did not match the observed population growth rate for either population (Fig. 3e).

3.2.2. *Cumulative effects*

The cumulative effects PVA scenario with all threats included (prey abundance, PCBs, vessel noise/presence and vessel strikes) was closer to the observed population sizes than any of the single threat models (Fig. 3f). The cumulative model included interactions between prey abundance and vessel noise/presence and PCB impacts, where the impact of vessel noise and PCBs was only applied when prey abundance was low (less than the long term mean index) (Table A11). The cumulative model approached the realised population growth for both populations closely, especially in the NRKW population (Fig. 3f). The mean model NRKW population size in 2017 was 309 (± 76 SD) individuals, the recorded NRKW population in 2017 was 308 individuals. The average model SRKW population size in 2017 was 134 (± 41) individuals, and the recorded SRKW population in 2017 was 77 individuals. Using the historical (rather than drawn randomly from the defined distribution) Chinook index values for 2000–2017 resulted in the cumulative effects

model approaching the observed population growth even more closely, especially for SRKW (Fig. 3f). Historical values are a useful model validation, but the use of the distribution is needed in order to define a model that can be used for projection into the future.

To further validate the model, we compared the observed and simulated population structure in the cumulative effects model. The relative proportions of juveniles and adults were similar for both SRKW and NRKW (Table A12). The NRKW model was extremely close to the observed values in its outputs (Modelled: 102 juveniles and 207 adults; Observed: 104 juveniles and 204 adults). The observed sex ratios for both populations were also similar to those produced by the cumulative effects models, which both predicted more females than males.

3.3. Model projection

Model scenarios were projected into the future to examine the long-term population growth rate and future of the populations. The projection of the cumulative effects model assumed that the current levels of threats continue into the future, with no changes in threats and no mitigation actions. Future outcomes differed according to whether the full or a subset of the prey abundance time series was used as input to the model. When Chinook salmon abundance was randomly drawn from the long-term mean abundance distribution (1979–2017), the cumulative model projected mean positive population growth for both populations, but with uncertainty among iterations and across years that included negative population growth: 1.6% (± 7.9 SD) for NRKW and 1.5% (± 8.1 SD) for SRKW (Fig. 4). The NRKW population size reached the arbitrarily-set carrying capacity (500 individuals) early in the projections and this affected the projected future population sizes (which would have been higher in the absence of a set carrying capacity). The probability of extinction (defined in the model as only one sex remaining) for both populations was 0% over 100 years. In contrast, when the cumulative effects model used the recent (2008–2017) distribution of Chinook salmon abundance indices the model projected negative population growth for SRKW (−2.5% ± 10.5), and a slightly lowered, but still positive, growth rate for NRKW (Fig. 4). Under the prey scenario using the recent time series, SRKW had a 26.1% probability of extinction and in those simulations where extinction occurred, the mean time to extinction was 86 years (± 11.3 years).

3.4. Sensitivity

The sensitivity of model parameters was tested to distinguish which threats had the highest impact on long-term population dynamics within the model structure. Sensitivity testing was performed for the cumulative effects scenario model projection for SRKW, which includes all four threat variables as well as the defined interactions between disturbance, contamination, and prey availability. The parameter of interest was varied across its range (minimum-maximum) by set increments, with the base values used for all other parameters (Table 2). The base threat levels were the original values used in the cumulative effects model. For the prey parameter sensitivity testing, the full range of Chinook index values for both stocks (1979–2017) was tested (minimum = 0.4, maximum = 1.8). The vessel noise/presence parameter began at the base level of noise (0.85, equivalent to 16.6% reduction in feeding rate) and increased to a maximum of 1.55, to represent the possibilities that either the reduction in feeding time or the time vessels were present could be higher than estimated. Strike risk was varied from 5% to as high as 50%. The PCB value tested included the base initial PCB tissue concentration for females, and included the full range of measured female PCB tissue concentrations. Male PCB tissue concentration was not used in sensitivity testing because the impact pathway occurs via maternal transfer. The most sensitive parameter for the long-term projection of the population was prey abundance (the value of the Chinook index), followed by vessel noise/presence (Fig. 5). Lacy et al. (2017) previously conducted sensitivity analyses on the effect of demographic parameters on population growth in a similar SRKW PVA model and found that variation in fecundity had the strongest effect on population growth for this population.

4. Discussion

The cumulative effects assessment suggests that resident killer whale

Table 2
Parameters and values used for testing sensitivity in the SRKW cumulative effects scenario projection, including the base value, the range, and increment of testing.

Parameter	Base	Minimum	Maximum	Increment
Prey availability (Chinook Index value)	1.00	0.40	1.80	0.10
Disturbance (model value)	0.85	0.85	1.55	0.10
Female PCB tissue concentration (mg kg-1 lw)	17.46	5.00	200.00	25.00
Strike risk (probability)	0.10	0.05	0.50	0.05

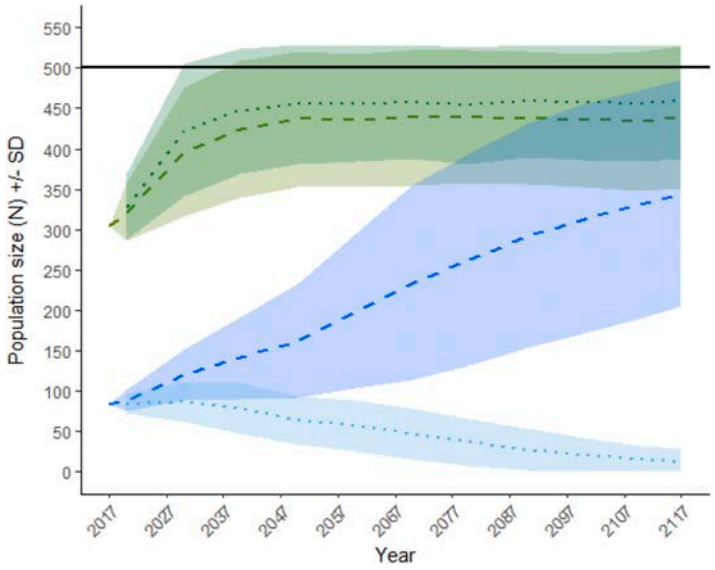


Fig. 4. Mean projection of the cumulative effects model 100 years into the future (starting in 2017) for NRKW (green) and SRKW (blue), under mean Chinook index ("mean prey": 1979–2017) or recent Chinook index ("recent prey": 2008–2017). Error bars represent ±1 standard deviation. Black horizontal line shows the arbitrary carrying capacity set for NRKW (500 individuals). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

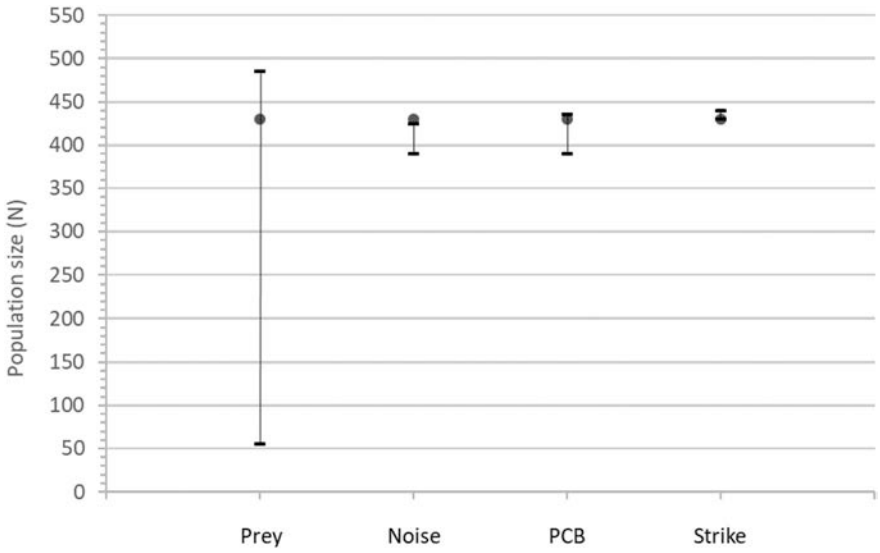


Fig. 5. Sensitivity of SRKW projected population size in the cumulative effects scenario to changes in the threat parameters: prey abundance, vessel noise/presence, PCB concentration and strike risk. Black circles represent the base value for each threat and the vertical bars represent the range of population size (N) with varying threat value (Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

populations are affected by the cumulative effect of anthropogenic threats and provides insights into the possible mechanisms behind the two populations' different trajectories. Chinook salmon abundance and its interactions with vessel noise/presence and PCB concentrations strongly influenced modelled killer whale population dynamics, highlighting the importance of considering threats collectively. The cumulative effects model fits the observed data, especially when recent low prey abundances were used, and is a more useful model than single threat models because it includes all threats and therefore can be used to examine tradeoffs in mitigation and management strategies. The cumulative effects PVA model can be used to project NRKW and SRKW population trajectories into the future. These projections are best used in a comparative evaluation of relative outcomes, rather than absolute predictions of abundance.

The projected population growth for both NRKW and SRKW was highly sensitive to the Chinook salmon abundance index. Under long-term mean Chinook salmon abundances, the modelled SRKW population was projected to increase; but when recent, lower Chinook salmon abundances were used, the SRKW population was projected to decline from present-day abundance, with a 26% chance of extinction within 100 years. Model projections were based on an assumption that modelled threat conditions will continue at the same levels as the present day with no mitigation. However, if the Chinook salmon stocks that SRKW depend upon continue to decline, this could affect the future outlook of the SRKW population, and potentially increase the probability of extinction above the model projection.

The findings of this cumulative effects assessment strongly support the significant role of prey availability in determining NRKW and SRKW population trajectories, and are consistent with previous work (Ford et al., 2010; Lacy et al., 2017; Vélez-Espino et al., 2015; Ward et al., 2009). The updated statistical analyses for the effect of prey availability on mortality and fecundity suggest that these impacts are still important to RKW, but the explanatory power of single-threat models has been reduced compared to previous studies. Sensitivity testing showed that prey abundance had the greatest effect on model results, within the bounds of the model structure. Improved mechanistic understanding of the other threats is still needed and could be used to advance the model for projections into the future. The cumulative effects model employed interactions of prey abundance with both vessel disturbance and contaminants, but these mechanisms have not been validated. The most uncertainty among the threats is related to the impacts of underwater noise and vessel disturbance. Additional research is urgently needed on the impacts of vessel presence and noise disturbance on resident killer whales. There are no comparable time series for vessel traffic and proximity to killer whales that would allow similar statistical testing to that done for prey availability. The current work contained a mechanistic model of PCB contamination but other contaminants are also a concern. PBDEs have also been found in high concentrations in these populations (Ross, 2006), although there was insufficient data available to include in the model. An important assumption made in this work is that the pathways of effects from threats to impacts are the same for both SRKW and NRKW; in other words, that the mechanisms by which threats affect individuals are the same for both populations. This assumption is the justification for using the same impact model structure for both populations, albeit with differing threat levels. The consequences of exposure to threats are assumed to be the same for both populations, while the level of exposure to threats is assumed to be population-specific. Differences in distribution, genetics, behaviour and other ecological characteristics at the sub-population (pod/clan) level may affect the exposure to threats and these nuances were not captured in the current assessment. The relationships between threats and resident killer whale mortality and fecundity were determined based on knowledge mostly obtained in the Salish Sea area in the summer/fall period but were assumed to be representative of relationships throughout the entire NRKW and SRKW ranges over the entire year.

Further, the two populations may exploit different prey stocks that themselves have varying population dynamics and availability to killer whale predation. All Chinook salmon stocks went through a period of decline in the 1990s, but since then have experienced stock-specific temporal variation (Ford et al., 2010). The ability and flexibility of killer whale populations to exploit different Chinook salmon stocks, other salmon species and indeed other fish taxa is not fully understood and may vary between NRKW and SRKW and through time. Potential prey competition between the two killer whale populations, and with other marine mammals, such as pinnipeds, may also affect prey availability and has not been included in the current models.

The positive population growth projected by the cumulative effects model under mean prey abundance assumes that the current levels of threats will not increase from present levels, which may not be the case in reality. Changing climate conditions and an increasing human population are having significant ongoing impacts on the marine environment and are likely to continue to affect killer whales and their prey into

the future (DFO, 2018; Harley et al., 2006; Walsh et al., 2020). Reductions in threats, such as through mitigation and management actions, may also improve future prospects for positive population trajectories. The USA and Canada have taken a number of management actions in recent years to support the recovery of the SRKW population, including Chinook commercial and recreational fishery closures in key killer whale feeding areas (DFO, 2018). Incorporating the effects of management actions, changing natural conditions, and changes to threat levels into iterations of the cumulative effects assessment may provide useful insights into the potential impacts of these actions on projected population trajectories.

Threats with low probability and high population consequences, such as oil spills or disease outbreaks, are difficult to include in simulation modelling. These threats should not be ignored in management and mitigation because they can have catastrophic consequences if the population were to be exposed. The *Exxon Valdez* oil spill in Alaska was linked to a significant decline in a resident killer whale pod (AB) that had been observed swimming through spilled oil; this pod suffered significant losses in the year following the spill, and had still not recovered to pre-spill levels 16 years after the event (Matkin et al., 1999; Matkin et al., 2008). One way to address high consequence, low probability events such as oil spills in model simulations could be to dramatically reduce the population to 50–75% of the current levels and test if the model population would be resilient enough to recover from such a catastrophe.

This cumulative effects assessment further advances the field by combining a detailed Pathways of Effects conceptual model with a Population Viability Analysis simulation model (after Lacy et al., 2017) to evaluate how the current state of human activities might affect the future persistence of the two imperilled killer whale populations. The incorporation of a PoE model allows the inputs and structure that inform the quantitative PVA to be explicit, and identifies areas lacking knowledge that were not able to be included but could be of value in future iterations. The cumulative effects PVA model could be a useful tool for testing the potential impacts of different theoretical mitigation and management scenarios for individual threats on population trajectories; for example to test whether the complete mitigation of acoustic disturbance would cause the projected population trajectory to increase over time and how long it may take for a change in population trajectory to be observable. Different parameters (e.g., increased vessel presence) can be input into the cumulative effects PVA model to consider the potential impacts of proposed developments and other anthropogenic changes. New information from ongoing and/or planned further research such as prey competition in key foraging areas, foraging efficiency, diet composition, prey field analysis, underwater acoustic monitoring and modelling, and contaminant sources and levels, will all help to inform future iterations of the PoE and PVA models. These models can help to adaptively inform and/or implement recovery measures, such as investigating the benefits of management actions to protect important areas, evaluating potential impacts of disturbance and prey competition from fisheries, assessing the potential impacts of salmon enhancement, and assessing industrial project impacts on killer whales and their habitat to provide advice on avoidance and mitigation measures. Population viability models have been used in conservation biology for over 30 years (Lacy, 2018) with many different approaches. The cumulative effects assessment case study described here builds on this considerable knowledge base and can provide guidance for assessments in other imperilled species.

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CRediT authorship contribution statement

Cathryn Clarke Murray: Conceptualization, Methodology, Formal Analysis, Investigation, Writing-Original draft preparation, Writing - Review and Editing, Supervision. **Lucie Hannah**: Conceptualization, Methodology, Investigation, Writing – Original Draft Preparation, Writing - Review and Editing. **Thomas Doniol-Valcroze**: Conceptualization, Writing – Review and Editing, Supervision. **Brianna Wright**: Investigation, Formal analysis, Writing – Review and Editing. **Eva Stredulinsky**: Investigation, Formal analysis, Writing – Review and Editing. **Jocelyn C. Nelson**: Formal analysis, Visualization, Writing – Review and Editing. **Andrea Locke**: Conceptualization, Writing – Review and Editing. **Robert C. Lacy**: Methodology, Software, Writing – Review and Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Estimated field metabolic rates and prey requirements of resident killer whales

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Estimated field metabolic rates and prey requirements of resident killer whales

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ABSTRACT

Killer whales are large animals that often feed in groups and thus have the potential to deplete prey populations. Determining predator energy requirements is essential to assessing whether prey availability is sufficient. This is important because one risk factor facing the endangered Southern Resident killer whale distinct population segment is limited prey availability. Body mass, field metabolic rate (FMR), and daily prey energy requirements (DPERs) were estimated for each individual in the population. FMRs were calculated from body mass, assuming they range from five to six times Kleiber-predicted basal metabolic rates. FMRs of adults were also calculated from resident killer whale activity budgets and the metabolic cost of swimming at speeds associated with daily activities. These two methods yielded similar results. Total FMRs varied by age and sex, which is partly due to the long developmental period and sexual dimorphism in killer whales. FMRs for males (465–4,434 kg) ranged from 35,048 to 228,216 kcal/d while FMRs for females (465–3,338 kg) ranged from 35,048 to 184,444 kcal/d. DPERs were calculated from FMRs assuming a standard digestive efficiency. Corresponding DPERs ranged from 41,376 to 269,458 kcal/d and 41,376 to 217,775 kcal/d, respectively.

Key words: energetics, *Orcinus orca*, killer whale, marine mammal, metabolism, prey consumption.

The daily energetic needs and prey consumption rates of apex predators are important areas of research, particularly because of their potential impact on ecosystems. Killer whales (*Orcinus orca*) represent the highest trophic level of any marine mammal (Pauly *et al.* 1998), and as a consequence, their energetic requirements and resulting prey consumption rates could be significant. However, these values are difficult to quantify. For example, the proposed impact of transient killer whale predation on marine mammal populations in the Northeast Pacific has resulted in considerable debate (*e.g.*, Springer *et al.* 2003, Williams *et al.* 2004, DeMaster *et al.* 2006, Trites

et al. 2007, Wade *et al.* 2007, Springer *et al.* 2008, Estes *et al.* 2009, Wade *et al.* 2009). One component of uncertainty is a basic understanding of the energetic requirements of killer whales (see Maniscalco *et al.* 2007). Indeed, for cetaceans in general, there is a paucity of information on energetic requirements and prey consumption rates. A key component in studying predator–prey interactions is an understanding of daily energy requirements of individual members of the population as well as the total energy requirements of the entire population.

Previous studies have used several different methods to assess the daily energy expenditure and prey consumption rates of adult resident (Kriete 1995, Williams *et al.* 2006) and transient (Baird and Dill 1996, Williams *et al.* 2004, Maniscalco *et al.* 2007) killer whales. For example, Williams *et al.* (2004) extrapolated field metabolic rates of adult transient killer whales from an allometric relationship of at-sea metabolic rates for marine mammals (Costa and Williams 1999). Other researchers (Kriete 1995, Williams *et al.* 2006, Maniscalco *et al.* 2007) estimated field metabolic rates of adult resident and transient killer whales from daily activity budgets of free-ranging animals and metabolic rates measured in captive killer whales performing behaviors that approximated wild killer whale activity states (from Kriete 1995). Baird and Dill (1996) estimated the rate of energy intake from observations of prey intake by wild transient killer whales. Alternatively, Barrett-Lennard *et al*. (1995) estimated daily caloric intake of transient killer whales based on daily fish ingestion by smaller, relatively sedentary captive whales with a correction factor of 25% to account for the difference in activity levels of captive and wild animals.

All of the previous studies have merit, yet additional approaches are warranted for several reasons. First, the estimates of daily field metabolic and prey consumption rates from some studies are similar, while the results of others differ significantly (for comparisons between studies see Williams *et al.* 2004, Williams *et al.* 2006, Maniscalco *et al.* 2007). Thus, there is some degree of uncertainty in our ability to estimate FMRs and prey consumption rates of killer whales, and therefore, other methods to calculate these values are needed. Second, only two previous studies estimated daily field metabolic or prey consumption rates of immature killer whales (Barrett-Lennard *et al.* 1995, Osborne 1999). Because a population of killer whales can be composed of a significant number of immature individuals, these segments of the population should not be ignored when modeling killer whale field metabolic rates, prey consumption rates, and potential impacts to the ecosystem. Third, none of the previous studies determined prey consumption rates for an existent population of killer whales with a known population size, including the number of individuals within each age and sex class. Because killer whales travel in family groups, refined estimates of daily prey requirements that are based on the demographics (*e.g.*, age and sex structure) of existent killer whale populations are essential to determining potential impacts on prey populations in an ecosystem.

Estimating daily prey energy requirements on the level of a marine mammal population is not a trivial task, particularly because so many variables impact daily energetic expenditure. Metabolic rates are influenced by age, body size, growth, reproductive status, activity level, and environmental conditions (Kleiber 1975, Costa *et al.* 1986, Kriete 1995, Costa 2002, Noren 2002, Williams *et al.* 2006, Maniscalco *et al.* 2007, Williams and Noren 2009, D. Noren, unpublished data). Furthermore, for marine mammals, metabolic rates are further affected by dive depth and duration, activity, and swimming speed (Webb *et al.* 1998, Hurley and Costa 2001, Rosen and Trites 2002, Hastie *et al.* 2006, 2007, Fahlman *et al*. 2008, Williams and Noren 2009). Thus, the proportion of time killer whales spend swimming at

different speeds during distinct activity states will impact FMRs, and consequently daily energetic needs.

The objective of this study was to estimate the daily energy expenditure and prey requirements for the entire distinct population segment of Southern Resident killer whales (SRKWs). These whales, which inhabit the eastern Pacific Ocean, ranging from central California to the northern Queen Charlotte Islands of British Columbia, suffered a 20% population decline from 1996 to 2001 (Krahn *et al.* 2004). This decline as well as several risk factors led to the population being listed as Endangered under the U.S. Endangered Species Act and Canada's Species at Risk Act. Because low abundance of their preferred prey, Chinook salmon (*Oncorhynchus tshawytscha*; Ford *et al.* 1998, Ford and Ellis 2006, Hanson *et al.*, in press), is linked to high mortality (Ford *et al.* 2009) and low fecundity (Ward *et al.* 2009), it is imperative that we have estimates of daily prey energy requirements for all members of the SRKW population. Resident killer whales travel in large matriarchal groups, so understanding the daily energetic needs on the level of the population, rather than on the level of the individual, is necessary to inform decisions regarding the conservation of SRKWs, the conservation of salmon, and the management of fishing activities which may limit Southern Resident killer whale prey resources.

Methods

Body masses, field metabolic rates (FMRs), and daily prey energy requirements (DPERs) were estimated for all individuals in the SRKW population (November 2008 census data, Center for Whale Research, http://www.whaleresearch.com), with the exception of calves aged 0–<1 yr old because delphinids at this age are primarily dependent on their mothers for nourishment (for review see Noren and Edwards 2006). Although many delphinid calves may nurse for up to 3 yr after birth (for review see Noren and Edwards 2006), wild killer whale calves can consume fish by 1-yr postpartum (Heyning 1988). Thus, for simplicity, FMRs and DPERs for 2- and 3-yr-old calves were calculated with the assumption that 100% of their daily energetic requirements are met through the consumption of prey, rather than milk.

Estimating Killer Whale Body Mass

There is no simple method to measure the body mass of free-swimming killer whales. Although body mass can be estimated from body length (Bigg and Wolman 1975), there are limited data on body lengths of wild killer whales, and not all age classes are represented. Similarly, there is a paucity of information on relationships between age and length and age and body mass of killer whales (for review see Clark *et al.* 2000). Because of this, a combination of published values and equations were used to estimate body masses of SRKWs.

For both male and female SRKWs 1–12 yr of age, body mass for each year of life was estimated using a Gompertz function that predicts female killer whale body mass from age in days (Clark *et al.* 2000). The growth rate of these captive-born animals through the age of 6 yr (36.0 cm/yr, Clark *et al.* 2000) was similar to the value (36.6 cm/yr) reported by Bigg (1982) for wild male and female killer whales, including southern and northern resident ecotypes, from the eastern North Pacific.

Because adult Atlantic killer whales (Christensen 1988, Duffield and Miller 1988) tend to be smaller than adult Northeast Pacific killer whales (Bigg and Wolman

1975, Bigg 1982), the growth curve from Clark *et al*. (2000), which was constructed almost exclusively from measurements made on Icelandic whales, was not used to estimate body masses for whales aged 13–≥20 yr. Instead, terminal body masses for adult male and female SRKWs were based on values from adult male and female Northeast Pacific resident killer whales reported by Bigg and Wolman (1975). Similar to body growth curves from Icelandic killer whales (Christensen 1988) and patterns of growth and food consumption rates in captive killer whales (Kastelein *et al.* 2000, 2001, 2003*a*), it was assumed that both male and female SRKWs complete their body growth and food consumption rates level off by approximately 20 yr of age.

Terminal body masses of adult female and male SRKWs were set to equal the largest estimated body masses of female and male Northeast Pacific resident killer whales that were taken by the live-capture fishery (Bigg and Wolman 1975). This is because the live-capture fishery focused primarily on smaller animals, thus the majority of masses reported by Bigg and Wolman (1975) were for juvenile animals. The terminal body mass for female SRKWs ≥20 yr old was set at 3,338 kg (estimated from Bigg and Wolman 1975). Due to a lack of data on changes in body mass with age in sexually mature female SRKWs, it was assumed that female body mass changes at a constant rate of approximately 107 kg/yr from the mass of 2,482 kg at the age of 12 (estimated according to methods from above) to the terminal mass of 3,338 kg for all adult females ≥20 yr of age (Fig. 1).

Killer whales are highly sexually dimorphic. Adult males have longer body length, larger body mass, greater girth, and larger flukes and fins than adult females (Nishiwaki and Handa 1958, Jonsgård and Lyshoel 1970, Bigg and Wolman 1975,

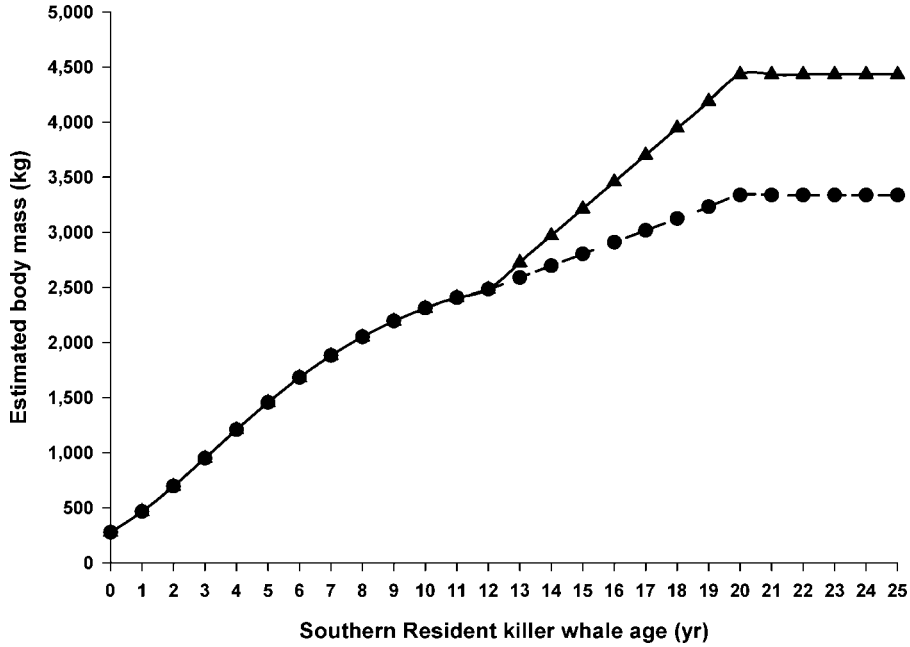


Figure 1. Relationship between body mass and age in years for male and female killer whales. The growth curves for male (▲) and female (●) killer whales are denoted by the solid and broken lines, respectively.

Clark and Odell 1999). Thus, the terminal body mass for male SRKWs ≥20-yr old was set at 4,434 kg (estimated from Bigg and Wolman 1975). To reach this large body size, male killer whales undergo a period of rapid growth, which begins at 13–14 yr of age (Christensen 1988). Due to a lack of data on changes in body mass with age in adolescent male SRKWs, it was assumed that male body mass changes at a constant rate of approximately 244 kg/yr from the mass of 2,482 kg at the age of 12 (estimated according to methods from above) to the terminal mass of 4,434 kg for all adult males ≥20 yr of age (Fig. 1).

Although it may be preferable to express SRKW male and female growth patterns as single nonlinear functions, there were insufficient data to do so. As more data become available, SRKW growth curves can be refined. In the meantime, this approach was deemed reasonable because realistic SRKW juvenile growth rates and adult body masses were incorporated into the estimates, which resulted in growth curves (Fig. 1) that are nearly identical in shape to growth curves of wild male and female Norwegian killer whales (Christensen 1988).

Estimating Field Metabolic Rates (FMRs)

The potential range of field metabolic rates (FMRs, the total metabolic cost of all physiological processes and activities of an animal in the wild) for killer whales of all age and sex classes were calculated from body mass assuming that daily metabolism ranges from five to six times Kleiber (1975) predicted BMR, according to the following equations:

$$\text{Lower bound FMR} = 350 M_b^{0.75} \tag{1}$$

$$\text{Upper bound FMR} = 420 M_b^{0.75} \tag{2}$$

where FMR is in kcal/d and M_b is body mass in kg.

This method was deemed appropriate for adult (≥20 yr of age) killer whales because FMRs of adult otariids and bottlenose dolphins (*Tursiops truncatus*) range from five to six times Kleiber-predicted BMR (calculated from Costa *et al.* 1991, Costa and Williams 1999, Costa 2002). For comparison, Williams *et al.* (2004) used the equation FMR = $406 M_b^{0.756}$ for adult transient killer whales in Alaska, which is near the upper bound of FMRs presented above.

It is plausible that the cost of reproduction in females and growth in juveniles may affect individual FMRs. However, results from previous studies on marine mammals suggest that energetic costs of gestation and lactation in females and growth in juveniles do not increase FMR values. For example, FMRs of lactating California sea lions (*Zalophus californianus*) range from five to six times Kleiber-predicted BMR (calculated from Costa *et al.* 1991), which are comparable to those of nonlactating otariids and delphinids (Costa and Williams 1999, Costa 2002). Similarly, resting metabolic rates do not differ between reproductive and nonreproductive female California sea lions during the late pregnancy or lactation periods (Williams *et al.* 2007).

Body size changes rapidly in young animals, so FMRs of immature animals (1–12-yr old), "sprouting" adolescent males (13–19-yr old), and young adult females (13–19-yr old) were estimated for each yr of life. Although body growth has the potential to increase daily metabolic rates, there is a paucity of information on how

the cost of growth affects FMRs in cetaceans. Data from juvenile sea lions suggest that these costs may not represent a large portion of daily energy expenditure. For example, the energy required for growth in immature Steller sea lions is small relative to their total energy needs (Winship *et al.* 2002). Furthermore, energetic costs of swimming juvenile sea lions (calculated from Feldkamp 1987, Williams *et al.* 1991, and Rosen and Trites 2002) range from three to six times Kleiber-predicted BMR. Thus, it was deemed reasonable to assume that FMRs of juvenile killer whales could also be calculated using Equations 1 and 2, similar to adult killer whales. Although the multiplier values for juveniles, adolescents, and adults are identical, the fact that FMR is proportional to $M_b^{0.75}$ means that smaller, younger individuals have significantly higher mass-specific FMRs than larger, older individuals, which is the typical mammalian pattern.

Comparing Predicted FMRs with FMRs Calculated from Daily Activity Budgets

To help determine whether FMRs calculated by the above methods are reasonable, FMRs were also calculated for adult (age $\geq$20 yr) male and female resident killer whales using cost of transport (*COT*) curves developed for killer whales (Williams and Noren 2009) and daily activity budgets that identified the proportion of time Northeast Pacific resident killer whales were engaged in each activity state in addition to the average swimming speed for each activity state (Northern Residents from Ford 1989, Southern Residents from Noren *et al*. 2009 and D. Noren, unpublished data). Specifically, FMRs were calculated with the assumption that whales swam at a constant speed specific to each activity state for the entire duration (proportion of a 24 h day) they were engaged in each activity state. The total metabolic cost of swimming during each activity state was calculated from *COT* curves from Williams and Noren (2009). Daily FMRs were then calculated by summing the total metabolic costs of swimming for all activity states that whales were engaged in daily (Table 1, 2).

These calculations are rather simplistic because the *COT* curves from Williams and Noren (2009) were constructed from speed and respiration rate data collected from Northern Resident killer whales during one activity state (travel/forage), and it is possible that *COT* curves may differ when whales are engaged in other activity states. However, Williams and Noren (2009) selected their data using strict criteria in an attempt to determine *COT* for swimming only, while excluding other associated costs of foraging (*e.g.*, diving and performing surface active behaviors). Thus, the *COT* curves from Williams and Noren (2009) should provide good estimates for the energetic costs associated with swimming over a range of speeds, and be applicable across most activity states. Although the energetic costs of surface active behaviors (*e.g.*, breaches, tail slaps, *etc*.) will not be accounted for in these calculations, these behaviors do not make up a substantial portion of Southern Resident killer whales' daily activity budgets (Noren *et al.* 2009). Furthermore, tail slaps, which are the predominant surface active behaviors performed (Noren *et al.* 2009), are not associated with high energetic costs (D. Noren, unpublished data). Consequently, the performance of surface active behaviors is not expected to significantly affect daily FMRs.

Estimating Daily Prey Energy Requirements (DPERs)

Digestive efficiency for killer whales is approximately 84.7% (Williams *et al.* 2004). This means that killer whales must consume more kcal/d than their predicted

Table 1. FMRs for adult male and female Northern Resident killer whales calculated from daily activity budgets.

Activity state[a] (% of 24 h day engaged in activity, mean swimming speed during activity)	Daily adult male (4,434 kg) FMR[b]	Daily adult female (3,338 kg) FMR[c]
Foraging (66.5%, 1.7 m/s)	780.7 MJ (186,585.8 kcal)	428.7 MJ (102,462.8 kcal)
Travelling (4.2%, 2.9 m/s)	50.4 MJ (12,038.8 kcal)	27.5 MJ (6,575.9 kcal)
Resting (13.2%, 0.8 m/s)	150.4 MJ (35,936.6 kcal)	83.2 MJ (19,883.7 kcal)
Socializing (11.6%, 1.1 m/s)	133.8 MJ (31,985.5 kcal)	73.8 MJ (17,641.3 kcal)
Beach-rubbing (4.5%, speed not available but assumed to be 0.8 m/s [speed for resting], since beach rubbing whales do not move through the area very quickly and rubbing behavior was often accompanied by resting among nearby animals ([Ford 1989]).	51.3 MJ (12,251.1 kcal)	28.4 MJ (6,778.5 kcal)
Total daily energy budget (24 h)	1,166.5 MJ (278,797.8 kcal)	641.6 MJ (153,342.2 kcal)
Daily energy budget relative to Kleiber (1975) predicted basal metabolic rate (BMR) values	7.3× Kleiber	5.0× Kleiber

[a]Percentage of time Northern Resident killer whales were observed in five activity states and mean swimming speed during each activity from Ford (1989). Ford (1989) reported percentages based on 416 total h of observations collected on 93 d. For this illustration, these percentages were also assumed to apply to a 24 h activity budget.

[b]Energy expenditure was calculated using the speed for each activity state from Ford (1989) and the cost of swimming at that speed (calculated from the *COT* regression equation for adult males from Williams and Noren 2009), with the assumption that whales maintained a constant swimming speed during the entire period they were engaged in each activity state.

[c]Energy expenditure was calculated using the speed for each activity state from Ford (1989) and the cost of swimming at that speed (calculated from the *COT* regression equation for adult females without calves from Williams and Noren 2009), with the assumption that whales maintained a constant swimming speed during the entire period they were engaged in each activity state.

FMR (Equations 1 and 2) to meet their daily energy demands. The estimated potential range of daily prey energy requirements (DPERs) for all killer whales takes digestive efficiency into account and was calculated from body mass, according to the following equations:

$$\text{Lower bound DPER} = 413.2 M_b^{0.75} \tag{3}$$

$$\text{Upper bound DPER} = 495.9 M_b^{0.75} \tag{4}$$

where DPER is in kcal/d and M_b is body mass in kg.

Table 2. FMRs for adult male and female Southern Resident killer whales calculated from daily activity budgets.

Activity state[a] (% of 24 h day engaged in activity, mean swimming speed during activity)	Daily adult male (4,434 kg) FMR[b]	Daily adult female (3,338 kg) FMR[c]
Foraging (21%, 1.1 m/s)	242.3 MJ (57,904.7 kcal)	133.6 MJ (31,936.9 kcal)
Travelling (70.4%, 2.2 m/s)	835.0 MJ (199,576.1 kcal)	457.4 MJ (109,314.2 kcal)
Resting (6.8%, 0.8 m/s)	77.5 MJ (18,512.8 kcal)	42.9 MJ (10,243.1 kcal)
Socializing (1.8%, 0.3 m/s)	19.7 MJ (4,711.9 kcal)	11.0 MJ (2,632.8 kcal)
Total daily energy budget (24 h)	1174.5 MJ (280,705.5 kcal)	644.9 MJ (154,126.9 kcal)
Daily energy budget relative to Kleiber (1975) predicted basal metabolic rate (BMR)	7.4× Kleiber	5.0× Kleiber

[a]Percentage of scan samples collected on a 10-min interval ($n = 571$ sampling intervals) that Southern Resident killer whales were observed in four activity states (Noren *et al.* 2009, D. Noren, unpublished data). The mean swimming speed for each activity state was calculated from speeds of individual male and female focal whales recorded during each state (D. Noren, unpublished data). Data were collected during daylight hrs only, but for this illustration, it is assumed that the percentages approximate percentages of a 24 h activity budget.

[b]Energy expenditure was calculated using the speed for each activity state (D. Noren, unpublished data) and the cost of swimming at that speed (calculated from the *COT* regression equation for adult males from Williams and Noren 2009), with the assumption that whales maintained a constant swimming speed during the entire period they were engaged in each activity state.

[c]Energy expenditure was calculated using the speed for each activity state (D. Noren, unpublished data) and the cost of swimming at that speed (calculated from the *COT* regression equation for adult females without calves from Williams and Noren 2009), with the assumption that whales maintained a constant swimming speed during the entire period they were engaged in each activity state.

It is possible that food consumption increases to compensate for the energetic costs of gestation, lactation, and growth. Results from the few studies conducted on marine mammals demonstrate that food intake can increase during some, but not all of these life processes. For example, food intake rates of captive killer whales (Kriete 1995, Kastelein *et al*. 2003*a*) and bottlenose dolphins (Kastelein *et al.* 2002, 2003*b*) do not increase significantly during gestation. Thus, it is also likely that DPERs of pregnant free-ranging killer whales do not increase. In contrast, food consumption is likely to increase during lactation. For instance, food consumption in lactating female California sea lions is greater than that of nonlactating females (Williams *et al.* 2007). Though, due to confounding energetic demands associated with the annual molt, which also increased food consumption in non-lactating females during the lactation period (Williams *et al.* 2007), it is not possible to determine the proportion of consumed prey that is attributed to lactation demands alone. Data on lactating odontocetes are also inadequate to establish an appropriate level of increased food

consumption for lactating, free-ranging killer whales. For example, lactating captive killer whales (Kriete 1995, Kastelein *et al.* 2003*a*) and bottlenose dolphins (Kastelein *et al.* 2002, 2003*b*) increase food intake rates by 1.5–2 times baseline levels, but food consumption rates are highly variable across individuals, across different lactation periods in females that have given birth more than once, and within a single lactation period (Kriete 1995, Kastelein *et al.* 2002, 2003*a*, *b*). In general, food intake rates increase only after the first month following birth but then decrease by the third or fourth month of lactation (Kastelein *et al.* 2003*b*). Several researchers have investigated lactation costs in terrestrial mammals, but it would be inappropriate to apply their results to lactating cetaceans because energy expenditure and caloric intake during lactation in mammals varies by several factors, including allometry, life history, phylogeny, and individual variation (Gittleman and Thompson 1988).

Given that pregnant captive delphinids do not increase food intake rates and data on food intake rates during lactation are equivocal, it was deemed appropriate to use Equations 3 and 4 to estimate DPERs of free-ranging pregnant and lactating killer whales. Similarly, Equations 3 and 4 were also used to estimate DPERs of growing juvenile and adolescent killer whales. This is because energy intake required for growth in immature captive killer whales (Kriete 1995) and free-ranging Steller sea lions (Winship *et al.* 2002) is negligible relative to total energy intake.

Results

Comparing Predicted FMRs with FMRs Calculated from Daily Activity Budgets

FMRs calculated from *COT* curves and daily activity budgets range from 5.0 to 7.4 times Kleiber (1975) predicted basal metabolic rates for adult resident killer whales (Table 1, 2). Even though the percentage of time spent in different activity states differs somewhat between Northern and Southern Resident killer whales, the resulting daily FMRs are very similar (Table 1, 2).

The results of these calculations suggest that FMRs of female killer whales are five times Kleiber (1975) predicted BMR values, which is the predicted lower bound FMR (Equation 1), and FMRs of males are 7.3–7.4 times Kleiber (1975) predicted BMR values, which is slightly greater than the predicted upper bound FMR (Equation 2). Relatively higher mass-specific FMRs for adult males (Table 1, 2) are likely due to the finding that mass-specific *COTs* at slower speeds are slightly higher in males compared to females (Williams and Noren 2009). In contrast, there is no sex difference in mass-specific *COTs* at faster speeds (Williams and Noren 2009). It is probable that differences in mass-specific *COTs* at slower speeds are artifacts of the methods used by Williams and Noren (2009) to determine *COT*, rather than a true elevation of mass-specific *COTs* in males relative to females. The elevated mass-specific FMR values for males (Table 1, 2) are likely due to the fact that the majority of speeds in the daily activity budgets are <2.0 m/s and do not necessarily indicate that mass-specific FMRs of adult males are higher than those of adult females.

Given that several assumptions were made during the construction of the *COT* curves (see Williams and Noren 2009) and that activities that reduce (*e.g.*, long-duration diving, rest) and increase (*e.g.*, social, surface active behaviors) metabolism were not accounted for in the calculations, FMRs estimated from *COT* curves and daily activity budgets were not expected to be identical to those estimated from Equations 1 and 2. However, the similarity is encouraging and provides some evidence to suggest

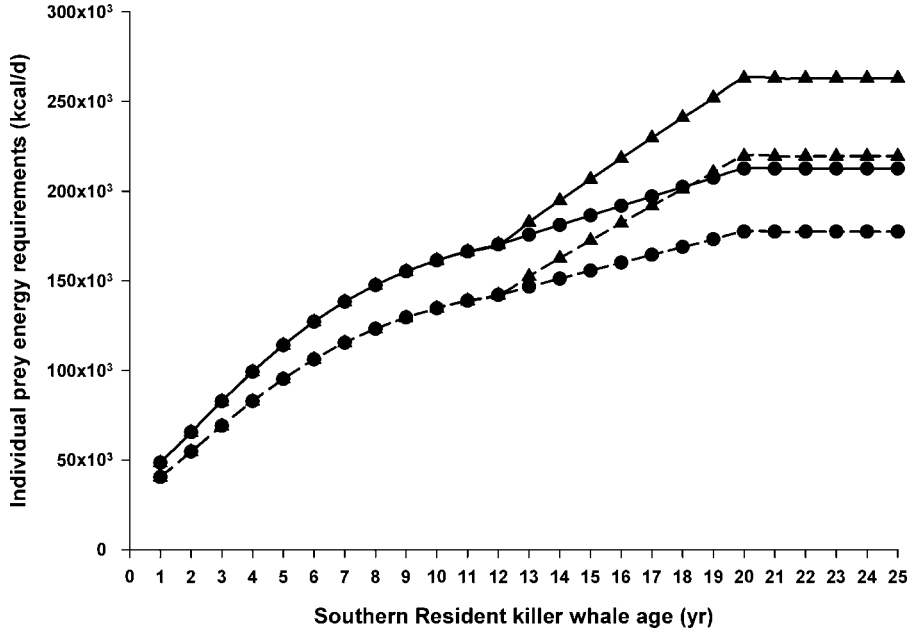


Figure 2. Relationship between daily prey energy requirements (DPERs) and age in years for male and female killer whales. Lower bound (broken lines) and upper bound (solid lines) estimates of DPERs (kcal/d) are presented for male (▲) and female (●) killer whales.

that FMRs of resident killer whales are likely to fall within the range of five to six times Kleiber (1975) predicted BMR, similar to other marine mammals.

Field Metabolic Rates (FMRs) and Daily Prey Energy Requirements (DPERs)

As expected, total FMRs and DPERs differ widely across Southern Resident killer whale age and sex classes (see online Table S1, Fig. 2). Not surprisingly, juvenile animals have the lowest total FMRs and DPERs, while adult males have the highest. Although males >12 yr old have higher lower and upper bound FMRs and DPERs than females of comparable age, there is some overlap in the range of values for males and females aged 13–18 yr old (Fig. 2). However, by 19 yr of age, FMRs and DPERs of males surpass those of females (Fig. 2).

Yet, when considering DPERs of the entire Southern Resident killer whale population, it is not the males, but the females that collectively have the highest total DPER. This is because 34.9% of the November 2008 population of SRKWs were older adult females (≥20 yr old), and thus a large portion of the population's total DPER is attributed to this segment (Fig. 3a, b). Specifically, the DPERs of all older adult females combined represent 40.5% of the population's total DPER (12,980,019–15,577,908 kcal/d). Although the number of adult males (≥20-yr old) in the November 2008 population was relatively small (7.2% of the population), and comparable to the number of animals in some of the juvenile/immature age classes, their larger body size ensures that the combined DPERs of all adult males is the second largest portion (10.4%) of the population's total DPER (Fig. 3a, b).

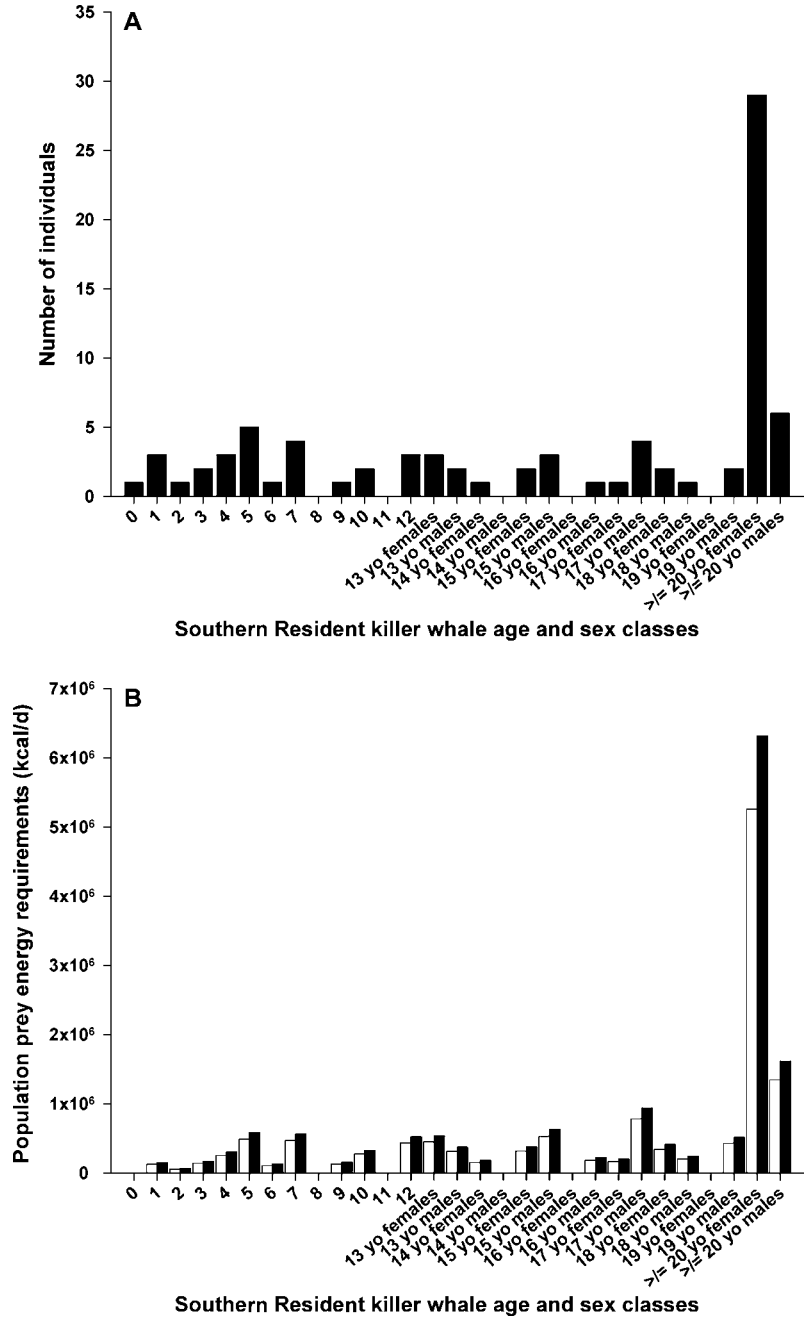


Figure 3. Number of individuals within each age and sex class (a) and total daily prey energy requirements (DPERs) for all killer whales combined within each age and sex class (b) from the Southern Resident killer whale population in November 2008 (Center for Whale Research, http://www.whaleresearch.com). Lower bound (white bars) and upper bound (black bars) estimated DPERs are presented. It is assumed that calves <1 yr of age receive all of their daily energy requirements through their mothers' milk, not *via* ingestion of fish.

Discussion

Because of the multitude of uncertainties associated with estimating body mass and field metabolic rates (FMRs) in free-ranging killer whales, it is not appropriate to provide point estimates of FMR and daily prey energy requirements (DPERs). Thus, upper and lower bounds for daily FMRs and DPERs were used to estimate a reasonable range of FMRs and DPERs for Southern Resident killer whales. Upper bound FMRs and DPERs are approximately 20% greater than lower bound FMRs and DPERs, respectively, for all age and sex classes.

The concurrence between FMRs calculated from Equations 1 and 2, which assumed that FMRs of resident killer whales are five to six times Kleiber-predicted BMR (similar to other marine mammals), and FMRs calculated from killer whale daily activity budgets and *COT* curves suggests that FMRs and DPERs of free-ranging killer whales fall within the ranges presented in the current study. Furthermore, the estimated FMRs and DPERS of adult male (FMRs: 43–51 kcal/kg/d, DPERs: 51–61 kcal/kg/d) and female (FMRs: 46–55 kcal/kg/d, DPERs: 54–65 kcal/kg/d) killer whales from the present study are similar to those reported previously for other adult killer whales (Kriete 1995, Baird and Dill 1996, Osborne 1999, Williams 1999, Williams *et al.* 2004, Williams and Noren 2009). Interestingly, these mass-specific FMRs are also similar to those of adult harbor porpoises (*Phocoena phocoena*), which were calculated from swimming speeds and estimates of partitioned daily activity levels (Yasui and Gaskin 1986).

As additional information on SRKW body size and cetacean energetics become available, FMR and DPER estimates should be refined. Given that the calculations are based on body mass, deviations from true body mass values will inevitably lead to errors in these estimates. For example, a 10% increase in body mass results in a 7% increase in both FMR and DPER values. Thus, accurate assessments of body mass are critical to improving FMR and DPER estimates. Also, as mentioned previously, the energetic costs of growth in young animals and adolescent males and lactation in females could increase DPERs, though the effect of these costs on DPERs is unclear. Until these can be better quantified, it is probably best to use DPERs calculated from the upper bound equation (Equation 4), which are 1.2 times greater than DPERs calculated from the lower bound equation (Equation 3), for growing and lactating whales. If, for example, upper bound DPERs were used to estimate prey consumption rates in lactating females over the course of 1 yr, the 3–4 mo (Kastelein *et al.* 2003*b*) of 1.5–2 times increased prey consumption rates (Kriete 1995, Kastelein 2002, Kastelein *et al.* 2003*a*, *b*) would be accounted for.

Although discrepancies between the estimated and actual DPERs of an individual lactating female killer whale may arise from using the above methods, these discrepancies will negligibly impact the accuracy of the SRKW population's total estimated annual DPER. This is because there are only a small number of lactating females with calves <1 yr of age in the population at any given time (number of calves <1 yr of age in November 2008: 1, average number ± SD of calves born per year: 3.1 ± 0.8, average percent ± SD first year survival of calves: 64.6 ± 30.8%, data from 1998 through 2008, Center for Whale Research, http://www.whaleresearch.com). Similarly, only 15.7% of the population were adolescent males (aged 13–19 yr old) in November 2008 (census data, Center for Whale Research, http://www.whaleresearch.com), so if the DPERs of these growing animals were slightly underestimated, the total SRKW population DPER would only be slightly underestimated.

Table 3. Comparison of daily prey energy requirements predicted for Southern Resident killer whales by Osborne (1999) and the present study.

Age and sex class[a]	DPER (kcal/d)[a]	Lower bound DPER (kcal/d)[b]	Upper bound DPER (kcal/d)[b]
Immature (1–6 yr)	85,000	41,376–108,525	49,657–130,246
Juvenile (7–12 yr)	100,000	118,019–145,299	141,640–174,380
Female >12 yr	160,000	149,972–181,458	179,988–217,775
Male >12 yr	200,000	155,885–224,521	187,085–269,458

[a]From Osborne (1999).
[b]From the present study.

This is the first study to estimate FMRs and DPERs of killer whales from all segments of a population during each yr of life until physical maturity (20 yr of age when body growth ceases). In contrast, Osborne (1999) presented distinct DPER estimates for immature (1–6 yr of age), juvenile (7–12 yr of age), male (>12 yr of age), and female (>12 yr of age) killer whales (Table 3). The results of this study suggest that there is a wide range of DPERs within each of the four groups (Table 3) defined by Osborne (1999). For example, DPERs of immatures (1–6-yr old) and juveniles (7–12-yr old) increase 2.6- and 1.2-fold over a 5-yr span in age, respectively. Similarly, DPERs increase 1.4-fold during the male growth spurt from the age of 13–20-yr old. These findings differ significantly from those of Osborne (1999) and are due to the prolonged developmental period and associated changes in body mass with age in killer whales. These comparisons demonstrate the importance of keeping life history patterns in mind when estimating daily prey energy requirements.

Estimating FMRs and DPERs are first steps in determining prey consumption rates (PCRs) for the Southern Resident killer whale population. The next step for management purposes is to know how many individual fish are consumed by these whales per year. From a mathematical perspective, converting DPERs (kcal/d) to fish/year is a relatively straightforward task, as long as the caloric densities of the fish consumed are known.

However, determining the number of fish consumed per year by the Southern Resident killer whale population is not a simple undertaking for several reasons. First, the caloric densities of fish vary by species, age, size, percentage lipid content, geographic region, and season (Brett 1995). Second, although SRKWs prefer to consume relatively rare Chinook salmon in the summer (Ford *et al.* 1998, Ford and Ellis 2006, Hanson *et al.,* in press), the diet composition of SRKWs during other seasons is not as well known. Data suggest that diets of resident killer whales not only change seasonally (Ford and Ellis 2006, Hanson *et al.*, in press), but that even within the summer season, killer whales may predominantly consume different species of salmon during particular months (Ford and Ellis 2006, Hanson *et al.*, in press). Third, differences in prey selectivity across pod members of different age and sex classes are not well understood (Ford and Ellis 2006).

Given the limited data on SRKW prey selectivity, it would be difficult to estimate annual PCRs for every prey item that is consumed by this population. However, to illustrate how diverse species-specific consumption rates can be, PCRs for Chinook and chum (*Oncorhynchus keta*) salmon were calculated. Specifically, lower and upper bounds for PCRs of Chinook and chum salmon were calculated from DPERs (kcal/d)

of Southern Resident killer whales and caloric densities (kcal/fish) of Chinook (average value for adults from the Fraser River: 16,386 kcal/fish)[1] and chum (average value for adults from the Puget Sound: 3,877 kcal/fish)[1] salmon, assuming a single-species diet (for simplicity). Chinook and chum salmon were used for this example because they are the two most prevalent salmon species in the diets of Northern and Southern Resident killer whales (Ford *et al.* 1998, Ford and Ellis 2006, Hanson *et al.*, in press). When subsisting only on Chinook, the daily consumption rate for the 82 animals $\geq$1 yr of age in the 83-member SRKW population ranges from 792 to 951 fish/d (289,131–347,000 fish/yr). Fish consumption increases significantly to 3,348–4,018 fish/d (1,222,003–1,466,581 fish/yr) when the population consumes only chum.

It is not surprising that Chinook salmon is the preferred prey of resident killer whales (Ford and Ellis 2006), given its larger size and greater mass-specific caloric content compared to other salmonid species (Groot and Margolis 1991). As a consequence, fewer Chinook salmon need to be consumed by killer whales to meet their DPERs. However, because PCR values are sensitive to assumptions about the size and caloric density of the fish consumed, they should be refined as additional data on prey selectivity become available.

Although coarse estimates for the number of individual fish consumed per day are presented here, the actual number of prey items available in the ocean will have to be much greater to ensure that the population of SRKWs meets their DPERs. This is because prey resources can be patchy and ephemeral. Thus, a much larger prey base will need to be available to SRKWs when the total area of the foraging ground and the energetic cost of searching for prey are considered. Consequently, upper bound PCR estimates likely represent a minimum starting point for how many prey need to be available to meet the metabolic demands of the SRKW population. Future studies on the foraging efficiency of resident killer whales should be conducted to provide additional information to improve these estimates.

In conclusion, this study provides the first estimates of body mass, FMRs, and DPERs for all members of an existent cetacean population. These estimates were based on the best available data and should be refined as additional data become available. In the meantime, however, the estimated DPERs presented here can be combined with data on salmon availability and SRKW foraging selectivity and efficiency to assess the degree to which SRKWs may be prey limited.

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Supporting Information

The following supporting information is available for this article online:

Table S1. Field metabolic rates (FMRs) and daily prey energy requirements (DPERs) for Southern Resident killer whales.

PLOS ONE

RESEARCH ARTICLE

Raising the bar: Recovery ambition for species at risk in Canada and the US

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Abstract

Routinely crossing international borders and/or persisting in populations across multiple countries, species are commonly subject to a patchwork of endangered species legislation. Canada and the United States share numerous endangered species; their respective acts, the Species at Risk Act (SARA) and the Endangered Species Act (ESA), require documents that outline requirements for species recovery. Although there are many priorities for improving endangered species legislation effectiveness, species recovery goals are a crucial component. We compared recovery goal quality, as measured by goal quantitativeness and ambition, for species listed under SARA and ESA. By comparing across ESA and SARA, the intent of the study was to identify differences and similarities that could support the development of stronger species' recovery goals under both legislations. Our results indicated that: (1) overall, only 38% of recovery goals were quantitative, 41% had high ambition, and 26% were both quantitative and with high ambition; (2) recovery goals had higher quantitativeness and ambition under ESA than SARA; (3) recovery goals for endangered species had higher ambition than threatened species under ESA and SARA, and; (4) no recovery goal aimed to restore populations to historic levels. Combined, these findings provide guidance to strengthen recovery goals and improve subsequent conservation outcomes. In particular, species at risk planners should seek to attain higher recovery goal ambition, particularly for SARA-listed species, and include quantitative recovery goals wherever possible.

Introduction

Biodiversity is eroding globally as species face unprecedented threats to their existence, including habitat loss and degradation [1,2], exploitation [3], invasive species [4], and climate change [5]. Among the concerted efforts to combat the biodiversity crisis, individual countries and

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territories often enact national endangered species legislation. Broadly, endangered species legislation aims to identify species at elevated risk of extinction, discern the threats they face, and use this knowledge to protect species and habitats, mitigate species declines, and facilitate species recovery, where feasible. Often far from infallible, national endangered species legislation warrants ongoing scrutiny and constructive change in order to improve the conservation outcomes for the species it is intended to protect.

Canada and the United States (US) share the longest international border in the world and are linked by prominent geographical features such as the Rocky Mountains, the Great Lakes, and countless additional marine, terrestrial, and freshwater ecosystems. In addition to growing lists of species at risk that are unique to each country, Canada and the US also share numerous at-risk species, including migratory (or otherwise mobile) species that traverse both countries and species represented by populations that occur in both countries (e.g., plants and non-migratory species). Two different national legislative acts, Canada's Species at Risk Act (SARA) and the US' Endangered Species Act (ESA), aim to identify and protect species at risk in their respective countries.

Identifying and protecting at-risk species in Canada involves multiple steps. Formed in 1977, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is an independent scientific body that assesses the status of species potentially at risk of extinction or extirpation within Canada [6]. COSEWIC status assessments, which represent the scientific basis for listing decisions, are subsequently forwarded to the Minister of the Environment [7]. The federal government then either accepts or rejects the Minister's recommendation, or refers the matter back to COSEWIC for additional information [7]. If accepted, the species is subsequently listed under SARA, which came into force in 2003. Species may be listed as extinct, extirpated, endangered, threatened, or of special concern [7]. A number of protections are then automatically applied to listed species on federal lands, including freshwater and marine systems [7]. SARA's protections may, upon request by the federal government, be extended to other lands under provincial or territorial jurisdiction [7]. Upon listing, SARA requires Recovery Strategies and Action Plans for endangered and threatened species within specific timeframes [7].

The US federal process for conserving at-risk species and the ecosystems on which they depend was established by ESA legislation enacted in 1973 [8]. Under ESA, species are listed as either endangered or threatened based on their biological status (e.g., population size) and the threats to their continued existence (e.g., habitat destruction, exploitation; [8]). Unlike SARA, species status assessments are conducted by federal agencies (US Fish and Wildlife Service, USFWS; National Marine Fisheries Service, NMFS) and are often initiated by public petitions [9]. Listing determinations are made by these same agencies, accepted or rejected by the Secretary of Commerce (NMFS) or the Secretary of the Interior (USFWS), and legalized when published in the Federal Register. In 1988, amendments to ESA legislation required the development of Recovery Plans for species listed under ESA to describe specific management actions necessary for their recovery [8], the timeframes for which are determined by the responsible federal agency (USFWS or NMFS; [10]).

Previous studies have highlighted the many differences and similarities between ESA and SARA [9,11,12]. Among the key differences, SARA is younger than the ESA and many species protections have yet to be fully implemented [13,14]. Further, while most species at risk in Canada and the US have failed to recover (i.e., the majority of COSEWIC-assessed species at risk: [13]; and most ESA-listed species: [15]), there is evidence that the ESA is effective over time, at least for some species [15]. Importantly, both acts require that Recovery Plans (ESA) and Recovery Strategies (SARA) be produced for species at risk [7,8]); these Recovery Plans and Strategies (hereafter "recovery documents") outline what is required to assist recovery,

recover and/or delist species, including the delineation of objectives for recovering species at risk.

Arguably, and beyond already identified significant issues relating to legislative effectiveness and bias (e.g., SARA: [16–18]; ESA: [19–21]), species recovery planning and subsequent follow-through are crucially important components of national endangered species legislation. Recent publications have drawn attention to variable and, at times, underwhelming ambition of recovery goals under both acts, in addition to a lack of quantitative goals [18,22]. Ambition, defined here as the extent to which recovery goals identify targets that will achieve species recovery, can range from low to high. As an example, ESA recovery goals for the endangered southern resident killer whale (*Orcinus orca*), one of the most intensively studied marine mammals on the planet, are quantitative and of relatively high ambition ("average growth rate of 2.3 percent per year"; [23]). In contrast, recovery goals under SARA are similarly high in ambition but entirely qualitative ("long-term maintenance of [. . .] an increasing size"; [24]). As a second example, although the recovery document contains substantive quantitative population-level information, recovery goals for the northern spotted owl (*Strix occidentalis caurina*) under ESA are qualitative with moderate ambition ("overall population trend [. . .] is stable or increasing"; [25]), whereas goals under SARA are quantitative and more ambitious ("more than 250 mature individuals"; [26]). A third example is the marbled murrelet (*Brachyramphus marmoratus*), another intensively studied species. ESA recovery goals published two decades ago are qualitative but of relatively high ambition ("stabilize and then increase" populations; [27]). Although quantitative, SARA recovery goals are of low ambition, with a short-term (20 year) target being to "halt the decline" and subsequently stabilize the population and nesting habitat areas at less than 30 percent decline compared to 2002 levels [28]. Although it remains unclear whether and how recovery goal ambition is linked to species recovery outcomes, the development of goals with high ambition is likely linked, if not fundamental, to meeting those same goals. In addition, inclusion of quantitative recovery goals offers defined, measurable benchmarks for recovery success (or failure), unlike qualitative goals [29].

Regardless of the drivers (political concerns, socioeconomic considerations, lack of information, and/or an absence of integrated conservation planning; e.g., [12]), varying quantitativeness and/or ambition of recovery goals in Canada and the US raises concerns over conservation effectiveness, efficiency, and ultimately, the persistence of at-risk species. To date, there have been few examinations of the recovery goals of the numerous species listed under endangered species legislation in Canada and the US, including cross-listed species (but see [12]). As multiple delayed recovery documents in Canada [30,31] have been released recently, there is a new opportunity to examine recovery goals for species listed under SARA and ESA.

Initially instigated over the unambiguous contrasts between ESA and SARA recovery goal quality, as measured by quantitativeness and ambition, for several high-profile species (e.g., southern resident killer whale, northern spotted owl, and marbled murrelet), this study's main objective is to compare and contrast recovery goal quality for species listed under SARA and ESA. Our focus on recovery goal quantitativeness and ambition was strategically identified for the potential to strengthen recovery goal objectives, with the ultimate intent being improved conservation outcomes for species at risk. By comparing across the two legislation types, our aim is to identify differences that could pinpoint areas for improvement as well as similarities that could identify weaknesses common to the development of quality recovery goals under both legislation types. Moreover, our analysis includes a subset of species that are cross-listed under both legislation types, the intent of which is to uncover cases that could benefit from increased cross-border sharing of information. Accordingly, study findings are intended to

inform and provide guidance for the improvement of recovery goals in aid of species conservation.

Methods

We compared the quantitativeness and ambition of recovery objectives for species listed under SARA in Canada and recovery criteria for species listed under the ESA in the United States. We first identified 57 species cross-listed under both SARA and ESA (SARA: http://www.registrelep-sararegistry.gc.ca/sar/index/default_e.cfm; ESA: https://www.fws.gov/endangered/index.html; S1 Table; documents archived 21 August 2019). Recovery documents are required for species listed as endangered or threatened; and endangered, threatened, or extirpated under ESA and SARA, respectively. ESA and SARA cross-listed species were included in our analysis if: (1) they were identified as being the same species or subspecies with a single recovery document under each legislation or; (2) they represented the same population (e.g., white sturgeon, *Acipenser transmontanus*, Kootenay River population) with population-specific recovery documents under both legislation types or; (3) they were equivalent but spatially discrete populations (e.g., beluga whale, *Delphinapterus leucas*), or Designatable Units (DU, Canada; e.g., Sockeye salmon, *Oncorhynchus nerka*) or Distinct Population Segments (DPS, US; e.g., Atlantic salmon, *Salmo salar*) with population-specific recovery documents under both legislation types. Hereafter, we refer to DUs, DPSs, species, subspecies, ecotypes, and subpopulations as "species". Where available, finalized recovery documents were used; in the absence of a finalized document, draft documents were examined. Two species listed as extirpated in Canada where recovery was deemed either not technically or biologically feasible were included in the summary table (S1 Table) but excluded from subsequent analyses (i.e., prairie population of grizzly bear, *Ursus arctos*; [32]; dwarf wedge mussel, *Alasmidonta heterodon*; [33]). We note that though the black-footed ferret (*Mustela nigripes*) and the karner blue (*Lycaeides melissa samuelis*) are also listed as extirpated in Canada, their recovery is currently considered feasible [34,35]; therefore, these species were retained in our analysis.

Secondly, additional species listed under ESA or SARA were randomly selected to be included in our analysis to supplement the small number of cross-listed species. In total, combining cross-listed and randomly sampled species, we sampled 15 species from each of seven natural taxonomic groupings (i.e., amphibian, bird, fish, invertebrate, mammal, plant, reptile), with exception of SARA-listed amphibians, where there were only 13 recovery documents available (total ESA, n = 105; total SARA, n = 103).

We extracted the recovery goals defined in the recovery documents for cross-listed and randomly selected species and evaluated their quantitativeness and ambition. In ESA recovery documents, recovery goals are defined as "criteria" for reclassifying or delisting, and in SARA documents, these goals are often referred to as "goals" or "objectives" for recovery or, commonly in more recent documents, as "population and distribution objectives". For ease of interpretation, hereafter, we use the term "recovery goals" to encompass the terms and criteria described above. To directly compare recovery goals, we scored each recovery document according to two attributes:

1. Quantitativeness of recovery goals: we first assessed whether the documents included quantitative or qualitative recovery goals. Goals were considered quantitative if a numeric target (e.g., population size, number of breeding pairs, percent population increase) was included. For plants, we also considered area of occupancy or extent occurrence as numeric population targets due to the difficulty of estimating number of individuals for some species. We scored only the recovery goal, and not the methods used to assess a species status or generate population trajectories within the entire recovery document. Some species' recovery

Table 1. Recovery ambition scoring guide for species' recovery plans and strategies under Canada's Species at Risk Act (SARA) and the US Endangered Species Act (ESA), modified from McCune et al. [18].

Ambition score	Recovery goal	Quantitative example	Qualitative example	Species with matching ambition score where one legislation is quantitative and the other qualitative
1	None stated (e.g. goal related to protection of area but not regarding population size)	SARA: none	SARA: Kirkland's warbler (*Setophaga kirtlandii*/ *Dendroica kirtlandii*)	None
		ESA: none	ESA: western prairie fringed orchid (*Platanthera praeclara)*	
2	Vague (e.g., "maintain an index of area of occupancy" [36], "achieve sufficient and viable populations" [37] —without clarification as to what this means) or less than current level	SARA: marbled murrelet (*Brachyramphus marmoratus*)	SARA: northern riffleshell (*Epioblasma torulosa rangiana*)	None
		ESA: sei whale (*Balaenoptera borealis)*	ESA: dwarf lake iris (*Iris lacustris*)	
3	Equal to current level (e.g., population is stable), or willing to accept current level or increase (e.g. "population is stable or increasing"[38], or "maintain or increase" [39])	SARA: none	SARA: short-tailed albatross (*Phoebastria albatrus*)	Species: Spalding's catchfly (*Silene spaldingii*)
		ESA: whooping crane (*Grus Americana*)	ESA: northern spotted owl (*Strix occidentalis caurina*)	Quantitative: ESA
				Qualitative: SARA
4	Restore to levels greater than current, restore to levels greater than current but less than historic, or restore to levels greater than current with historic levels unknown	SARA: northern spotted owl (*Strix occidentalis caurina*)	SARA: north Atlantic right whale (*Eubalaena glacialis*)	Species: golden paintbrush (*Castilleja levisecta*)
		ESA: short-tailed albatross (*Phoebastria albatrus)*	ESA: marbled murrelet (*Brachyramphus marmoratus*)	Quantitative: ESA
				Qualitative: SARA
5	Restore to historic levels; however, must include description of historic population extent and time period	SARA: none	SARA: none	None
		ESA: none	ESA: none	

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documents were quantitative throughout their methods sections (e.g., demographic analyses), but lacked a quantitative element in their recovery goal; these recovery goals were scored as qualitative. For example, despite extensive quantitative analyses in other sections of the ESA recovery plan for the northern spotted owl, the recovery goal of "overall population trend [. . .] is stable or increasing" [25] was scored as a qualitative goal. Where no goal was included, this attribute was assigned "NA".

2. Ambition of recovery goals: recovery goals were assigned an ambition score modified from McCune et al. [18]. Ambition, defined as the extent to which recovery goals delineate targets that will achieve species recovery, was described using a five-point scale that ranged from low to high (Table 1).

Additionally, recovery goals in SARA recovery documents were often separated into short- and long-term objectives; typically these two time periods were based on the life history of the species in question, with several exceptions where time frames were not clarified (in these cases, objectives were categorized as long-term). When present, the two time frames were assessed separately. The two time frames often received different scores for both recovery goal quantitativeness and ambition and thus, as a conservative approach for the direct comparison between SARA and ESA recovery documents, we used the "best case scenario" from the two SARA goals by choosing quantitative over qualitative goals and using the higher ambition score. Once completed, 10% of recovery documents were randomly re-sampled and evaluated again by three trained individuals; on average, repeatability scoring for recovery goal ambition score and recovery goal quantitativeness was 90%.

Data analysis

We used Fisher's Exact tests to examine similarities and differences in quantitativeness and ambition in relation to legislation type, species status, and natural taxonomic grouping. For simplicity, we compared goals with ambition scores of 4 (i.e., the highest-ranked goals in the data set) to all lower ranked goals (i.e., 1, 2, or 3). For comparisons by status, we focused on species listed as threatened versus endangered due to the small number of species in our data-set (n = 2) listed as extirpated under SARA. All data were analyzed and graphed using R statistical software [40].

Results

Considering all recovery documents examined in this study, 38% (78/208) of recovery goals were quantitative and 41% (85/208) had high ambition (i.e., an ambition score of 4). Only 26% (55/208) of recovery goals were both quantitative and had high ambition. Overall, quantitative goals were associated with higher ambition (Table 2). Specifically, the odds of a quantitative

Table 2. Comparisons of the quantitativeness and ambition of recovery goals (n = 208) by legislation, status, natural grouping, and habitat. Odds ratios and confidence intervals were obtained from Fisher's Exact Tests. See Methods for further detail. Cells shaded grey with italicized text denotes odds ratios with confidence intervals that overlap one (i.e., include the possibility of no difference).

Comparison		Proportion of Goals (%)		Odds Ratio (95% CI)
Quantitativeness		**Quant**	**Qual**	
of Ambition 4	Overall	55/78 (71)	30/130 (23)	7.9 (4.0–15.8)
Goals	ESA	36/51 (71)	17/54 (31)	5.1 (2.1–13.1)
	SARA	19/27 (70)	13/76 (17)	11.1 (3.7–36.6)
Legislation		**ESA**	**SARA**	
Quantitative		51/105 (49)	27/103 (26)	2.6 (1.4–5.0)
Ambition 4		53/105 (50)	32/103 (31)	2.4 (1.3–4.4)
Status		**Endangered**	**Threatened**	
Quantitative	Overall	62/147 (42)	15/59 (25)	2.1 (1.1–4.5)
	ESA	42/77 (54)	9/28 (32)	*2.5 (0.9–7.2)*
	SARA	20/70 (29)	6/25 (19)	*1.7 (0.6–5.7)*
Ambition 4	Overall	68/147 (46)	17/59 (29)	2.1 (1.1–4.4)
	ESA	42/77 (54)	11/28 (39)	*1.8 (0.7–5.0)*
	SARA	26/70 (37)	6/31 (19)	*2.4 (0.8–8.3)*
Natural Grouping		**ESA**	**SARA**	
Quantitative	Mammals	11/15 (73)	5/15 (33)	*5.2 (0.9–35.6)*
	Birds	12/15 (80)	10/15 (67)	*1.9 (0.3–15.8)*
	Reptiles	6/15 (40)	1/15 (7)	*8.7 (0.8–457.9)*
	Amphibians	5/15 (33)	1/13 (8)	*5.6 (0.5–306.3)*
	Fish	6/15 (40)	6/15 (40)	*1 (0.2–5.5)*
	Invertebrates	1/15 (7)	2/15 (13)	*0.5 (0–10.2)*
	Plants	10/15 (67)	2/15 (13)	11.7 (1.7–147.7)
Ambition 4	Mammals	11/15 (73)	6/15 (40)	*3.9 (07–25.9)*
	Birds	8/15 (53)	7/15 (47)	*1.2 (0.2–6.9)*
	Reptiles	7/15 (47)	0/15 (0)	*Infinity*
	Amphibians	7/15 (47)	2/15 (13)	*4.5 (0.6–56.3)*
	Fish	7/15 (47)	10/15 (67)	*0.5 (0.1–2.4)*
	Invertebrates	6/15 (40)	3/15 (20)	*2.6 (0.4–20.4)*
	Plants	7/15 (47)	4/15 (27)	*2.3 (0.4–15.0)*

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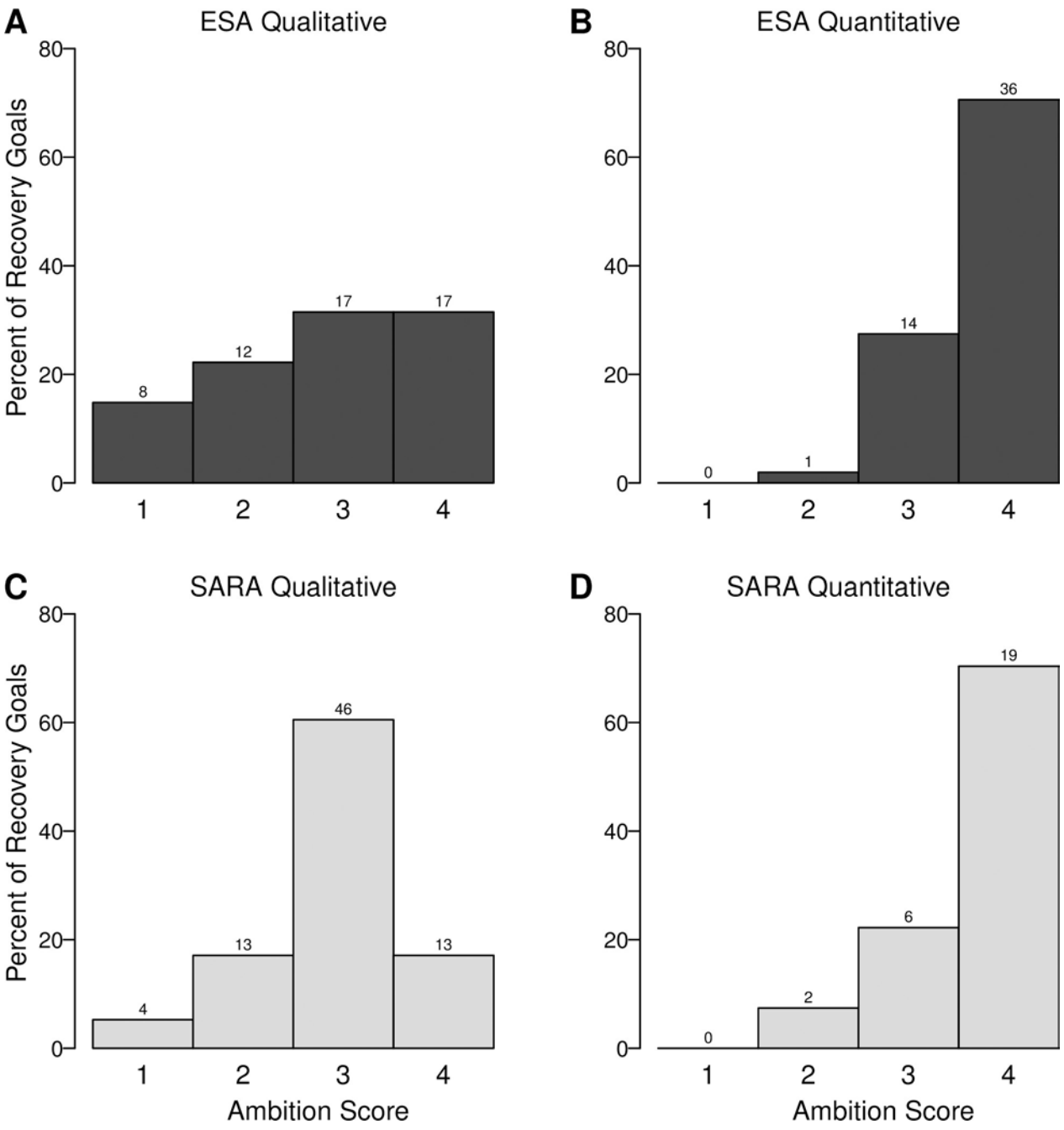


Fig 1. Ambition of qualitative and quantitative recovery goals for species (n = 208) listed under the United States' Endangered Species Act (ESA) and Canada's Species at Risk Act (SARA). Bars show the percent of recovery goals with ambition scores 1–4 for (A) qualitative goals under the ESA, (B) quantitative goals under the ESA, (C) qualitative goals under SARA, and (D) quantitative goals under SARA. Ambition of recovery goals within published recovery documents was scored on a scale from 1 to 5; however, no goals qualified for an ambition score of 5 (see Methods). The number of recovery goals in each category is displayed above each bar.

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goal receiving an ambition score of 4 were 7.9 times higher than for a qualitative goal. The trend of quantitative goals having higher ambition was consistent in both legislation types (Table 2). However, and relevant to evaluating the potential redundancy of the scoring system applied in this study, the two metrics of recovery goal quality (i.e., quantitativeness and an

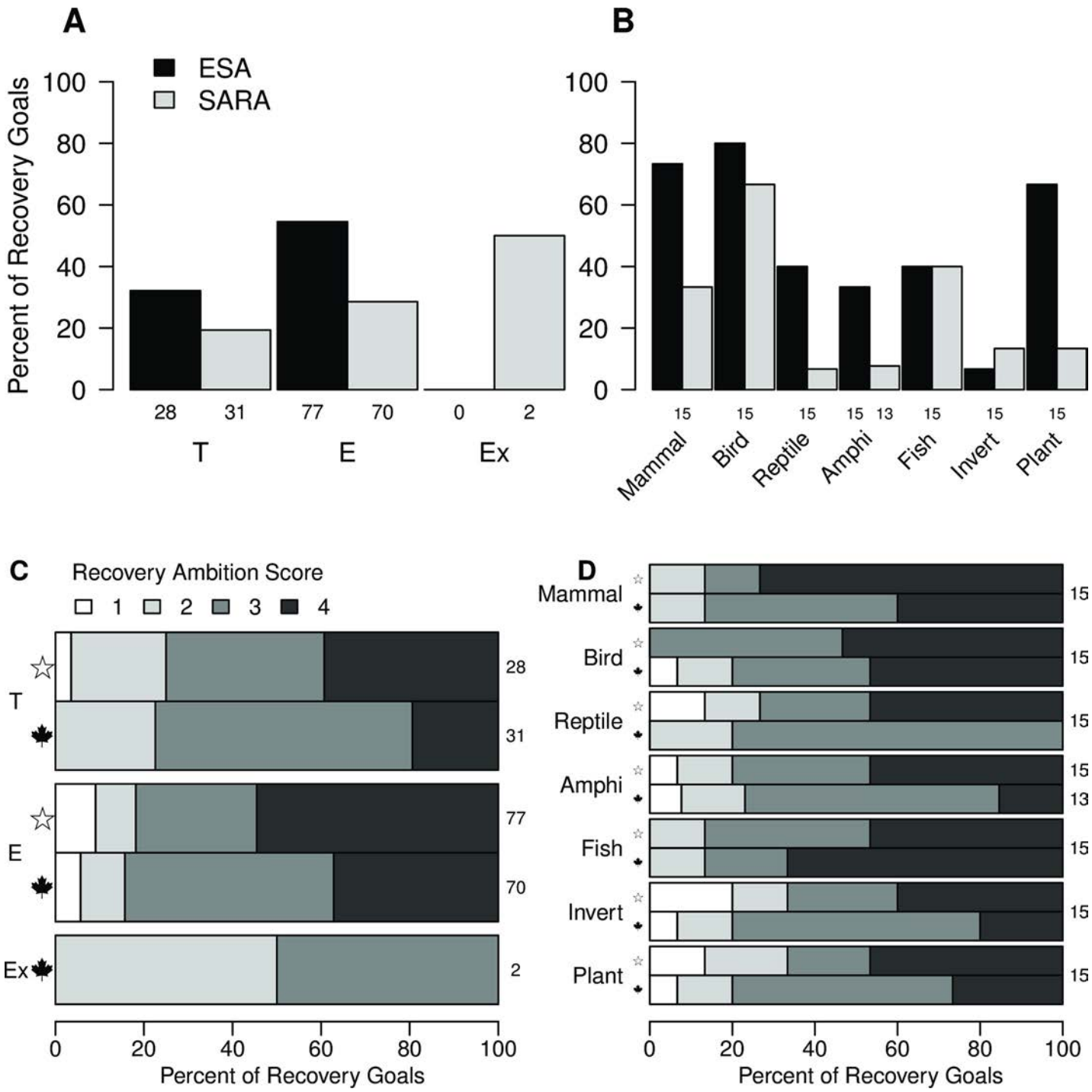


Fig 2. Quantitativeness and ambition of recovery goals for species (n = 208) listed under both the United States' Endangered Species Act (ESA) and Canada's Species at Risk Act. Percent of quantitative recovery goals (A) by species status (i.e., threatened [T], endangered [E], or extirpated [Ex]), and (B) by natural grouping. Ambition of recovery goals listed under the ESA (denoted by a star) and SARA (denoted by a maple leaf) (C) by status and (D) natural grouping, Ambition of recovery goals within published recovery documents was scored on a scale from 1 to 5; however, no goals received an ambition score of 5 (see Methods). Sample sizes are displayed to the right of bars.

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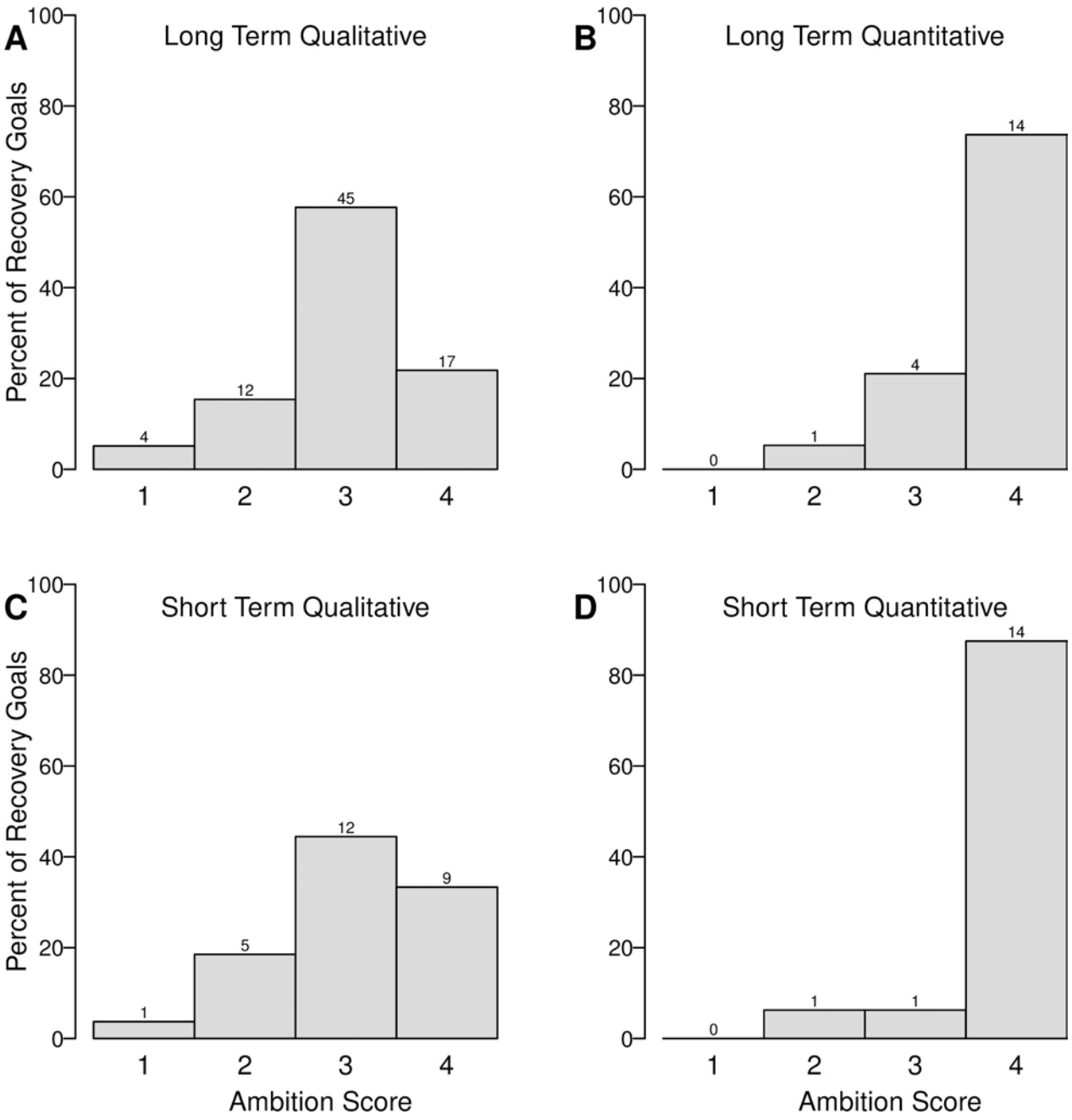


Fig 3. Ambition of qualitative and quantitative long-term (n = 97) and short-term (n = 43) recovery goals for species listed under Canada's Species at Risk Act (SARA). Bars show the percent of recovery goals with ambition scores 1–4 for (A) long-term qualitative goals, (B) long-term quantitative goals, (C) short-term qualitative goals, and (D) short-term quantitative goals. Ambition of recovery goals within published recovery documents was scored on a scale from 1 to 5; however, no goals received an ambition score of 5 (see Methods). The number of goals in each category is displayed above each bar. Sample sizes are uneven because seven recovery plans contained only long-term goals and one strategy contained only short-term goals.

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ambition score of 4) differed for 25% (53/208) of goals evaluated. In other words, 25% of goals were scored as either quantitative with low ambition (23/208) or qualitative with high ambition (30/208).

Comparing between legislation types, ESA recovery goals were more quantitative and had higher ambition than SARA recovery goals (Fig 1; Table 2). Specifically, the odds of a quantitative goal were 2.6 times higher under ESA than SARA (Table 2). Similarly, the odds of a goal receiving an ambition score of 4 were 2.4 times higher under ESA than SARA (Table 2). The trend of ESA goals having higher ambition than SARA goals occurred primarily among qualitative goals, where the mode ambition scores were 4 and 3 for ESA and SARA, respectively (Fig 1A and 1C). By contrast, the proportion of quantitative goals with an ambition score of 4 were similar for both ESA and SARA (Fig 1B and 1D). Notably, no recovery goals scored an ambition score of 5 (Fig 1).

Quantitativeness and ambition also differed by species status (Table 2). Overall, the odds of a goal being quantitative were 2.1 times higher for endangered than for threatened species (Fig 2A; Table 2). Similarly, the odds of a goal receiving an ambition score of 4 were 2.1 times higher for endangered than for threatened species (Fig 2C; Table 2). When considering each legislation type separately, the trend of goals for endangered species being more quantitative and ambitious than those for threatened species were consistent; however, the confidence intervals of the odds ratios for each legislation type overlapped one (i.e., included the possibility of no difference by status; Table 2; Fig 2A and 2C).

The trend of ESA being more quantitative and having higher ambition than SARA was largely consistent across natural taxonomic groupings (Fig 2B and 2D; Table 2). One exception was in fish, where SARA goals had a similar proportion of quantitative goals and a higher proportion of goals with an ambition score of 4 compared with ESA goals (Fig 2B and 2D). A second exception was for invertebrates, where the proportion of quantitative goals was low for both legislation types (Fig 2B). Comparing across natural groupings, the greatest difference in quantitativeness between legislation types occurred in plants, where the odds of a quantitative goal were 11.7 times higher under ESA than SARA (Fig 2B; Table 2). The difference in recovery goal ambition was greatest in reptiles; however, it was not possible to calculate an odds ratio because no SARA goals for reptiles had an ambition score of 4 (Fig 2D; Table 2).

The majority of long- and short-term recovery goals for SARA-listed species were qualitative ($\frac{78}{97} = 80\%$ and $\frac{27}{43} = 63\%$ respectively; Fig 3). In both the long-term and short-term, quantitative goals had higher ambition (mode = 4; Fig 3B and 3D) than qualitative goals (mode = 3; Fig 3A and 3C).

The majority of species cross-listed under SARA and ESA had recovery documents ($\frac{36}{57} = 63\%$, including three extirpated species in Canada; S1 Table). Twelve $\left(\frac{12}{57} = 21\%\right)$ cross-listed species had only one recovery document, either by SARA or ESA. Only two species are currently without a recovery document from either country ($\frac{2}{57} = 4\%$), one of which is the Vancouver Island marmot, which is considered a Foreign Species under ESA. Lastly, seven species ($\frac{7}{57} = 12\%$) were listed as Special Concern under SARA (where no Recovery Strategy is required) and as endangered or threatened under ESA (four of which had Recovery Plans).

Our study findings for the subset of species listed under both legislation types (n = 34; S2 Table; S1–S3 Figs) were largely consistent with findings from the full complement of recovery documents examined in this study (n = 208; Table 2). An exception is that the trend of endangered species having a higher proportion of quantitative goals compared with threatened species is consistent for both legislation types in the larger data set, whereas the trend is reversed for species listed under SARA in the cross-listed data set (S2 Table). Relevant to potential information-sharing between countries, 18 of 34 species (53%) listed under both legislation types had goals that were quantitative under one legislation but not the other, including 13 cases where ESA goals were quantitative but SARA goals were not and 5 cases where SARA goals were quantitative and ESA goals were not. Similarly, 18 of 34 the cross-listed species

(53%) had high ambition (ambition score of 4) under one legislation but not the other, including 14 cases where ESA goals had high ambition but SARA goals did not and 4 cases where SARA goals had high ambition but ESA goals did not.

Discussion

Endangered species legislation is essential to protect and recover at-risk species, but its successful implementation is inherently difficult, requiring considerable time, cost, and species-specific information. Previous assessments of national endangered species legislation and associated processes have identified multiple areas for improvement (e.g., listing process bias, critical habitat designation, and delays; [21,30]); recovery documents also offer a potentially rapid, strategic avenue for improving species' conservation status [e.g., [29]. Although reviews of recovery documents provide guidance on threat monitoring [20], the biological relevance of recovery criteria [41], and recovery document scope [42], this study focused on the quality (i.e., quantitativeness and ambition) of recovery goals as a key component of effective recovery documents. Overall, 38% of goals were quantitative, 41% had high ambition (i.e., an ambition score of 4), and 26% were both quantitative and highly ambitious. Comparing between legislation types, ESA recovery goals generally were more quantitative and had higher ambition than those put forward under SARA. Common to both legislations, recovery goals for endangered species were more quantitative and had higher ambition than those for threatened species. By focusing on listed species with recovery documents, our study provides an appraisal of recovery goal quality for species at risk, and is intended to contribute to efforts to strengthen recovery goals and subsequent conservation outcomes for species in Canada and the US.

One of our main findings was that only 38% of recovery documents assessed had recovery goals that were quantitative. This finding is highly relevant, as recovery goal quality may affect conservation outcomes. As a key example, Gerber and Hatch [29] found that quantitative recovery goals were associated with improved status of ESA-listed species. Further, quantitative recovery goals have been praised for providing consistency, efficiency, transparency, and legitimacy; consequently, recent reviews have called for their inclusion in recovery documents whenever possible [43]. Despite these strengths, quantitative conservation targets have been criticized for their rigidity that may not be adaptive to complex ecological variation (e.g., climate change response) or socioeconomic criteria [44], for their application in situations when they are not biologically founded [45,46], and in cases where inherent uncertainty around targets is not reported [47]. When these concerns can be addressed, our results indicate that recovery goal quantitativeness should be improved where possible.

Regarding ambition, only 41% of goals had high ambition (i.e., received an ambition score of 4). Although recovery goals with higher ambition were more likely to be quantitative, the two measures of goal quality differed (i.e., were scored as either quantitative with low ambition or qualitative with high ambition) for 25% of species examined (see Table 1 for examples). These differences suggest that both measures of recovery goal quality should be considered when developing recovery goal targets. An important next step, however, would be to explore the relationships between recovery goal ambition and species' conservation status outcomes under SARA and ESA.

Contributing new knowledge regarding the differences and similarities between ESA and SARA, this study also finds that SARA recovery goals are generally less quantitative and of lower ambition than those put forward under ESA. While recovery goal quality could be improved under both legislative acts, this appears to be particularly the case for SARA-listed species in Canada. Further, for the subset of species cross-listed under both ESA and SARA, there is evidence of varying goal quality between the two legislations, with SARA-listed species

having lower recovery goal quality in general, in terms of both ambition and quantitativeness. Recovery goals with underwhelming ambition (i.e., ambition score 1 or 2) have been previously identified for SARA-listed species [17], but direct comparison with ESA species and the subset of cross-listed species has not been previously undertaken. Whereas McCune et al. [17] speculated that a species' economic importance may influence recovery goal ambition, other factors may also contribute to reduced recovery goal quality under SARA.

Although there are a litany of potential drivers for the observed differences in recovery goal quality between ESA and SARA, several fundamental explanations represent starting points for further study. First, ESA is older than SARA and has been subject to amendments, arguably greater academic scrutiny [19,42,48], and more legal challenges (e.g., Centre for Biological Diversity; http://www.biologicaldiversity.org) as compared to SARA (but see [17,18]). Funding also differs greatly between the two legislations; for example, in 2007, the average amount spent per species was 1.3 million USD under ESA versus 0.2 million USD under SARA [49,50]. Although little explored, funding disparities could potentially influence any stage of endangered legislation implementation, including the setting and achievement of recovery goals. For example, Miller et al. [51] found that species listed under the ESA with higher funding were more likely to have either stable or increasing status. Institutional perspectives and language typically used in the two recovery document types also frequently differed; these differences may have affected recovery goal quality. As an example, ESA recovery documents tended to use more explicit language (e.g., "stable populations or increasing"; [27]) compared with often vague language used in SARA recovery documents (e.g., "maintain long-term, self-sustaining, viable populations"; [52]). Finally, fundamental differences in the requirements laid out by the two acts may also influence recovery goal quality [9]; as an example, recent ESA recovery documents are required to include criteria necessary for delisting [8], unlike SARA.

As a third major finding, recovery goal quantitativeness and ambition were higher for species listed as endangered as compared to threatened under ESA and SARA. Higher recovery goal quality for endangered species could be related to a greater urgency to increase endangered populations rather than maintain or slow their decline [53]. Alternatively or concomitantly, the difference could relate to better knowledge of endangered species, leading to quantitative, high ambition recovery goals for endangered species [43,54]. Regardless of the drivers, differences in recovery goal quality for endangered and threatened species have implications for the timing of recovery interventions in a species' pathway to recovery, including a failure to recover. Although allocating resources to the most endangered species can have benefits in the short term, investments in less endangered species benefit more species in the longer term [55]. Further examination of these differences, and potential ramifications for conservation outcomes, remain to be explored.

In the midst of a global extinction crisis, effective conservation actions for recovering species at risk are crucial. When setting targets for at-risk species recovery, low quality recovery goals may undermine or stymie conservation efforts and, thus, are counterproductive. Given the potentially negative conservation outcomes associated with low quality goals, [e.g., [19], our results provide clear guidance for developing higher quality goals for recovery planning. Specifically, our findings highlight that recovery goals could be improved by focusing on the development of unambiguous, high-ambition (i.e., increasing population), and quantitative recovery goals wherever possible. Further, differences in recovery goal quality between ESA and SARA indicate that greater international information sharing [11] could provide a synergistic benefit in achieving conservation outcomes (e.g., via data and expertise sharing, joint recovery planning, and cross-border species management) for species cross-listed under both legislative acts. Ultimately, increasing recovery goal ambition for species with lower threat status could result in stronger conservation outcomes, although this topic warrants additional

exploration. As a final point, attention to recovery goal quality is important because recovery documents are accessed by diverse users, including those without a scientific background and/or species-specific knowledge; by extension, recovery goals should be straightforward, explicit, and standalone. Although many other aspects of endangered species legislation require improvement, increasing recovery goal quality represents a strategic opportunity to effect meaningful and urgently needed conservation outcomes.

Supporting information

S1 Table. Identity and status of cross-listed species at risk under Canada's Species at Risk Act (SARA) and the US Endangered Species Act (ESA). Recovery documents not finalized as of 21 August 2019 are denoted with "NF". "Pop(s)" refers to population(s) identified by the recovery documents.
(DOCX)

S2 Table. Comparisons of the quantitativeness and ambition of recovery goals by legislation, status, natural grouping, and habitat for species listed under both SARA and ESA (n = 34). Odds ratios and confidence intervals were obtained from Fisher's Exact Tests. See Methods for further detail. Shading shows where the trend was opposite between the subset of paired data (n = 34) and the larger set of recovery documents (n = 208).
(DOCX)

S1 Fig. Ambition of qualitative and quantitative recovery goals for species (n = 34) listed under the United States' Endangered Species Act (ESA) and Canada's Species at Risk Act (SARA). Bars show the percentage of recovery goals with ambition scores 1–4 for (A) qualitative goals under the ESA, (B) quantitative goals under the ESA, (C) qualitative goals under SARA, and (D) quantitative goals under SARA. Ambition of recovery goals within published recovery documents was scored on a scale from 1 to 5; however, no goals qualified for an ambition score of 5 (see Methods). The number of goals in each category is displayed above each bar.
(TIF)

S2 Fig. Quantitativeness and ambition of recovery goals for species (n = 34) listed under both the United States' Endangered Species Act (ESA) and Canada's Species at Risk Act. Percent of quantitative recovery goals (A) by species status (i.e., threatened [T], endangered [E], or extirpated [Ex]), and (B) by natural grouping. Ambition of recovery goals listed under the ESA (denoted by a star) and SARA (denoted by a maple leaf) (C) by status and (D) natural grouping. Ambition of recovery goals within published recovery documents was scored on a scale from 1 to 5; however, no goals received an ambition score of 5 (see Methods). Sample sizes are displayed to the right of bars.
(TIF)

S3 Fig. Ambition of qualitative and quantitative long-term and short-term recovery goals for species (n = 34) listed under Canada's Species at Risk Act (SARA). Bars show the percent of recovery goals with ambition scores 1–4 for (A) long-term qualitative goals, (B) long-term quantitative goals, (C) short term qualitative goals, and (D) short-term quantitative goals. Ambition of recovery goals within published recovery documents was scored on a scale from 1 to 5; however, no goals received an ambition score of 5 (see Methods). The number of goals in each category is displayed above each bar. Only species cross-listed under the United States' Endangered Species Act are shown. Sample sizes are uneven because seven recovery plans

contained only long-term goals and one strategy contained only short-term goals.
(TIF)

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FEATURE ARTICLE: REVIEW

From diatoms to killer whales: impacts of pink salmon on North Pacific ecosystems

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ABSTRACT: In response to a climate regime shift in 1977 and general heating of the North Pacific Ocean, pink salmon *Oncorhynchus gorbuscha* abundance reached record highs during 2005–2021, comprising 70% of all Pacific salmon. Pink salmon are approximately 25 times more numerous in odd- than even-numbered calendar years in some major North Pacific ecosystems, a unique demographic pattern analogous to repeating whole ecosystem treatment–control experiments. We found compelling examples indicating that in odd years, predation by pink salmon can initiate pelagic trophic cascades by reducing herbivorous zooplankton abundance sufficiently that phytoplankton densities increase, with opposite patterns in even years. Widespread interspecific competition for common-pool prey resources can be dominated by pink salmon, as indicated by numerous biennial patterns in the diet, growth, survival, abundance, age-at-maturation, distribution, and/or phenology of ecologically, culturally, and economically important forage fishes, squid, Pacific salmon and steelhead trout *Oncorhynchus* spp., seabirds, humpback whales *Megaptera novaeangliae*, and endangered southern resident killer whales *Orcinus orca*. In aggregate, the evidence indicates that open-ocean marine carrying capacity in the northern North Pacific Ocean and Bering Sea can be mediated by top-down forcing by pink salmon and by ocean heating, and that large-scale hatchery production (~40% of the total adult and immature salmon biomass) likely has unintended consequences for wild salmon, including Chinook salmon *O. tshawytscha*, and many other marine species. Further investigation of the effects of pink salmon on other species will increase our knowledge of ecosystem function and the important role top-down forcing plays in the open ocean

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Pink salmon returning to Prince William Sound, Alaska hatcheries have contributed to record-setting abundances in recent years and to impacts on other marine species.

Photo: Preston and Teresa Cole, https://taps-photography.pixels.com/

KEY WORDS: North Pacific ecosystems · *Oncorhynchus gorbuscha* · Competition · Trophic cascade · Carrying capacity · Climate change · Ocean heating · Ecosystem services

1. INTRODUCTION

Some upper trophic level species play crucial roles in the natural histories of other species and the structure and function of ecosystems. Such interactions have been well documented in terrestrial (Carpenter et al. 1995, Painter et al. 2015), freshwater (Carpenter

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et al. 1985, Naiman et al. 1988, Ellis et al. 2011, Beschta & Ripple 2019), and nearshore marine environments (e.g. Paine 1977, Estes et al. 1998, Christianen et al. 2023), primarily from treatment–control experiments. This has been poorly documented in the open ocean, where experiments are generally impractical because of the great spatial scales, challenging logistics, and expense. Although considerable progress has been made in identifying top-down effects in ocean ecosystems (e.g. Baum & Worm 2009), most inferences have been based on before–after comparisons of change following predator removals or additions. Examples include the slaughter of great whales in the 19th and 20th centuries in the North Pacific and Southern Oceans (Springer et al. 2003, 2006, Roman et al. 2014), the collapse of cod *Gadus morhua* stocks in the NW Atlantic (Frank et al. 2005), and the invasion of killer whales *Orcinus orca* into the eastern Canadian Arctic (Breed et al. 2017, Matthews et al. 2020).

Pink salmon *Oncorhynchus gorbuscha* in the North Pacific Ocean (NPO) exhibit a unique, exaggerated biennial alternation between high and low abundance that can be viewed as a simple, natural treatment–control 'experiment' (Ruggerone & Nielsen 2004), even though all variables cannot be controlled. Many pink salmon populations are predictably much more abundant in odd-numbered calendar years than in even-numbered years (Irvine et al. 2014), thus in this analogy, odd years are equivalent to treatment years and even years are equivalent to control years. The biennial cycles repeat over many decades (Fig. 1), creating reliable replication that can be used to identify effects of pink salmon on the ecosystem. A growing body of evidence suggests that biennial patterns in the biology of many marine species in the NPO can be linked directly and indirectly to pink salmon, and that pink salmon can initiate pelagic trophic cascades.

Our goal here is to synthesize information on those biennial patterns and evaluate evidence that they are caused by direct and indirect effects of pink salmon. Such evidence provides novel information about the influences of top-down predation on the structure and function of open ocean ecosystems, and has important biological and policy value for understanding the ocean's carrying capacity. If, for example, the forage demand of billions of additional salmon released from industrial-scale hatcheries pushes closer to the ocean's carrying capacity, this may have deleterious effects on wild salmon as well as non-salmon species, such as decreased survival rate, productivity, and body size (e.g. Cooney & Brodeur 1998, Perry et al. 1998). Governments and managers often assume hatchery and wild populations do not compete for prey (Holt et al. 2008), or with other species in pelagic food webs, yet the overall benefits and costs of hatchery production to ecological and societal well-being is a matter of considerable debate (e.g. Kaeriyama & Edpalina 2004, Harrison & Gould 2022).

We show that pink salmon can have major top-down impacts on species and food webs that include 5 major taxa — phytoplankton, zooplankton, fishes, marine birds, and marine mammals — over vast regions of the NPO, and through a transhemispheric teleconnection on terrestrial ecosystems in the southern hemisphere (Table 1). In aggregate, the weight of evidence leads to a robust conclusion: pink salmon can exert strong top-down effects on a common pool of prey resources that affect many other species and influence pelagic ecosystems of the NPO. These effects, in turn, may affect human subsistence and cultural, recreational, and economic values in both the northern and southern hemispheres. The examples of direct and indirect effects of pink salmon presented here are likely not the only ones that exist, and other researchers with multi-year data sets might seek additional biennial patterns waiting to be found, and explanations for them.

2. BACKGROUND

Pink salmon life history characteristics are uniquely suited for testing hypotheses about top-down interactions with other marine species. These fish are widely distributed throughout epipelagic waters of the NPO; e.g. those from eastern Kamchatka, Russia, migrate eastward to approximately 150° W (Radchenko et al. 2018), suggesting that they have the potential to interact with species across the Bering Sea (BS) and Gulf of Alaska (GOA), including North American salmon. Major populations spawn in Alaska, British Columbia (BC), Puget Sound (WA), the Russian Far East, and northern Japan (Takagi et al. 1981). Their overall abundance increased steadily after the mid-1970s, reaching unprecedented levels during 2005–2021, when annual abundance averaged 522 million adults, or nearly 70% of all Pacific salmon (Fig. 1). Approximately 82 million adult pink salmon per year (16% of total) originated from hatcheries during 2005–2015 (Ruggerone & Irvine 2018).

Pink salmon have benefited from climate change, beginning with a major climatological regime shift in 1977 (Mantua et al. 1997) and heating of the NPO, as indicated by a strong positive correlation between

Table 1. Evidence for interactions between pink salmon and plankton, forage fishes, squid, Pacific salmon, seabirds, and whales. Evidence includes biennial or cyclic patterns, and positive (+) and negative (–) correlations (Pearson's correlation or linear regression) when available. Biennial patterns without correlation analyses indicate negative effects of pink salmon on other species. For seabirds, biennial patterns with correlation analyses apply only to omnivores: for planktivores, biennial patterns in Births, Productivity, and Phenology indicate positive correlations with pink salmon. See Section 3 and Supplement 2 at www.int-res.com/articles/suppl/m719p001_supp2.xlsx for details. SH: southern hemisphere; NH: northern hemisphere; NP: North Pacific; AI: Aleutian Islands; BS: Bering Sea; GOA: Gulf of Alaska; PWS: Prince William Sound; SOG: Strait of Georgia; AK: Alaska; BC: British Columbia; OR: Oregon; WA: Washington; WC: West Coast; R: river; I: island

Species	Diet	Growth	Fecundity	Births	Productivity	Abundance	Age-at-maturation	Distribution	Phenology	Body condition	Ecosystem	Population location
Plankton												
Phytoplankton						Biennial, +					BS, AI, central NP	
Zooplankton		Biennial, +				Biennial, –					BS, AI, central NP	
Forage fishes and squid												
Herring		Biennial, –				–					PWS, Sitka Sound	PWS, Sitka Sound
Atka mackerel		Biennial, –									AI	AI
Sand lance						Biennial					Salish Sea	Salish Sea
Pacific Ocean perch						Biennial, –					GOA	GOA
Squid spp.						Biennial					BS, W NP	BS, W NP
Berryteuthis anonychus						Biennial, – and cyclic					BS, GOA	BS, GOA
Pacific salmon												
Sockeye	Biennial	Biennial, –	Assumed –		Biennial, –	Biennial, –	Biennial, +				NP, BS, Salish Sea	Kamchatka, AK BC, WA, PWS
Chum	Biennial, –	Biennial, –	–		Biennial, –	Biennial, –	Biennial, +	Biennial, –		–	NP, BS, Kuril I, Salish Sea	Japan, Russia, Norton Sound, Kuskokwim R, Yukon R, Bristol Bay, SE AK, BC, Salish Sea, WC
Coho	Biennial	Biennial, –	Biennial, –		Biennial, –						W NP, GOA, Salish Sea	SE AK, Kuskokwim R, Russia, SOG
Chinook	Biennial	Biennial, –	–		Biennial, –	Biennial, –	–				NP, BS, Salish Sea	Kamchatka R, Yukon R, Kuskokwim R, Nushagak R, Columbia R, Central AK, SE AK, Salish Sea, AK, BC, WA, OR
Steelhead	–	–			–	Biennial, –					NP	Thompson R, Keogh R, Chilcotin R (BC), Columbia R
Pink	Biennial					Biennial and cyclic					NP, BS, Salish Sea, PWS	Russia, Japan, AK BC, WA
Seabirds												
NH Seabirds	Biennial		Biennial, –	Biennial, –	Biennial, –				Biennial, –	Biennial, –	BS, AI, GOA, PWS	Buldir I, Chowiet I, Pribilof Is, PWS
SH Seabirds						Long-term, –				Biennial, –	BS	Australia, Tasmania
Whales												
Humpback whale				Biennial							SE AK	SE AK
Killer whale				Biennial	Biennial					Biennial	Salish Sea	Salish Sea / WC

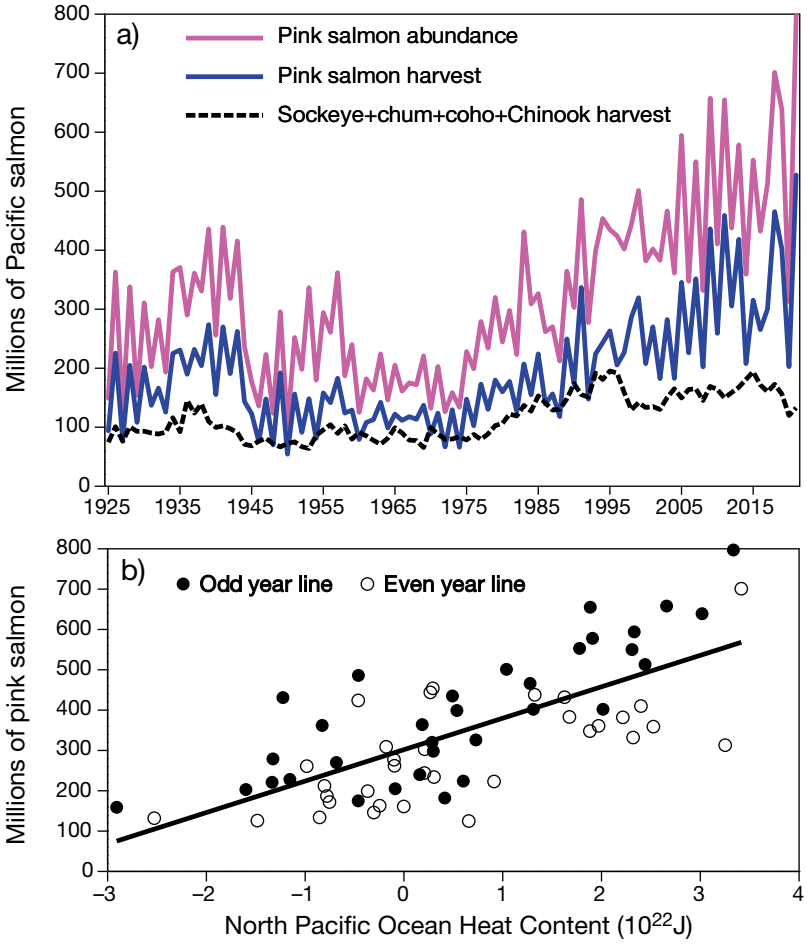


Fig. 1. (a) Annual abundance of adult pink salmon (catch plus spawners) returning from the North Pacific Ocean; commercial harvest of pink salmon; and the combined commercial harvest of sockeye, chum, coho, and Chinook salmon in Asia and North America, 1925–2021 (Ruggerone & Irvine 2018, Ruggerone et al. 2021, NPAFC 2022a). (b) Relationship between pink salmon abundance (odd and even years combined) and annual heat content for the North Pacific Ocean (0–700 m) during the year of juvenile pink salmon entry to the ocean, 1955–2021 (linear regression, df = 1, 65, $p < 0.001$, $R^2 = 0.51$; updated from Radchenko et al. 2007, NOAA 2022)

the Ocean Heat Index in the year they go to sea and adult abundance in the following year (Fig. 1b), and the use of ocean temperature to forecast adult returns (Radchenko et al. 2007, Krovnin et al. 2021, Bugaev et al. 2022). Pink salmon numbers are increasing in the Arctic (Dunmall et al. 2016, Farley et al. 2020), and they recently colonized the North Atlantic Ocean and Barents Sea following intentional stocking by Russia in the White Sea region (Sandlund et al. 2019, Diaz Pauli et al. 2023, Lennox et al. 2023).

Pink salmon have a fixed 2 yr anadromous life cycle in which they spawn in rivers during summer and fall, emerge as fry and emigrate to sea in spring, migrate over 5500 km, and then return to spawn and die after 1 winter at sea (Heard 1991). Odd- and even-year lines are separate, genetically isolated populations. Most notably, they have a unique, exaggerated biennial pattern of abundance in many regions of the NPO. For example, pink salmon sampled in the central BS were approximately 25 times more abundant in odd years than in even years during 1990–2010 (Davis 2003, Morita & Fukuwaka 2020). Potential mechanisms supporting the biennial fluctuations include negative interactions between odd- and even-year lines at sea and in fresh water (Heard 1991), and genetic adaptations of the odd-year line to warmer spawning temperatures (Beacham & Murray 1988).

Growth of pink salmon is relatively slow during the first 8 mo at sea but accelerates after winter, leading to prodigious consumption to fuel a rapid 5-fold increase in body weight by the time they spawn in summer to early fall (Heard 1991, Karpenko & Koval 2012). In the ocean, young pink salmon feed on various zooplankton species, primarily large calanoid copepods and euphausiids, and increasing amounts of squids and forage fishes as they grow (Brodeur 1990, Karpenko et al. 2007, Davis et al. 2009, Graham et al. 2021). Pink salmon <500 g consume zooplankton and small fishes; those >500 g consume zooplankton, fishes, and juvenile squid; and those >1000 g also consume adult squid (*Berryteuthis anonychus*) in spring and summer after overwintering at sea (Davis 2003, Aydin et al. 2005, Shaul & Geiger 2016). Their forage demand during 2005–2021 averaged approximately 4.35×10^6 Mt yr^{-1}, based on the methodology of Cooney & Brodeur (1998) and updated abundance values. About 90% of the forage demand occurs in oceanic rather than coastal habitats, especially during their second spring/summer at sea when they consume squid and small fishes and grow rapidly. A key question given such high consumption is whether the bottom-up processes supporting pink salmon are sufficient to also support other marine species.

Scientists have searched for biennial patterns in atmospheric and physical oceanographic variables

that might underpin the biennial patterns observed and summarized here, but none have been found. Physical variables that have been associated with interannual and decadal-scale changes in primary, secondary, and/or tertiary production — Northern Hemisphere Zonal Index, solar radiation flux, surface wind speed, sea surface temperature (SST), salinity, density, nutrient levels, integrated mean water column temperature, average winter sea ice extent in the BS, vertical stability index, North Pacific Index, North Pacific Gyre Oscillation, Pacific Decadal Oscillation, and Southern Oscillation Index — have displayed no systematic biennial variability (e.g. Polovina et al. 1995, Mantua et al. 1997, Shiomoto et al. 1997, Sugimoto & Tadokoro 1997, Kobari et al. 2003, Brown et al. 2011, Jorgensen 2011, Litzow et al. 2020a, Thoman et al. 2020, Belkin & Short 2023). Recently, Ohlberger et al. (2023, their Fig. 5g) presented a time series of average summer SST in the BS between 1962 and 2020 that revealed a weak biennial pattern in 1976–1998. Since then, summer SST has been highly irregular between years, unlike the highly regular biennial patterns in biological variables we summarize here.

3. THE EVIDENCE

3.1. Pelagic trophic cascades

Evidence of trophic cascades in open ocean ecosystems is uncommon, although here we document 5 compelling examples, linked to pink salmon, from the NPO and BS spanning multiple decades. The cascades flow downward from pink salmon to large copepods to diatoms: diets of pink salmon include large copepods, primarily *Neocalanus* spp., that consume diatoms in the BS (Davis et al. 2005, Karpenko et al. 2007, Campbell et al. 2016).

In the most recent example, Batten et al. (2018) used continuous plankton recorder data to develop indices of abundance of phytoplankton (primarily large diatoms) and zooplankton (primarily large calanoid copepods) in the BS and Aleutian Islands region during summer, 2000–2014. Three lines of evidence suggested that predation by maturing pink salmon during spring and summer altered the abundance of large copepods, which in turn altered the abundance of diatoms. First, copepods were less abundant and diatoms more abundant in odd years of higher pink salmon abundance (Fig. 2a–c). Second, diatom abundance was negatively correlated with copepod abundance, and copepod abundance was negatively correlated with adult pink salmon abundance (Fig. 2d–f). Third, in 2013, when pink salmon abundance was exceptionally low for an odd year, copepod abundance rebounded to high levels that year and diatom abundance was low (Fig. 2a–c). Evidence for a trophic cascade was strong in both the southcentral BS and eastern Aleutian Islands region, although reduced or absent in the western Aleutian Islands. These findings illustrate the importance of variability in pink salmon abundance and its effects across the ecosystem, which in that study was greater than physical oceanographic variability, according to the authors.

Earlier studies also found evidence of direct effects of pink salmon on summer plankton standing stocks in the central subarctic NPO and the eastern BS. Sugimoto & Tadokoro (1997) reported negative correlations between zooplankton biomass anomalies and Asian pink salmon abundance, and between chlorophyll *a* (chl *a*) concentration (a proxy for phytoplankton biomass) and zooplankton, during 1954–1981. They suggested that top-down predation by pink salmon increased interannual variations in zooplankton and in turn phytoplankton, whereas bottom-up factors were more important at decadal or longer scales. Toge et al. (2011) also reported a positive correlation between chl *a* concentration in the central BS and regional pink salmon abundance during 2002–2008 while noting the apparent trophic cascade through zooplankton.

Pink salmon are usually, but not always, more abundant in odd than even years, and plankton communities reflect those shifts in abundance. Shiomoto et al. (1997) quantitatively sampled pink salmon in the BS, and macrozooplankton (mostly copepods) and chl *a* just south of the central Aleutian Islands during 1985–1994. Early in their research (1985–1988), few differences existed between even- and odd-year pink salmon numbers, macrozooplankton biomass, or chlorophyll concentrations. However, beginning in 1989, odd-year pink salmon abundance and chl *a* notably increased while odd-year macrozooplankton biomass declined. We found negative correlations between the estimates of Shiomoto et al. (1997) of maturing pink salmon abundance and macrozooplankton biomass (Pearson's correlation, $p = 0.040$), and between their macrozooplankton biomass and chl *a* levels ($p = 0.086$). The authors also reported that zooplankton biomass in the central NPO remained low throughout summer of odd years after maturing pink salmon had migrated into the BS, an observation that is consistent with relatively low summer/fall marine scale growth of Bristol Bay sockeye salmon *Oncorhynchus nerka* in odd years (Ruggerone et al. 2005).

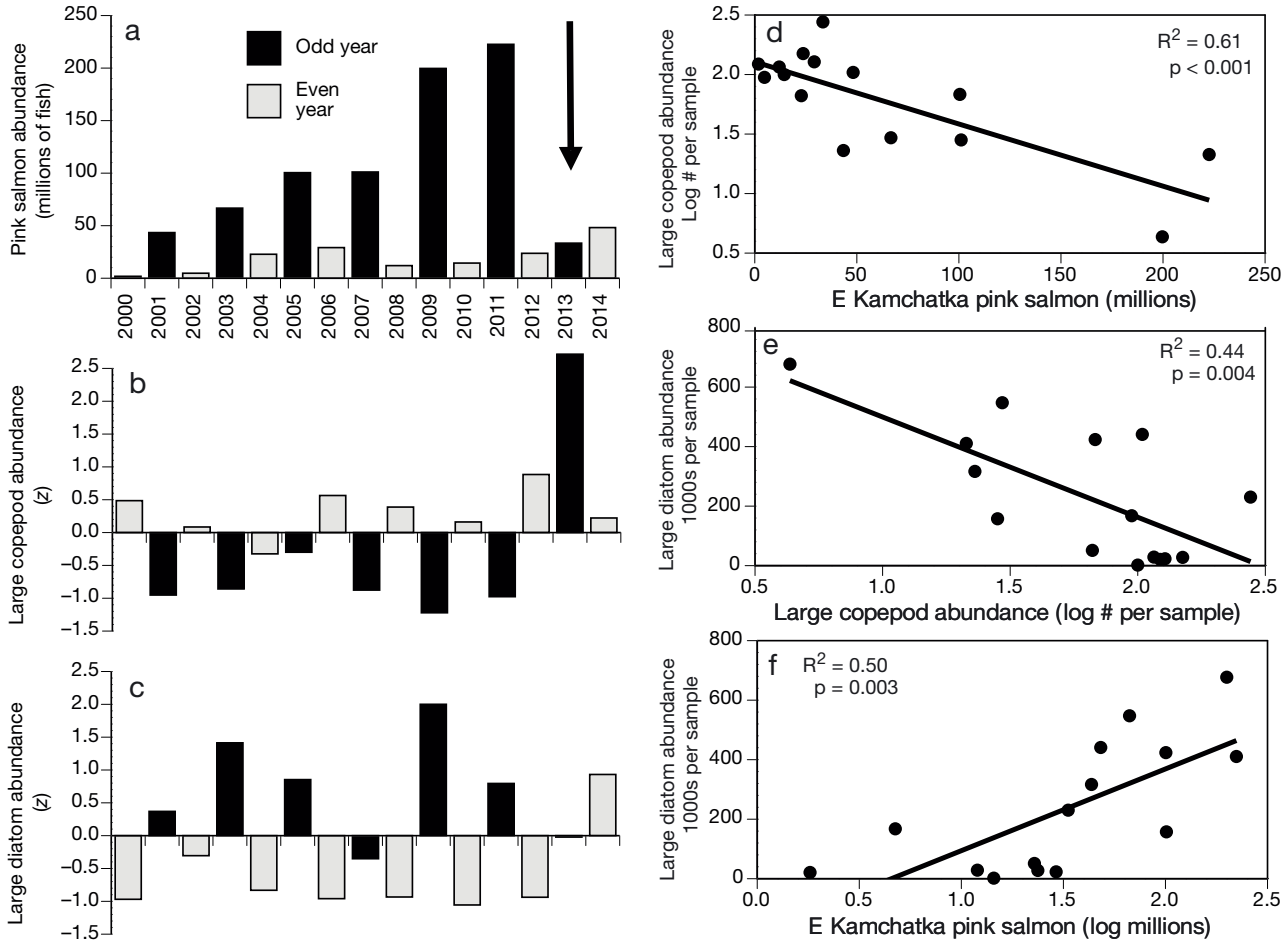


Fig. 2. Three lines of evidence supporting the pink salmon trophic cascade hypothesis in the southern Bering Sea and Aleutian Islands. (a) Biennial pattern of eastern Kamchatka pink salmon, the primary population in this region. (b) Normalized abundance of large copepods. (c) Normalized abundance of large diatoms. (d) Relationship between abundances of eastern Kamchatka pink salmon and large copepods. (e) Relationship between abundances of large copepods and diatoms. (f) Relationship between abundances of eastern Kamchatka pink salmon and large diatoms in 2000–2014. In 2013 (arrow in panel a), pink salmon abundance declined sharply, zooplankton abundance increased substantially, and diatom abundance declined. In 2014, diatom abundance was high for an even year, possibly in response to the marine heatwave that was occurring at the time (DiLorenzo & Mantua 2016). Redrawn from: Batten et al. (2018)

The trophic cascade described here requires tight coupling between phytoplankton and zooplankton, such that changes in the standing stock and grazing pressure by the herbivorous zooplankton have measurable effects on phytoplankton abundance. It then would be expected that in even years of relatively low pink salmon abundance, and thus higher copepod abundance, food limitation might have consequences for copepod growth and body size. A 20 yr study from 1979 to 1998 identified biennial patterns in the abundance of *Neocalanus cristatus*, *N. plumchrus*, and *N. flemingeri* in the central subarctic Pacific and attributed them to pink salmon predation (Kobari et al. 2003). Notably, they also documented biennial patterns in the growth of those copepods, with growth higher in odd years of lower copepod abundance. In addition, they found a positive correlation between body size of *N. cristatus*, the largest of the 3 species, and chl *a* concentration.

3.2. Forage fishes

3.2.1. Pacific herring

As with many forage fishes, Pacific herring *Clupea pallasii* are widely distributed and highly important to marine ecosystems (Surma et al. 2018). Herring are also important to Indigenous people and subsistence fishermen (Thornton & Moss 2021), and they support commercial fisheries.

Sitka Sound, Alaska, has one of the largest herring populations in North America. We found that herring

growth (proportional increase in mean annual body weight) was lower in 5 adult herring age groups when emigrating from Sitka Sound in the spring of odd years and returning in the following even years compared with those emigrating in even years, 1996–2018 (Fig. 3a). The magnitude of year-to-year variation in herring growth was negatively correlated with that of adult pink salmon abundance (Prince William Sound [PWS], Southeast Alaska (SEAK), and BC stocks) for each herring age group, especially younger fish (Fig. 3b). Adult herring emigrate from Sitka Sound in spring after spawning and feed in offshore continental shelf waters, possibly from PWS to BC (D. Hay pers. comm.), where in odd years they may encounter fewer zooplankton prey during spring, summer, and fall as a result of

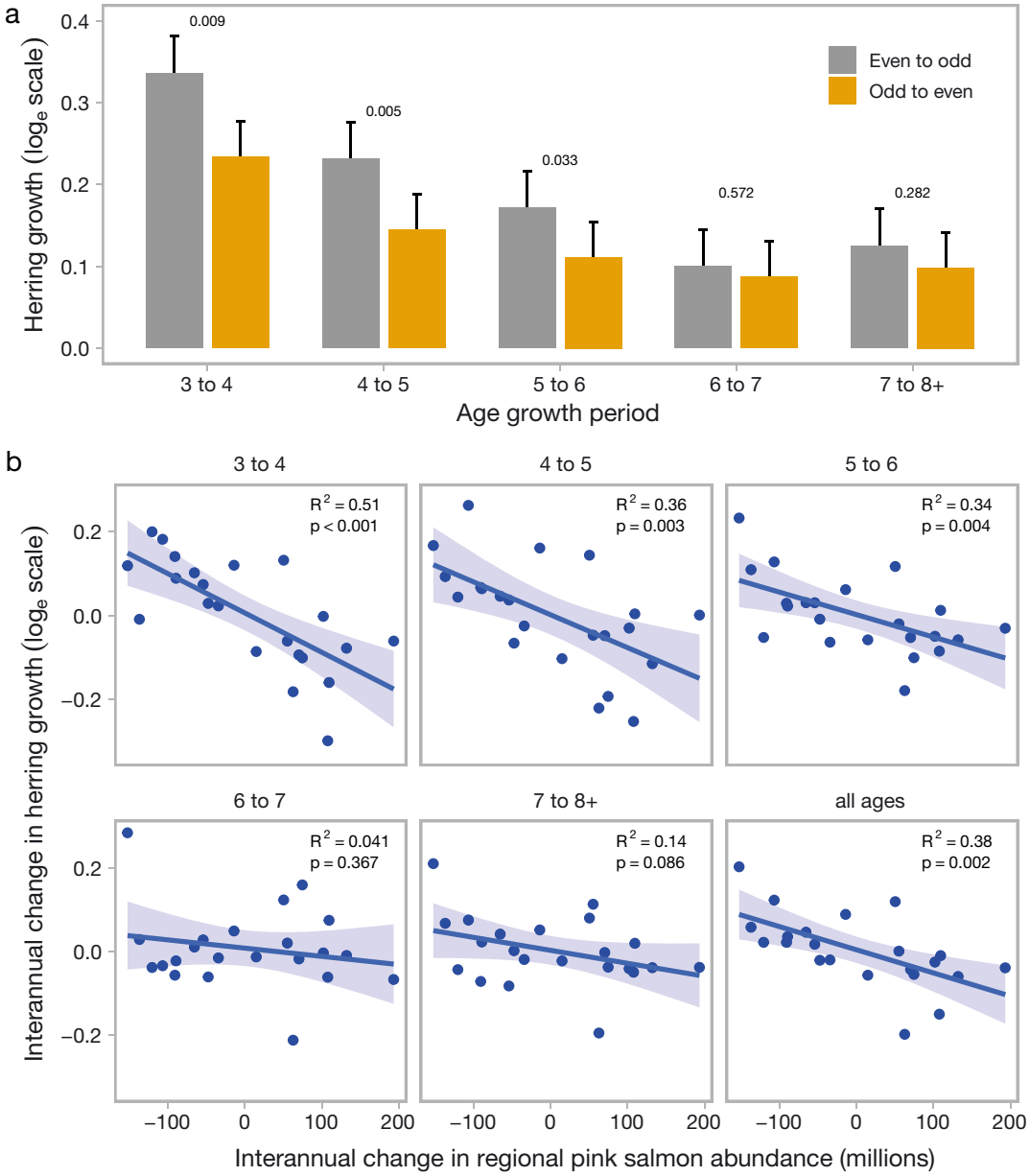


Fig. 3. (a) Biennial pattern in age-specific annual proportional increase in mean weight (growth index, ±95% CI) of adult herring returning to Sitka Sound, Alaska, from 1996 to 2018; and (b) relationships between the magnitude of year-to-year variation of age-specific mean growth of herring and the magnitude in year-to-year variation in abundance of pink salmon returning to North America, where interannual change (G) in year $i = G_i$ – avg. (G_{i-1}, G_{i+1}). In panel (a), 'Even to odd' refers to proportional growth from even to odd years (e.g. $\log_e$[weight-at-age in year t+1/weight-at-age in year t]); t-test p-values are shown above each growth period in (a), and linear regression statistics are shown in panel (b). Herring weight-at-age measured in the commercial fishery prior to spawning. Data sources: S. Dressel unpubl. data, Hebert (2019), Ruggerone & Irvine (2018)

numerous maturing pink salmon. These relationships were weaker during the previous 16 yr period (not shown), possibly because several year classes failed to produce many herring and because the magnitude of variation in pink salmon abundance was smaller.

In PWS, herring recruitment declined sharply after the 'Exxon Valdez' oil spill in 1989, and the population has yet to recover, leading to several studies of factors inhibiting recovery. A statistical examination of 19 hypotheses for the lack of recovery and subsequent analyses found competition with hatchery pink salmon (up to 600 million released per year) had the greatest support (Deriso et al. 2008, Pearson et al. 2012). This conclusion was based on the large reduction in herring spawning biomass associated with hatchery releases, sympatry of pink salmon fry and age-1 herring in nearshore habitats during late spring and summer, diet overlap, and field studies indicating reduced food intake by juvenile herring in the presence of juvenile pink salmon. Other studies have found equivocal support for this hypothesis, but recommended further study of pink salmon effects on the PWS food web (Cooney 1993, Ward et al. 2017, 2018).

3.2.2. Sand lance

Sand lance *Ammodytes personatus* recruitment and abundance in the Salish Sea were 13 times higher in odd versus even years, corresponding with the strong biennial pattern of pink salmon (Baker et al. 2019). In this region, maturing pink salmon are approximately 45 times more abundant in odd years, leading to exceptionally high abundances of juvenile pink salmon in the following even year that may reduce sand lance prey (Osgood et al. 2016, Sisson & Baker 2017).

3.2.3. Atka mackerel

Atka mackerel *Pleurogrammus monopterygius* are important prey of Pacific salmon and other fishes, marine birds, and marine mammals and the target of a commercial fishery in the Aleutian Islands (Davis 2003, Lowe et al. 2018). Atka mackerel feed heavily on *Neocalanus* spp. and euphausiids (Yang 1999, 2003, Rand et al. 2010), a diet that overlaps extensively with that of pink salmon.

Matta et al. (2020) found a conspicuous biennial pattern in the growth of Atka mackerel otoliths (an index of annual body growth; Fig. 4): a Pearson's negative correlation between otolith growth and the abundance of eastern Kamchatka pink salmon ($p = 0.005$), and a positive correlation between otolith growth and the abundance of large copepods ($p = 0.023$). The abundance of large copepods in the region of their study was negatively related to pink salmon abundance ($p = 0.002$).

3.2.4. Pacific Ocean perch

Pacific Ocean perch (POP) *Sebastes alutus* is a long-lived, commercially important rockfish that mainly occupies continental slope and shelf habitats from California to Japan (Hulson et al. 2021). POP are considered to be semi-demersal, but limited sampling at sea indicates larvae and juveniles inhabit

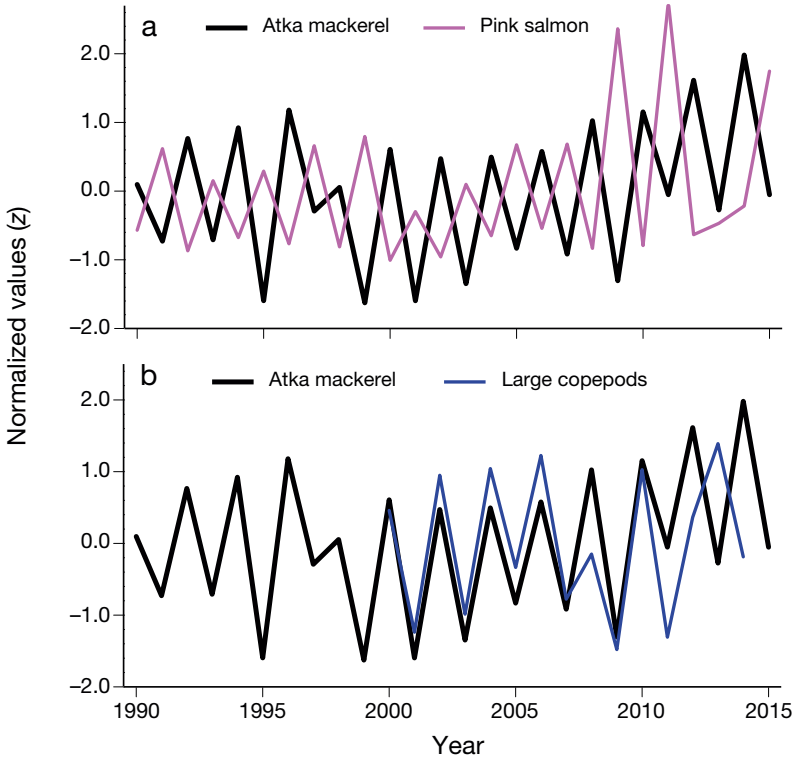


Fig. 4. Relationships between anomalies in otolith growth of Atka mackerel and (a) the normalized abundance of eastern Kamchatka pink salmon (negative), and (b) the abundance of large copepods (positive) in the central Aleutian Islands. Pink salmon data from Ruggerone & Irvine (2018); Atka mackerel and large copepod data from Matta et al. (2020) and M. Matta and S. Batten, with permission

epipelagic waters far from adult habitats (Kendall et al. 2007, Boldt & Rooper 2009). Juvenile POP primarily consume copepods.

We analyzed age-2 POP recruitment estimates from the GOA (Hulson et al. 2021) and found a pronounced biennial pattern from 1999 through 2019, corresponding to a period of relatively high POP abundance and high interannual variation in numbers of pink salmon returning to North America (Fig. 5). Age-2 POP recruits (typically <160 mm) averaged 45% fewer fish in odd (101 million fish) versus even years (183 million fish) during 1999–2019, suggesting a negative interaction with pink salmon during the growing season (Fig. 5), even though abundances of both species increased after 1977. Over the 43 yr period 1977–2019, approximately 50% of the interannual variability in age-2 POP abundance was explained by interannual variation in the abundance of pink salmon, which also consume copepods, and POP female spawning biomass 2 yr earlier (Fig. 5). Ortiz & Zador (2022) also reported that POP recruitment in the Aleutian Island region exhibited a biennial pattern; abundances of age-3 POP were often higher in odd years.

3.3. Squid

Subadult and adult squid are highly important prey of many fishes, birds, and marine mammals in the NPO (Aydin 2000). For example, large proportions of salmonid diets were squid (subadult and adult *Berryteuthis anonychus*, <150 mm) in the Subarctic Current region of the GOA during 1994–1998: e.g. pink (40–80% of prey weight), sockeye (>85%), coho *O. kisutch* (>95%), and Chinook salmon *O. tshawytscha* (100%), and steelhead *O. mykiss* (50–100%) (Kaeriyama et al. 2004). Bioenergetic modeling indicated a substantial increase in salmon growth when consuming high-energy *B. anonychus*, which is especially important to maintaining growth as temperature increases (Aydin 2000), particularly among larger salmon (Beauchamp 2009). *B. anonychus* is the most abundant squid in the GOA and is distributed primarily south of 53° N and west from North America to about 160° W.

The primary effect of pink salmon on *B. anonychus* abundance appears to be via predation on subadults and adults, rather than competition with juveniles for prey (Shaul & Geiger 2016). In the northwestern GOA, the abundance of *B. anonychus* paralarvae

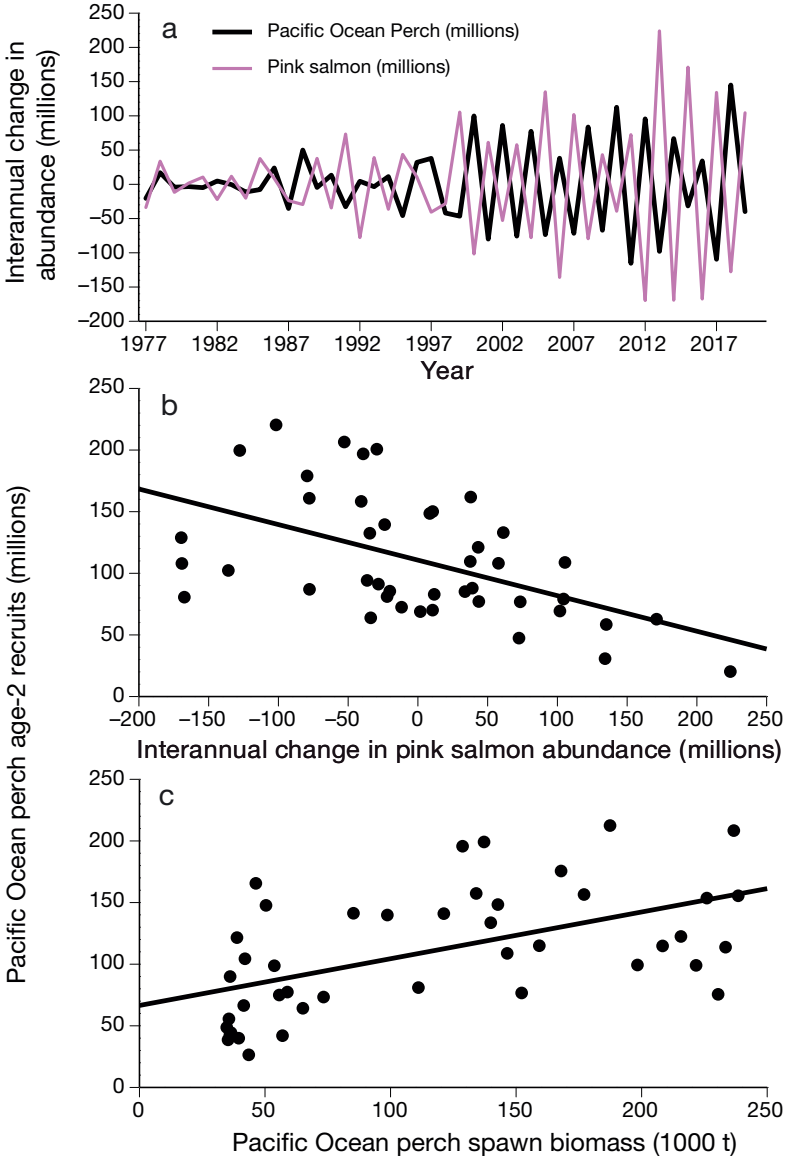


Fig. 5. (a) Interannual change in abundances of age-2 Pacific Ocean perch (POP) in the Gulf of Alaska and pink salmon returning to North America during 1977–2019; and regression-corrected plots of (b) age-2 POP recruits in relation to interannual change in abundances of North American pink salmon ($p < 0.001$) and (c) age-2 POP recruits in relation to the parent spawning biomass ($p = 0.019$). Cochrane-Orcutt multiple regression accounted for autocorrelation ($R^2 = 0.50$; overall df = 2, 39; $p < 0.001$). Interannual change in abundance (A) in year $i = A_i$ – avg. (A_{i-1}, A_{i+1}). Data source: Hulson et al. (2021)

was negatively correlated with maturing pink salmon abundance during the previous year, as expected from predation by maturing pink salmon on the parent squid (r = −0.55, p = 0.009, Jorgensen 2011). Over a 19 yr period, paralarvae were 95% less abundant in even versus odd years, leading to fewer adult squid in the following odd year (Jorgensen 2011). Jorgensen (2011) could not explain the biennial pattern using oceanographic variables. *B. anonychus* appears to have a 2 yr life cycle, which leads to a strong and consistent biennial cycle when combined with predation by biennial pink salmon. In odd years when pink salmon are highly abundant, squid are less common in diets of all salmon species in the BS (Fig. 6) and the Alaska Gyre in the GOA (Aydin 2000, Kaeriyama et al. 2004).

B. anonychus are critical prey for marine fishes, birds, and mammals, such that substantial predation by pink salmon on squid, as in spring and summer of odd years, can reverberate through the offshore ecosystem (Aydin 2000). Furthermore, the 2 yr lifespan of *B. anonychus* and predation on them by biennially-abundant pink salmon sustains and perhaps exacerbates biennial patterns in squid abundance.

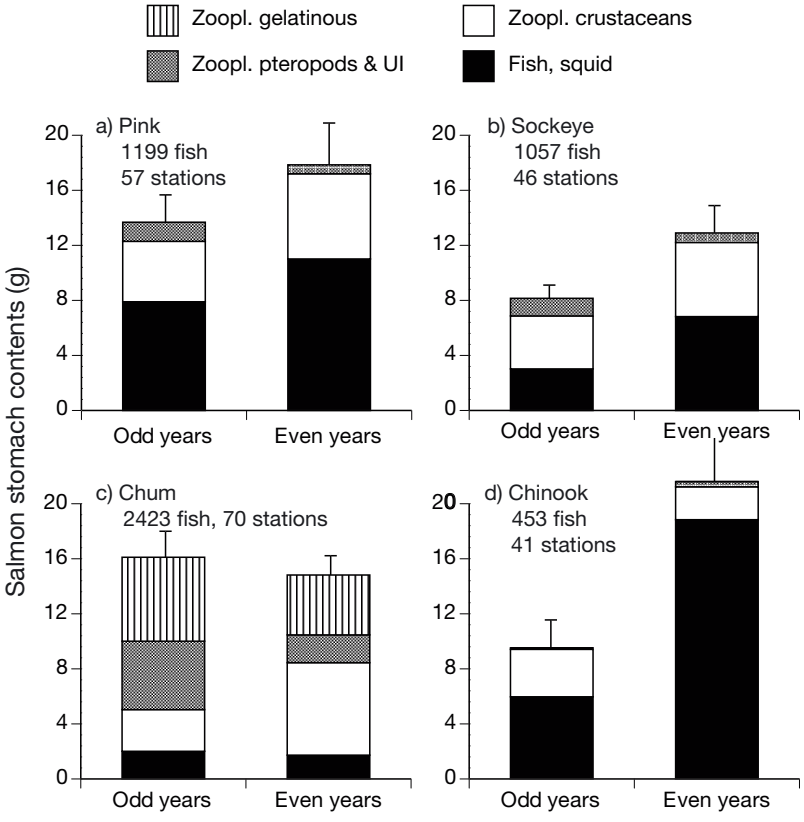


Fig. 6. Mean weights of stomach contents from (a) pink, (b) sockeye, (c) chum, and (d) Chinook salmon sampled in the central Bering Sea during odd and even years, 1991–2000 (UI = unidentified). Error bars: SE. Data source: Davis (2003)

3.4. Pacific Salmon

Biennial variation in the abundance of pink salmon may lead to biennial feeding patterns by other species of Pacific salmon if they are out-competed for common prey, as detailed below. For example, in odd years when pink salmon are typically most abundant, Davis (2003) found that over a 10 yr period, Chinook, sockeye, and pink salmon in the BS consumed fewer nutritionally valuable prey such as squid, fishes, and euphausiids, and all salmon species consumed more low-calorie prey than in even years (Fig. 6). Those high-quality prey are among the principal conduits of energy flow through pelagic food webs that include zooplankton, forage fishes, squids, salmon, seabirds, and marine mammals (Brodeur et al. 1999, Aydin 2000).

Stable isotope signatures of Chinook and coho salmon and steelhead have been used as evidence that they typically feed on higher trophic level prey than pink salmon, and thus there is little direct competition between them (Welch & Parsons 1993, Kaeriyama et al. 2004, Johnson & Schindler 2009). However, diet composition of pink salmon during the second year at sea is more accurate for identifying potential competition with salmon species that consume squid and fishes than stable isotope signatures, which fail to reflect the consumption of squid and fishes by pink salmon during their second year at sea when forage demand is especially great. Muscle isotope signatures require many months after a diet shift from plankton to fish and squid to be partially detected, and years to accurately reflect the new diet (e.g. Madigan et al. 2021; see Text S1 in Supplement 1 at www.int-res.com/articles/suppl/m719p001_supp1.pdf).

3.4.1. Sockeye salmon

Sockeye salmon migrate long distances during their 2 or 3 yr at sea where they can interact with nearby and distant populations of pink salmon. For example, Bristol Bay sockeye

salmon range from the Kamchatka Peninsula to Kodiak Island (Myers et al. 2007, Habicht et al. 2010, Espinasse et al. 2020), and ocean age-1 Fraser River, BC, sockeye salmon have been observed in the central NPO (176.2° E) approximately 4000 km from their natal river (Neville & Beamish 2022).

Among Pacific salmon species, sockeye salmon have the greatest diet overlap with pink salmon (Brodeur 1990, Kaeriyama et al. 2000, Qin & Kaeriyama 2016). Both species are primarily planktivores, but each can switch to higher trophic level prey such as small fishes and squid as they grow in their second season at sea. During a 10 yr study in the central BS (52–58° N), the diet of sockeye salmon averaged 47% fish and squid, 44% zooplankton, and 9% other prey by weight (Fig. 6). However, in odd years, when pink salmon were approximately 40 times more abundant, total prey weight consumed per sockeye salmon declined 36% versus only 23% among pink salmon. In odd years, the consumption of energy-rich fishes and squid declined 50 to 58% in sockeye salmon, respectively, but only 25 to 32% in pink salmon (Fig. 6; Davis 2003). Likewise, in odd years, consumption of higher caloric-value euphausiids and copepods declined 46 to 50% in sockeye salmon compared with only 37 to 48% in pink salmon, respectively. In contrast, lower caloric-value pteropods and amphipods increased in diets of both sockeye (13%) and pink salmon (72%) in odd years. These data suggest that pink salmon were able to consume fishes, squid, and energy-rich zooplankton more effectively than sockeye salmon when availability of these key prey was limited (Ruggerone et al. 2003).

In the western NPO, only trace amounts of squid were observed in the stomachs of sockeye and pink salmon during odd years, whereas both species contained 50 times more squid by weight in even years during 1956–1963 (Ito 1964). This observation, which preceded the large increase in pink salmon abundance after the 1977 regime shift, occurred when Asian pink salmon abundance averaged 67% more fish in odd (200 million) versus even years (120 million; Ruggerone & Irvine 2018).

Despite the tremendous amount of research on sockeye salmon over the past 75 yr, and the odd–even year differential in consumption of squid noted above, interactions between them and pink salmon were largely unknown until the early 2000s (Peterman 1982, Bugaev et al. 2001, Ruggerone et al. 2003). In the past 20 yr, however, a growing body of evidence indicates that pink salmon influence the growth, age, survival, and abundance of sockeye salmon throughout their range in North America.

A quantitative analysis of 47 sockeye salmon populations, representing approximately 90% of all sockeye salmon ranging from the Fraser River in southern BC to the Kuskokwim River region in southwestern Alaska, found strong associations between sockeye salmon productivity ($\log_e$ recruits per spawner) in brood years 1976–2009 and NPO pink salmon abundance and SST during early life at sea (Connors et al. 2020). Based on these relationships, it was estimated that a 119 million increase in pink salmon abundance (i.e. 1 SD above the mean) was associated with a 9% decline in sockeye salmon productivity in the BS and the GOA, and a 21% decline in productivity in BC and SEAK (Fig. 7a), whereas a 1.5°C increase in SST (1 SD) was associated with a 23% increase in sockeye salmon productivity in the BS and a 9% increase in the GOA, but with a 12% decline in BC and SEAK. The mean annual return of approximately 82 million hatchery pink salmon during 2005–2015 was estimated to reduce sockeye salmon productivity by 5% in the BS, 6% in the GOA, and 15% in BC and SEAK.

Sockeye salmon have a diverse life history, especially in northern areas, that can mask detection of biennial pink salmon effects. Sockeye salmon typically enter the ocean after spending 1 or 2 winters in freshwater, then return to their natal rivers to spawn after 2 or 3 winters at sea, thereby encountering both odd-year (abundant) and even-year (few) pink salmon. Therefore, age-specific analyses of sockeye salmon are often needed to unravel the apparent effects of pink salmon on sockeye salmon growth, age-at-maturation, survival, and abundance.

Analyses of annual and seasonal sockeye salmon scale growth at sea revealed strong interactions with pink salmon. For example, over a 43 yr period, odd-year scale growth of Bristol Bay sockeye salmon averaged 6.2 and 10% less than adjacent even-year growth during the second and third years at sea, respectively (Fig. 8a; Ruggerone et al. 2003, 2016a). Scale growth declined with increasing abundances of pink salmon returning to Russia (the primary overlapping population), explaining 33 and 58% of second- and third-year scale growth variability, respectively, during 1965–2009 (Fig. 8b; Ruggerone et al. 2016a). Analysis of seasonal scale circuli measurements indicated that the biennial divergence in sockeye salmon growth began in early spring (third season at sea) or late spring (second season at sea) and continued through summer and fall; no biennial pattern was detected during winter when most pink salmon were distributed farther south than

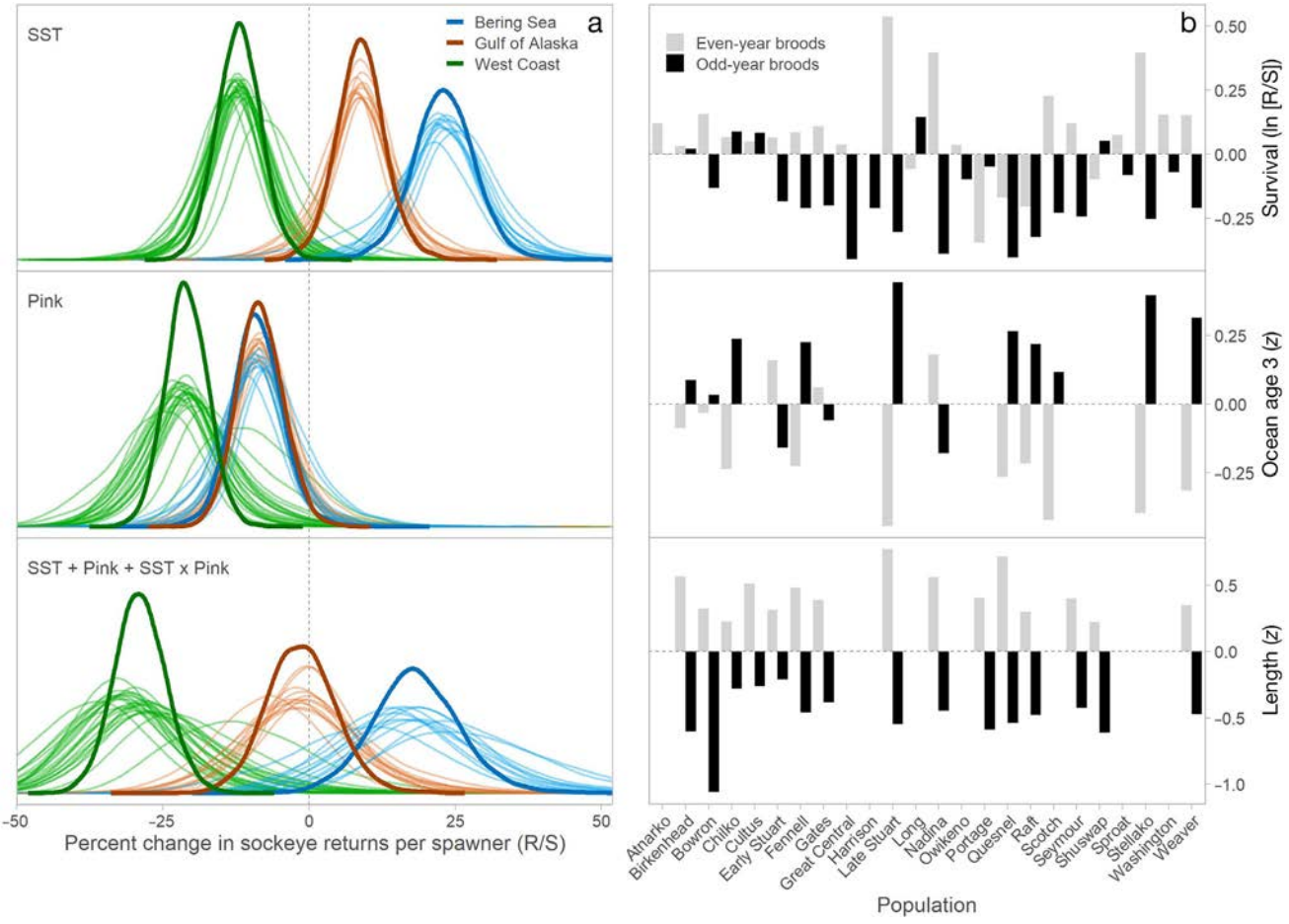


Fig. 7. (a) Posterior probability distributions of the predicted effect of sea surface temperature (SST; top), pink salmon competitors (middle), and the combined effect from all covariate terms (bottom), on survival of 47 sockeye salmon populations originating from the Bering Sea, Gulf of Alaska, and west coast of North America (Southeast Alaska and British Columbia). Posterior hyperdistributions of the covariate effects are in bold lines, with individual stock-specific posterior distributions illustrated by the thin lines. Covariate effects are standardized (i.e. per standard deviation unit increase in each covariate), which equates to 1.5°C SST and 119 million pink salmon above the mean. (b) Mean survival (top), proportion of ocean age-3 sockeye salmon in the adult return (middle), and length-at-age of 24 sockeye salmon populations from British Columbia and Washington state during odd- versus even-numbered brood years, 1978–2005 (bottom). Values are normalized (z) relative to the entire data time series, except survival, which is the mean residual ($\log_e$ recruits per spawner) from the recruitment relationship. Data sources: Ruggerone & Connors (2015), Connors et al. (2020)

sockeye salmon (Ruggerone et al. 2005). Biennial patterns in sockeye salmon scale growth were not observed during the first year at sea or during the homeward migration, presumably because abundance of pink salmon is low in Bristol Bay (Ruggerone & Irvine 2018). Biennial scale growth of sockeye salmon returning to watersheds in the GOA region (Chignik, Cook Inlet, PWS, Copper River, and SEAK) was also observed during the second and third years at sea (low growth in odd years), but not consistently during the first year at sea (P. Rand & G. Ruggerone unpubl. data).

Size-at-age of returning Bristol Bay sockeye salmon was negatively correlated with both abundance of Russian pink salmon during the year prior to return and abundance of Bristol Bay sockeye salmon during the year of return, 1958–2003 (Ruggerone et al. 2003, 2007). Eight sex- and age-specific statistical models explained on average 45% of the variability in adult sockeye salmon length. The models indicated that competition with pink salmon reduced the length of female sockeye salmon more than that of males, suggesting a possible adverse effect on future abundance because salmon fecundity is associated with body size (Quinn 2005). A recent analysis of Bristol Bay sockeye salmon size-at-age over a 60 yr period, which considered SST, also found that pink and sockeye salmon abundance had the greatest ex-

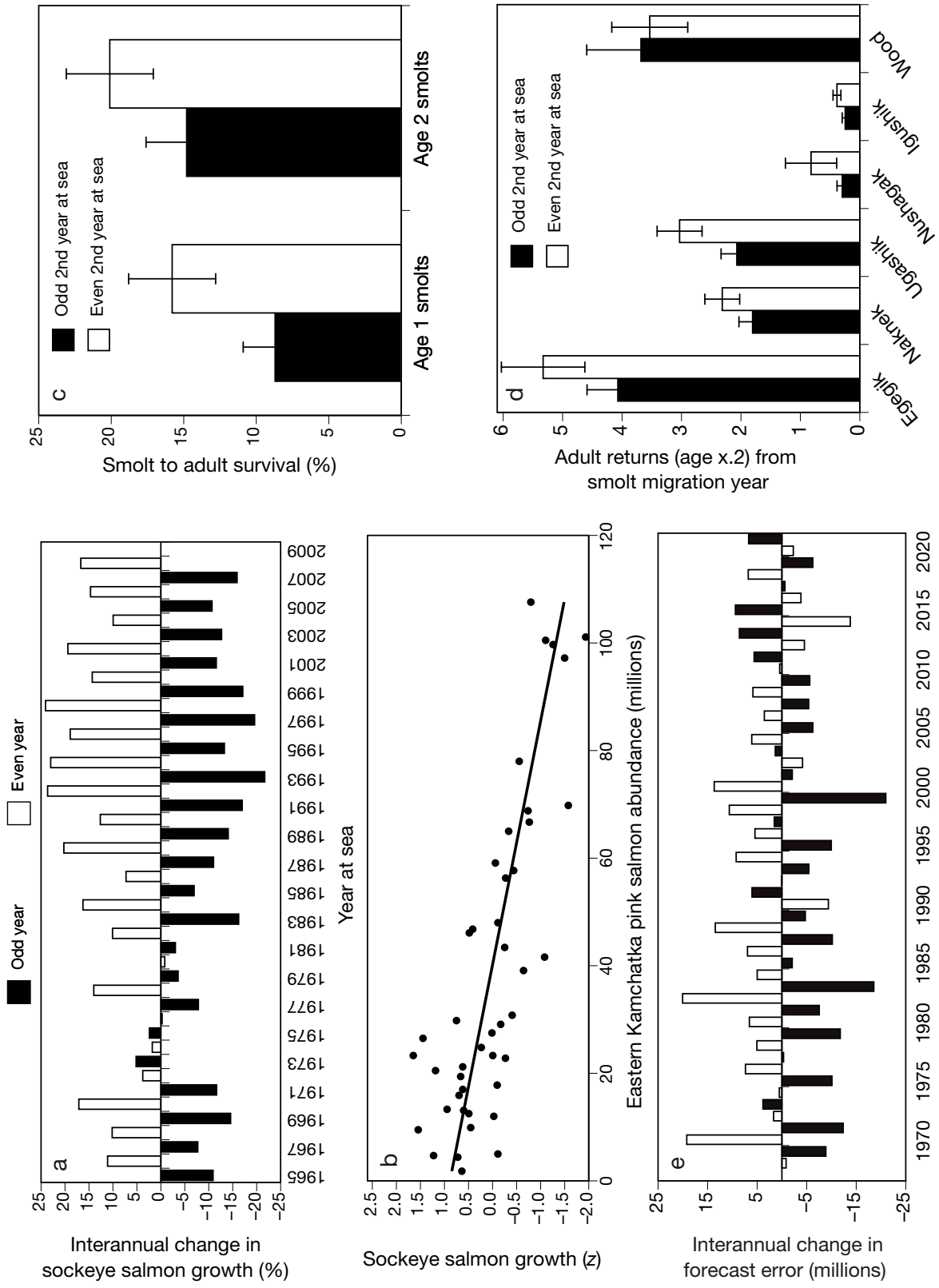


Fig. 8. Examples of biennial patterns and correlation analyses among Bristol Bay sockeye salmon (a,b) testing the hypothesis that pink salmon affect sockeye salmon growth at sea, (c) smolt to adult survival, (d) adult returns from smolt migrations, and (e) adult sockeye salmon forecast error, 1968–2021. Interannual change in scale growth or forecast error (G) in year $i = G_i$ – avg. (G_{i-1}, G_{i+1}). Mean scale growth values in (a,b) represent Kvichak, Egegik, Naknek, Ugashik, and Wood River stocks during the third year at sea, 1965–2008. Second-year growth shows similar patterns (not shown). Smolt-to-adult survival (c) is the annual mean for Kvichak, Egegik, and Ugashik stocks, 1977–1997. Mean annual adult returns of ocean age-2 salmon (d) are from odd- or even-year smolt migrations, 1977–2019, excluding 1999 as an extreme outlier. Error bars are ±1 SE. Updated from Ruggerone et al. (2003, 2016a)

planatory power (Ohlberger et al. 2023). Oke et al. (2020) reported a negative correlation between body size of sockeye salmon in Alaska (128 populations, up to 60 yr) and the abundance of pink salmon in the NPO.

Smolt to adult survival of Bristol Bay sockeye salmon was significantly lower for fish entering the southeastern BS during even years compared with odd years, 1977–1997 (Fig. 8c, $p < 0.02$; Ruggerone et al. 2003). Specifically, smolt survival declined 35%, on average, when they entered Bristol Bay in even years and competed with highly abundant Russian pink salmon during their second year at sea (odd year). Survival of younger age-1.2 salmon declined 59% compared with 30% among age-1.3 and age-2.2 salmon and 19% among age-2.3 salmon that interacted with pink salmon in both odd (second year) and even (third year) years at sea.

Age-specific adult sockeye salmon returns to Bristol Bay from odd- versus even-year smolt migrations also revealed apparent interactions with pink salmon (Ruggerone et al. 2003). Adult returns of ocean age-2 sockeye salmon from 6 stocks declined 21%, or 3.3 million adults per even year, on average, in 1977–2019 when they competed with abundant odd-year pink salmon during their second growing season at sea (Fig. 8d). Ocean age-2 sockeye salmon primarily interacted with pink salmon during a single second year at sea, i.e. either abundant pink salmon in an odd year or few pink salmon in an even year. Adult returns of ocean age-3 sockeye salmon declined only 6% when emigrating in even years (odd second year) because ocean age-3 sockeye salmon interacted with both even- and odd-year pink salmon. Overall, during 1977–2019, approximately 85 million fewer adult sockeye salmon returned from even-year smolt migrations that encountered abundant pink salmon in the following year than from odd-year smolt migrations that encountered fewer pink salmon.

Interannual variation in forecast error (i.e. error relative to error during the 2 adjacent years) was used to further test the hypothesis that pink salmon affect the survival and abundance of Bristol Bay sockeye salmon (Ruggerone et al. 2016a). Forecast error of southeastern Bristol Bay sockeye salmon (Kvichak, Naknek, Egegik, and Ugashik stocks) was biased high during even-numbered years (avg. 4.0 million fish yr^{-1}), and biased low during odd-numbered years (avg. −3.9 million fish yr^{-1}), 1968–2021 (Fig. 8e). High-biased forecasts in even return years reflect interaction with abundant pink salmon during the previous odd year in which sockeye salmon growth is reduced (Fig. 8a,b); seasonal scale-growth measurements demonstrated little effect of pink salmon during the homeward migration (Ruggerone et al. 2005, 2016a). Likewise, low-biased forecasts in odd return years reflect interaction with fewer pink salmon and greater sockeye salmon growth during the previous even year (Fig. 8a,b). After standardizing forecast error relative to adjacent years, forecasts in even years were biased high in 63% of the years and biased low in 22% of the years. Interannual variation in forecast error increased with interannual variation in the abundance of eastern Kamchatka pink salmon during the previous year, 1968–2008 (linear regression, $p < 0.01$, $r = 0.41$, after accounting for autocorrelation). Forecast error was greater for ocean age-2 than for ocean age-3 sockeye salmon because age-2 sockeye salmon interact with either odd-year or even-year pink salmon, whereas age-3 sockeye salmon interact with both pink salmon lines (Ruggerone et al. 2016a). Interannual variation in forecast error shifted after 2009 (Fig. 8e), possibly reflecting an increase in the proportion of sockeye salmon spending 3 rather than 2 winters at sea in response to younger age of smolts (Nielsen & Ruggerone 2009, Cline et al. 2019) and the exceptional abundance of Bristol Bay sockeye salmon since 2014 (Ruggerone et al. 2021).

Interannual variation in forecast error of northwestern Bristol Bay sockeye salmon (Wood River, Nushagak, and Igushik stocks combined) was also biased high in even years (avg. 0.79 million fish yr^{-1}) and biased low in odd years (avg. −1.06 million fish yr^{-1}), 1968–2021. This pattern was not as consistent nor as strong as it was for the southeastern stocks, possibly reflecting the more easterly distribution of Wood River (Bristol Bay, Alaska) sockeye salmon in the NPO and less interaction with eastern Kamchatka pink salmon (Ruggerone et al. 2016a).

The annual return of sockeye salmon to Bristol Bay exceeded 50 million fish from 2015 to 2021 at the same time when pink salmon returns to Russia were exceptionally large (Ruggerone et al. 2021). We hypothesize that this counterintuitive relationship occurs because Bristol Bay sockeye salmon encounter few pink salmon during their first season at sea (Ruggerone et al. 2003, 2005, 2016a) and because both species in the north have benefited from recent marine heatwaves, especially during early life at sea (e.g. Ruggerone et al. 2005, 2007). Greater sockeye and pink salmon abundance, however, led to reduced growth during late life at sea and reduced adult size-at-age of sockeye salmon. Our findings suggest that early growth at sea is critical to salmon survival and subsequent abundance, but that reduced growth at later marine life stages can also affect survival,

although to a lesser extent. For Bristol Bay sockeye salmon, favorable early marine conditions have likely overwhelmed competition effects with pink salmon during the second and third seasons at sea (Connors et al. 2020).

This pattern of abundance is reversed among sockeye salmon in the south. Sockeye salmon in BC and SEAK have encountered unfavorable early and late marine conditions in recent decades, leading to declining survival and abundances (Connors et al. 2020). An analysis of up to 36 sockeye salmon populations from Puget Sound, WA, through SEAK during the past 55 yr revealed that high abundance of NPO pink salmon in the second year of sockeye salmon life at sea was associated with lower sockeye salmon productivity, reduced adult length-at-age, and delayed maturation (Ruggerone & Connors 2015). While accounting for SST, they predicted that an increase from 200 million to 400 million pink salmon would lead to a 39% reduction in productivity of Fraser River sockeye salmon, an estimate that is consistent with that of Connors et al. (2020). Furthermore, biennial patterns in sockeye salmon life history characteristics were significant: productivity was low, length-at-age was small, and age-at-maturation was delayed when sockeye salmon encountered highly abundant pink salmon (Fig. 7b). The greatest statistical support for models occurred when sockeye salmon were aligned to interact with immature pink salmon during their second season at sea and continued to interact with maturing pink salmon as they migrated to their natal river. Less support was found for negative interactions during the first season at sea. In contrast, McKinnell & Reichardt (2012) found some support for negative effects of juvenile pink salmon in northern BC on first-year scale growth of Fraser River sockeye salmon, but no support in the Strait of Georgia.

Several studies reported evidence for adverse effects of adult pink salmon on the growth and survival of juvenile sockeye salmon. Marine survival rate residuals of Babine Lake (Skeena River, BC) sockeye salmon were inversely related to the abundance of adult pink salmon returning to northern BC during the year of sockeye smolt emigration to sea in 1961–1977 (Peterman 1982). Sockeye salmon survival was positively correlated with juvenile pink salmon abundance in the year of outmigration. Thus, Babine Lake sockeye salmon may experience both compensatory and depensatory mortality in relation to pink salmon. In PWS, productivity of sockeye salmon returning to the Copper River, Coghill Lake, and Eshamy Lake in 1981–2011 was inversely related to abundance of returning hatchery pink salmon, but no effects were found on wild pink, chum *O. keta*, or Chinook salmon (Ward et al. 2017, 2018). In support of the competition hypothesis, Martinson et al. (2008) reported decreased scale growth of sockeye salmon emigrating from the Karluk River (Kodiak Island, AK) during years when large numbers of adult pink salmon returned to the same area, while providing some evidence for diet overlap between juvenile sockeye salmon and adult pink salmon.

Russia produces approximately 15% of the annual sockeye salmon returns from the NPO (Ruggerone & Irvine 2018). Bugaev et al. (2001) reported that the length and weight of sockeye salmon returning to the Ozernaya River (Kuril Lake, Kamchatka) during 1970–1994 was reduced in years when the ocean abundances of Kamchatka pink salmon were high. The effect of pink salmon abundance on sockeye growth was greater than that of sockeye salmon abundance, owing to the much higher abundance of pink salmon. Additional studies provided evidence that trophic competition between pink and sockeye salmon at sea influenced the growth of Russian sockeye salmon ([Krogius 1960, Birman 1985] in Bugaev et al. 2001). Sano (1963) found that both the size of sockeye and pink salmon caught in the western NPO and the average weight of their stomach contents were smaller in odd years, when pink salmon abundance was high.

3.4.2. Chum salmon

Chum salmon are highly abundant and widely distributed in the NPO (Myers et al. 2007). Most fish (60%) are from hatcheries in Japan, Russia, and Alaska (Ruggerone & Irvine 2018). They enter the ocean as young-of-the-year fry during spring and primarily consume zooplankton while typically spending 3 or 4 yr at sea (Graham et al. 2021). Their unusually large stomach is uniquely adapted to process large quantities of low-calorie gelatinous plankton (cnidarians, ctenophores, and salps), which is thought to be an evolutionary response to reduce competition with other salmon species, especially highly abundant pink salmon (Welch 1997).

Despite this adaptation, there is evidence for competition between chum and pink salmon. For example, in odd years when maturing pink salmon are highly abundant in the BS during June and July, zooplankton abundance has been found to be negatively correlated with pink salmon abundance (Section 3.1). Consequently, in odd years, chum salmon consumed 40% more low-calorie gelatinous zooplankton and

30% more pteropods, and 40% less high-calorie prey than in even years when few pink salmon were present, 1991–2007 (Fig. 6; Tadokoro et al. 1996, Davis 2003, Kaga et al. 2013). Furthermore, in odd years, the distribution of immature chum salmon shifts southeastward from the BS (e.g. a 50% reduction in abundance in the BS) to the eastern NPO, based on Japanese research in 1972–2000, presumably to find higher densities of prey (Azumaya & Ishida 2000, Davis 2003).

Besides changes in chum salmon diet and distribution, a number of studies reported additional effects of competition between chum and pink salmon. For example, chum salmon sampled in the BS exhibited reduced second- and third-year body growth, reduced condition factor, and lower gonad weight (maturity rate index) with increasing local abundance of pink salmon in the previous year, 1971–2010 (Morita & Fukuwaka 2020); slower growth was linked to delayed maturation (Morita & Fukuwaka 2007). Lipid content of chum salmon in the BS was negatively related to local pink salmon abundance (2002–2007) after accounting for chum salmon body size; pink salmon abundance had a greater effect on lipids than chum salmon abundance (Kaga et al. 2013). In the central NPO south of the Aleutian Islands (1959–1995), third-year scale growth of chum salmon was negatively correlated with abundance of Asian pink salmon (Walker et al. 1998). In the western NPO, prey weight consumed by chum salmon was 27% lower during odd years when maturing pink salmon were abundant (Sano 1963), and feeding rates of immature chum salmon near the Kuril Islands were lower in years of high juvenile pink salmon abundance (Ivankov & Andreyev 1971). However, Shuntov et al. (2017) argued that positive correlations over time between pink and chum salmon weights and pink and chum salmon numbers in the Sea of Okhotsk and the western BS were evidence that environmental factors drove size and abundance rather than competition for prey; there is considerable debate about how applicable those results are to other geographic regions (Shuntov et al. 2017).

Likewise in western Alaska, scale growth of Kuskokwim River (1968–2010), Yukon River (1965–2006), and Bristol Bay (1965–2006) chum salmon was negatively correlated with pink salmon abundance, especially during their third and fourth years at sea; these and other studies also considered oceanographic variables (Agler et al. 2013, Frost et al. 2021). Productivity of Norton Sound chum salmon was negatively correlated with Asian pink salmon abundance in addition to chum salmon abundance (Ruggerone et al. 2012). Scale growth of chum salmon returning to SEAK (1972–2004) and to southern BC (1971–2010) was negatively correlated with the abundance of pink salmon or pink and chum salmon (Yasumiishi et al. 2016), and to the combined biomass of pink, chum, and sockeye salmon during each year at sea (Debertin et al. 2017).

In the Salish Sea, where maturing pink salmon are approximately 40 times more abundant in odd versus even years, chum salmon exhibited strong biennial variations in abundance, size, age-at-maturity, and productivity (recruits per spawner), consistent with the hypothesis of competition for food with pink salmon (Gallagher 1979, Ruggerone & Nielsen 2004, Litz et al. 2021). Overall, chum salmon returns were 32% lower in high pink salmon years (odd) compared to low pink salmon years (even) during the last 5 decades (Litz et al. 2021). This pattern was reinforced by early maturation of chum salmon produced from odd-year broods that interact with adult and juvenile pink salmon (15% more age-3 than age-4) compared with those produced from even year broods (17% more age-4 than age-3). Scale growth of Quilcene River (Salish Sea) chum salmon during the third season at sea (1973–2004) was negatively correlated with the combined abundances of pink and chum salmon while also considering the effect of climate indices (Yasumiishi et al. 2016). Likewise, scale growth of Puget Sound chum salmon (brood years 1997–2012) was negatively correlated with local pink salmon abundance during the first year at sea and with NPO pink salmon abundance during the third year (Anderson et al. 2021). In the Strait of Georgia during 1966–1969, chum salmon fry were smaller in even years when pink salmon fry were abundant versus odd years when few juvenile pink salmon were present (Phillips & Barraclough 1978), and fry-to-adult survival of Fraser River chum salmon declined 44% (from average of 1.53 to 0.85% survival) when they entered marine waters in even-numbered years with numerous juvenile pink salmon, 1961–1979 (Beacham & Starr 1982). Chum salmon on the Washington (USA) coast, where few pink salmon spawn, also exhibited biennial patterns in abundance, age, and productivity, suggesting that factors such as intra- and interspecific competition occurring in the northeast Pacific contributed to those patterns (Ruggerone & Nielsen 2004, Debertin et al. 2017, Litz et al. 2021).

3.4.3. Coho salmon

Coho salmon typically spend approximately 16 mo at sea, and many individuals from North America

migrate into the GOA and the eastern NPO (Godfrey et al. 1975, Myers et al. 1996). Coho salmon occupy a somewhat higher trophic level than pink salmon because they eat more fishes and squid throughout their life (Welch & Parsons 1993, Kaeriyama et al. 2004, Johnson & Schindler 2009). However, diet overlap between them increases during the second season at sea as pink salmon grow and begin to capture small fishes and squid (Ito 1964, Pearcy et al. 1984, Brodeur et al. 2007). Consumption of squid by pink salmon becomes more pronounced during their final 2 or 3 mo at sea, especially after they reach 1 kg (Davis 2003, Aydin et al. 2005). Maturing coho salmon also consume some zooplankton, but depend primarily upon energy-rich squid.

Over a period of 50 yr (1970–2019), the average weight of coho salmon caught in the SEAK troll fishery declined with increasing biomass of pink salmon harvested in North America (an index of abundance) and increased with broad-scale SST, as indexed by the Pacific Decadal Oscillation (PDO; Shaul & Geiger 2016). An updated version of the statistical model used by Shaul & Geiger (2016) explained 68% of the variability in average annual coho salmon weight, which exhibited a strong biennial pattern that was opposite of adult pink salmon abundance (Fig. 9). Interannual variation in coho salmon weight explained by adult pink salmon biomass was slightly greater (55%) than variability explained by the PDO (45%).

The most likely mechanism responsible for those relationships involves predation by maturing pink salmon on squid (*B. anonychus*), a key prey of maturing coho salmon. The biennial life cycles of pink salmon and squid contribute to distinct biennial abundances of maturing squid that are consumed by a single cohort of ocean age-1 coho and pink salmon (Jorgensen 2011, Shaul & Geiger 2016). Thus, evidence indicates that predation by abundant odd-year pink salmon leads to fewer squid available to maturing coho salmon in odd years (Kaeriyama et al. 2004, Jorgensen 2011) and to their reduced growth and body size (Shaul & Geiger 2016). Adult coho salmon weight was explained by average North American pink salmon biomass 2 and 4 yr earlier, owing to a long-term influence of distinct even- and odd-year

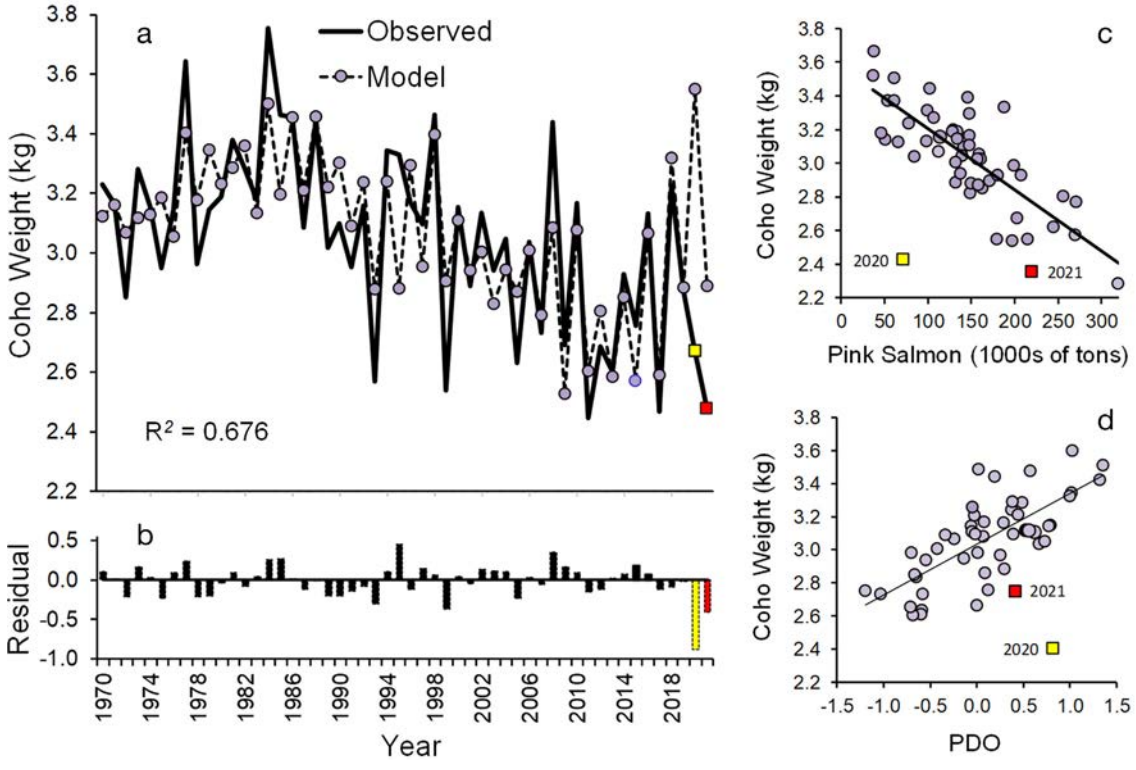


Fig. 9. Southeast Alaska troll-caught coho salmon average dressed weight (ocean age-1) compared with (a) predicted weight based on a multiple regression model with 2 variables: the standardized April–March Pacific Decadal Oscillation (PDO) Index (average for lag 0, 2, and 4 yr) and the standardized average commercial catch of pink salmon in North America (excluding the Bering Sea and Aleutian Islands) lagged by 2 and 4 yr. (b) Model residuals. Also shown are partial residual plots for (c) pink salmon abundance and (d) the PDO index. The multiple-regression model developed by Shaul & Geiger (2016) using 1970–2014 data was refitted for 1970–2019, with 2020 and 2021 values indicated on the partial residual plots by yellow and red squares, respectively

pink salmon lines preying on even- and odd-year lines of maturing squid. In the season of coho maturation, it is possible that pink salmon were too small (<1 kg) to strongly influence squid abundance during winter through late spring when coho salmon began intensive feeding on squid. High average PDO values during the year of maturation and 2 and 4 yr earlier were positively correlated with coho salmon weight, presumably through increased abundance of squid in response to warmer conditions associated with positive PDO index values.

Pink salmon biomass was linked to additional population characteristics of coho salmon in SEAK. Coho salmon survival at sea (1990–2014) was negatively correlated with both pink salmon biomass ($r = -0.58$, $p < 0.05$) and coho salmon body length ($r = -0.67$, $p < 0.05$), which was influenced by pink salmon abundance (Shaul & Geiger 2016). The ratio of female to male coho salmon was lower in odd years ($p = 0.012$), and the per capita egg biomass of maturing coho salmon, which provides an index for the reproductive potential of the spawning coho salmon population, was negatively correlated with pink salmon biomass ($r = -0.60$, $p < 0.05$). The investigators provided evidence that coho salmon body size and survival were primarily influenced during late marine life when coho salmon are offshore. These findings suggest that pink salmon adversely affect both coho salmon survival and future coho salmon abundance by reducing the reproductive potential of the survivors through a combination of lower egg biomass and lower survival of female versus male coho salmon in odd years (Shaul & Geiger 2016).

After 50 yr of strong correlation, the pink salmon–climate statistical model of Shaul & Geiger (2016) failed to predict the extremely low body size of SEAK coho salmon in 2020 (2.67 kg) and 2021 (2.48 kg), both of which followed warm conditions during 2016–2020 and poor GOA pink salmon returns on the even-year line in 2016 and 2018 (Fig. 9). However, total pink salmon returns to North America and Asia in 2018 and 2019 (avg. 670 million fish) were the largest consecutive years on record since 1925 when records were first kept (Ruggerone et al. 2021), raising the question of whether Asian pink salmon, which are typically west of most SEAK coho salmon, may have contributed to the small size of coho salmon in 2020 and 2021. Lastly, the PDO index covers a large region of the NPO and may not have reflected mesoscale effects of marine heat waves in the GOA region.

Studies in other regions are consistent with the findings of Shaul & Geiger (2016), indicating an adverse effect of pink salmon on coho salmon growth, survival, and abundance. Ogura et al. (1991) also reported that final-year growth rates of coho salmon in the western NPO, 1978–1987, were lower in odd years when maturing pink salmon were highly abundant. In the Kuskokwim River in western Alaska, commercial coho salmon harvests in odd years averaged 33% less (avg. 225000 coho salmon) compared with even years (avg. 336000 coho salmon) during 1965–2007 (*t*-test, $p < 0.001$, Ruggerone & Nielsen 2009). Further south in the Strait of Georgia, where diet overlap of juvenile coho and pink salmon was high during 1998–2009, the proportion of coho salmon with empty stomachs increased approximately 37%, and the abundance and survival of hatchery coho salmon by September declined approximately 73 and 80%, respectively, in even years when juvenile pink salmon were highly abundant (Beamish et al. 2010).

3.4.4. Chinook salmon

Subadult Chinook salmon have been found extensively in offshore areas of the NPO and BS, where they overlap with pink salmon (Major et al. 1978, Myers et al. 1996; Text S1). Diet overlap between Chinook and pink salmon can be considerable, especially during the second season at sea for pink salmon, when they are large enough to consume squid and small fishes. The small energy-rich squid *B. anonychus* is a major component in the diet of Chinook salmon (and other salmon species) in the GOA, central NPO, and central BS, and is also consumed heavily by maturing pink salmon in these same waters. For example, during a 10 yr study in the central BS (52–58° N), the diet of Chinook salmon averaged 80% fish and squid, 19% zooplankton, and 1% other prey by weight, and the diet of pink salmon averaged 60% fish and squid, 34% zooplankton, and 6% other prey (Fig. 6; Davis 2003). In odd-numbered years, when pink salmon were approximately 40 times more abundant than in even years, total prey weight consumed per Chinook salmon declined 56% versus only 23% among pink salmon (Fig. 6). In odd years, Chinook salmon consumed 72% less squid and 44% less fish, but 44% more euphausiids compared with even years (Fig. 6). In odd years, pink salmon consumed 32% less squid, 25% less fish, and 29% less zooplankton compared with even years (Fig. 6). These data suggest that pink salmon consumed fishes and squid more efficiently than Chinook salmon when availability of key prey was low. Other studies indicate that the degree of overlap in

the consumption of squid, small fishes, and euphausiids varies with region (Davis et al. 2009, Qin & Kaeriyama 2016). Collectively, this evidence suggests that pink salmon may directly and indirectly affect Chinook salmon growth and survival by consuming the same prey and by altering the food web that supports small fishes, squid, and zooplankton consumed by Chinook salmon.

Chinook salmon harvests, abundances, and average body sizes in northern regions where freshwater habitat is mostly intact have been declining for several decades (Bigler et al. 1996, Lewis et al. 2015, Ohlberger et al. 2018, Welch et al. 2021), and several studies have suggested Chinook survival and growth may be inversely related to pink salmon abundance at sea (e.g. Cunningham et al. 2018, Oke et al. 2020). We examined the time series of annual Chinook salmon commercial harvests in Alaska and BC from 1952 to 2021. Commercial harvests reflect fishing effort, based on abundance predictions and fishery regulations (PSC 2022), and can provide a first-order approximation of abundance, although they can also be confounded by changes in fishery regulations and effort over time. Consistent with the hypothesis that pink salmon affect Chinook salmon, we found that harvest trends during the 70 yr period were opposite those of pink salmon abundance trends (Fig. 10a).

Body size of adult Chinook salmon in Alaska also declined with increasing abundance of pink salmon since 1952. Average weight of commercially caught Chinook salmon was relatively stable over time when abundance of pink salmon was low during 1952 to 1975 (Fig. 10b). Immediately after the 1977 ocean regime shift, body size of Chinook salmon reached its maximum (9.3 kg) and then declined steadily over time as pink salmon abundance increased (Fig. 10b). Chinook salmon body size reached the long-term minimum during 2015–2021 (avg. 5.7 kg) when pink salmon abundance was peaking (564 million yr^{-1}) and when marine heat waves became more frequent (Ross et al. 2021). We note, however, that these trends in size and commercial harvest can be confounded with other long-term trends in oceanographic and freshwater processes, and so should be interpreted with caution. Also, the Japanese salmon fishery on the high seas removed, on average, 334 000 Chinook salmon per year from 1955 to 1980, then harvests declined steadily until its termination in 1991 (NPAFC 2022a). Most of the Chinook salmon had originated from western and central Alaska (Rogers et al. 1984; Text S1), suggesting that Chinook salmon harvests in Alaska would have been even higher during the period when pink salmon abundance was low. Other factors contributing to long-term declines in catch and size of North American Chinook salmon have been hypothesized, including size-selective predation by resident killer whales (Ohlberger et al. 2018, 2019; Text S1).

Lewis et al. (2015) demonstrated a consistent decline in Alaskan Chinook salmon length-at-age and age-at-maturation over a 30 yr period while noting the potential influence of competition for prey with other salmon species. Our analyses of these data

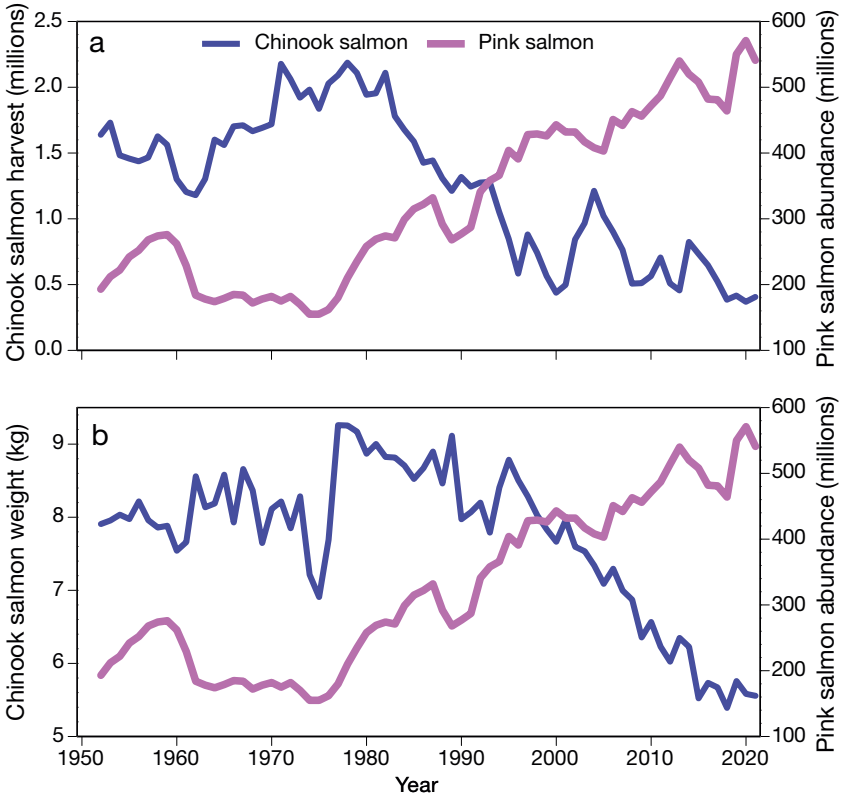


Fig. 10. Time series of (a) Chinook salmon commercial harvests in Alaska and British Columbia, and (b) average weight of Chinook salmon in Alaskan harvests in relation to average pink salmon abundance returning from the North Pacific Ocean 1 to 4 yr prior to the Chinook salmon harvest during 1952–2021 (e.g. harvest in year 2000 was related to average pink salmon abundance during 1996–1999, corresponding to the period of species overlap and potential direct and indirect effects of pink salmon). Data sources: Ruggerone et al. (2010, 2021), Ruggerone & Irvine (2018), NPAFC (2022a)

and the aggregate length of troll-caught Chinook salmon reveal that mean length of age-1.4 Chinook salmon from all 11 populations declined coincident with increasing pink salmon abundance, although the relationship was weak in 2 populations (Table S1, Fig. S1.1). The populations ranged from the Yukon River in the northeastern BS to the Copper River in the northeastern GOA, and the Unuk River in SEAK. Likewise, average length of 9 of 10 age-1.3 populations of Chinook salmon declined with increasing pink salmon abundance, including 4 weak relationships (Table S1). Average age of 4 of 5 Chinook salmon populations declined with increasing abundance of pink salmon, including 1 weak relationship (Table S1). In the Yukon River, the decline in body size led to a 24–35% reduction in the reproductive potential of female Chinook salmon since the 1970s (Ohlberger et al. 2020). In the Kamchatka River, Russia, scale analysis of Chinook salmon revealed biennial growth patterns during the first and second years at sea, 1935–1955, that may have been related to pink salmon (Grachev 1967).

Analyses of survival across the entire life cycle of Chinook salmon found support for the adverse effect of pink salmon on 2 Yukon River populations using a Bayesian life-cycle model (Cunningham et al. 2018), but no support using dynamic factor analysis of data from 15 populations throughout Alaska (Ohlberger et al. 2016); those studies also considered a number of other variables. Both studies aligned pink salmon abundance with the second season at sea (brood year plus 3 yr) of Chinook salmon rather than each year in which Chinook salmon interact with pink salmon. In contrast, while also considering the effect of oceanographic variables, moderate to strong support was found for an adverse effect of Russian pink salmon abundance on annual scale growth of Yukon, Kuskokwim, and Nushagak Chinook salmon during the third and fourth years at sea over a period of 30 yr or longer (Ruggerone et al. 2016b; Supplement 2 at www.int-res.com/articles/suppl/m719p001_supp2.xlsx). Survival of 2 of the 3 major stocks of Chinook salmon in western Alaska declined with the running 2 yr abundance of Russian pink salmon during the third and fourth years at sea. The percentage of age-6 (age-1.4) and older Chinook salmon in each stock declined with increasing abundance of pink salmon, but support was weak in 1 stock. The decline over time in abundance, growth at sea, and the proportion of older Chinook salmon led the investigators to hypothesize that mortality during late marine life had increased in response to competition with pink salmon and to predation by salmon sharks and other marine predators (Manishin et al. 2021).

Lastly, in the Japanese high seas salmon fishery in the western/central BS and NPO, we found a biennial pattern in the catch of Chinook salmon during 1955–1981. The mean catch in odd years (254 000 ± 40 000 fish [SE]) was 39% lower than the catch in even years (417 000 ± 60 000 fish, *t*-test, $p = 0.03$). Chinook salmon catch was negatively correlated with pink salmon catch (linear regression, $r = -0.63$, $p < 0.001$; Text S1, Fig. S1.2). Scale pattern analysis indicated that most of the Chinook salmon originated from western and central Alaska.

Chinook salmon growth and survival may also be affected by pink salmon in coastal seas. In the Salish Sea, subyearling ocean-type Chinook salmon smolts released from 13 hatcheries experienced a 59% decline in marine survival, on average, when released during even years compared with those released during odd years, 1984–1997 (Fig. 11a; Ruggerone & Goetz 2004). Juvenile pink salmon were highly abundant in even years (avg. ~8 million odd-year spawners, 1983–1996) but rare in odd years (<0.5 million even-year spawners). Additional analyses of over 53 million coded-wire-tagged Chinook salmon indicated that the biennial mortality pattern was established during the first year at sea, i.e. within the Salish Sea. No biennial pattern in Chinook salmon survival was observed along the Washington coast and southern Vancouver Island, where few pink salmon spawn. During 1972–1983, overall survival of juvenile Chinook salmon was high and tended to be highest when emigrating with juvenile pink salmon in even years, a change from 1984–1997 possibly related to the 1982–83 El Niño and a shift from predation- to competition-based mortality (Ruggerone & Goetz 2004). Subsequent analyses of subyearling and yearling hatchery Chinook salmon from 1983 to 2012 found lower density-dependent survival and fewer adult returns of hatchery Chinook salmon when released into the Salish Sea during even years when juvenile pink salmon were abundant (Kendall et al. 2020). In odd years, when few juvenile pink salmon were present, density-dependent survival of Chinook salmon was not apparent and survival was higher. From 1970 to 2015, abundance and size of adult natural-origin Chinook salmon in the Salish Sea were negatively correlated with pink salmon abundance (Losee et al. 2019).

Diet overlap between juvenile pink and Chinook salmon in the Salish Sea is relatively low, and researchers hypothesized that pink salmon indirectly influenced Chinook salmon growth and survival (Ruggerone & Goetz 2004, Kendall et al. 2020). Several lines of evidence support a hypothesis of trophic

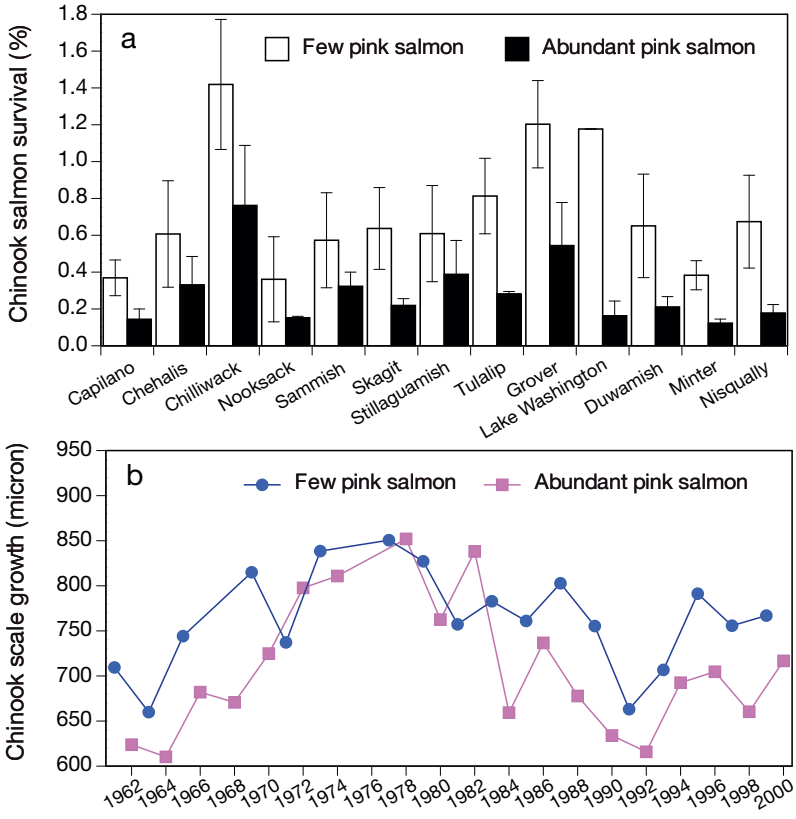


Fig. 11. (a) Mean smolt to adult survival (±1 SE) of subyearling Chinook salmon (tagged ocean type) released from 13 hatcheries in the Salish Sea (Washington and British Columbia) during even years (numerous juvenile pink salmon) and odd years (nearly zero juvenile pink salmon), 1984–1997, and (b) mean early marine scale growth (circuli 11 to 34) corresponding to residence in the Salish Sea of adult Skagit River Chinook salmon (ocean type) during even and odd years, 1961–2000. Data sources: Ruggerone & Goetz (2004); Text S1

interaction. (1) Juvenile pink salmon enter the Salish Sea approximately 2 mo before subyearling Chinook salmon. (2) We found that first-year marine scale circuli measurements of surviving adult Skagit River Chinook salmon were 7% narrower, on average, during even years than odd years, 1961–2000 (*t*-test, $p < 0.01$, df = 35, Fig. 11b; Text S1). (3) During 1983 to 1997, returning coded-wire-tagged Chinook salmon were smaller at age and tended to delay maturation when released into Salish Sea watersheds in even years when juvenile pink salmon were abundant (Ruggerone & Goetz 2004). (4) Early marine growth and survival of Salish Sea Chinook salmon increased with fewer juvenile pink salmon (Claiborne et al. 2021).

Approximately 11–38% of Chinook salmon sampled for genetic stock identification in the southeastern BS during 2005–2010 originated from the Pacific Northwest, raising concern that climate warming may be shifting salmon from the Pacific Northwest into a crowded BS where temperatures are cooler (Larson et al. 2013). In support of this hypothesis, Buckner et al. (2023) analyzed the growth of 48 stocks of Chinook salmon returning to hatcheries and spawning grounds in the Columbia River Basin, Oregon coast, and Washington coast (brood years 1976–2013), and found that growth of subyearling and yearling far-north migrating Chinook salmon was negatively associated with pink salmon abundance. The effect of pink salmon on Chinook salmon growth was stronger than that of the tested oceanographic variables (see their Fig. 4). Growth of subyearling Chinook salmon populations that did not migrate as far north was also negatively associated with pink salmon abundance, but to a lesser extent; growth of yearling Chinook salmon in the southern distribution area was not associated with pink salmon abundance.

3.4.5. Steelhead

Steelhead migrate long distances during their typical 1 to 3 winters at sea, leading to a broad distribution across the NPO. Ocean age-0 steelhead migrate farther offshore than other salmonids in their first year at sea, and many immature steelhead from North America have been sampled west of 180° and off the Kuril Islands, Russia (Myers 2018). Steelhead in the open ocean are opportunistic foragers, but they specialize to some degree on a few species of micronekton, including cephalopods (especially *B. anonychus*) and small mesopelagic fishes, and zooplankton such as adult euphausiids, pelagic decapods, amphipods, and pteropods (Myers 2018).

Steelhead feed at a somewhat higher trophic level than pink salmon, but they also share many common prey, leading Atcheson et al. (2012a) to conclude that ocean age-0 and older steelhead may compete with maturing (ocean age-1) pink salmon. In the central NPO, consumption of highly energy-dense mesopelagic forage fishes and squids was negatively correlated with abundance of eastern Kamchatka pink salmon, whereas the percentage of empty stomachs increased with increasing pink salmon abundance

(Atcheson et al. 2012b). These researchers recognized that pink salmon are less abundant in the central NPO than in the central BS, but suggested that large runs of adult pink salmon may deplete prey resources as they migrate through broad North Pacific regions from winter to spring (Myers 2018). They also hypothesized that the surface orientation of foraging steelhead may be a mechanism to reduce trophic interactions with pink salmon.

Steelhead survival indices in BC provide evidence that pink salmon may adversely affect their survival at sea. Adult recruit per spawner anomalies of critically endangered Thompson River summer-run steelhead in the interior of the Fraser River watershed were negatively correlated with the biomass of NPO pink salmon that overlapped their final 2 yr at sea during 1978–2012 (Fig. 12a; Text S1). Smolt-to-adult survival of Keogh River (northeast Vancouver Island) winter-run steelhead was negatively correlated with pink salmon biomass in 1977–2018 (Fig. 12b). Approximately 46 and 49%, respectively, of the annual variability in the Thompson River and Keogh River steelhead survival indices were explained by pink salmon abundance. In the Chilcotin River (interior Fraser River), steelhead recruit per spawner anomalies were negatively correlated with pink salmon abundance (r= –0.65), but autocorrelation was high and reduced the significance of the relationship (linear regression, df = 1, 38, p = 0.14). Predation by local populations of seals on adult and post-smolt steelhead is also considered a key factor in the decline of these steelhead populations (COSEWIC 2020, Wilson et al. 2022). We found that seal and NPO pink salmon abundances are highly correlated, so it is not possible to quantify their relative influence on the decline of steelhead. However, Friedland et al. (2014) reported that smolt-to-adult survival of Keogh River steelhead (1977–1999) was correlated with their scale growth during the first year at sea, especially during summer and fall when they overlap with abundant pink salmon in the north (Myers 2018; Text S1).

In the Columbia River Basin, we found that B-run summer steelhead exhibit a pronounced biennial pattern of abundance, suggesting strong interactions with pink salmon at sea (Fig. 12c). These fish are

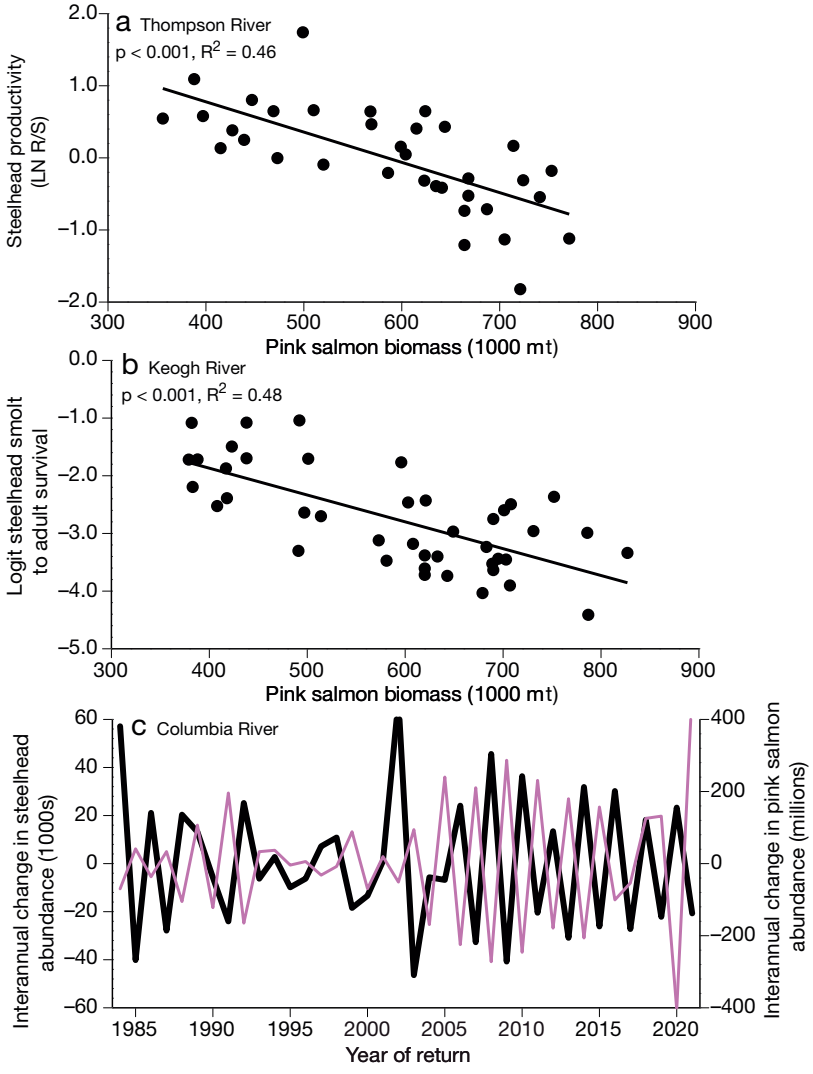


Fig. 12. Potential influence of North Pacific Ocean (NPO) pink salmon abundance on (a) the productivity (return per spawner, R/S) of Thompson River summer-run steelhead (Fraser River watershed, BC), brood years 1978–2012, and (b) smolt to adult survival of Keogh River winter-run steelhead (NE Vancouver Island), smolt years 1977–2018. (c) Interannual change in abundances of Columbia River B-run summer steelhead (black line) and North Pacific pink salmon (pink line) during 1984–2021, where interannual change in abundance (A) in year $i = A_i$ – avg. (A_{i-1}, A_{i+1}). Pink salmon biomass is the average biomass 3 and 4 yr after the brood year for Thompson steelhead (mostly 5 yr old fish that spend 2 winters at sea and the last winter in freshwater), and average biomass 1 to 3 yr after the smolt migration of Keogh River steelhead (up to 3 winters at sea), accounting for overlap at sea and different age composition of the 2 steelhead populations. Autocorrelation in the linear regressions was inconclusive (a) or non-significant (b). Data sources for our analyses: Ratzburg (2021), WDFW/ODFW (2022), R. Bison unpubl. data

listed as 'threatened' under the US Endangered Species Act. Returning B-run steelhead counted at Bonneville Dam were 38% less abundant in odd versus even years during 1984–2021 (*t*-test, p = 0.014, n = 38). Furthermore, odd-year pink salmon have become more dominant in recent years (Irvine et al. 2014), and this is reflected in the negative correlation between interannual change in abundances of B-run steelhead and NPO pink salmon over the past 38 yr (Fig. 12c; linear regression, p = 0.014 after accounting for autocorrelation).

In contrast to B-run steelhead, A-run summer steelhead abundance did not differ between odd and even years (*t*-test, p = 0.24, n = 38). B-run steelhead typically spend 2 yr at sea and migrate farther north and west and potentially interact with more abundant pink salmon than A-run steelhead, which spend only 1 yr at sea (Myers 2018). Importantly, the biennial abundance pattern shown by B-run, but not A-run, steelhead suggests substantial mortality after the first year at sea, consistent with late marine mortality observed in other salmon species described here.

3.4.6. Pink salmon

In comparison with other Pacific salmon, pink salmon appear to be well-adapted to foraging in a warming ocean given that the ocean supports more pink salmon now than at any other time since detailed record keeping began in 1925. Pink salmon stomachs are often much fuller than those of other salmon species, they typically consume higher caloric prey than chum and sockeye salmon, and they have high daily rations (Fig. 6; Davis 2003, Karpenko et al. 2007, Karpenko & Koval 2012, Shuntov et al. 2017, Radchenko et al. 2018). Bioenergetic analyses show that body growth declines less in pink salmon (–31%) than in chum (–52%), sockeye (–43%), and coho salmon (–33%) when ocean temperature increases from 5 to 9°C and daily ration is constant (Davis et al. 1998). Growth of smaller salmon is more efficient than growth of larger salmon as temperature rises (Beauchamp 2009). These studies suggest that the strength of density-dependence at sea among pink salmon may be weaker than within other salmon species.

Intraspecific studies of pink salmon at sea often examine interactions between hatchery and wild fish because approximately 1.35 billion juvenile pink salmon are released into the NPO each year, 1990–2021, of which 66% are released in Alaska, primarily in PWS (NPAFC 2022b). Multiple studies reported that adult run size and returns per spawner of PWS wild pink salmon declined in response to increased hatchery production (Hilborn & Eggers 2000, 2001, Amoroso et al. 2017). In contrast, abundances of wild pink salmon in adjacent regions of Alaska increased during this period, further indicating increased hatchery production of pink salmon influenced the decline of wild pink salmon in PWS.

Increased intraspecific competition for prey in PWS and at sea was identified as a key mechanism affecting wild PWS pink salmon. In support of the competition hypothesis, the food demand of juvenile pink salmon in PWS reportedly exceeded the standing stock of preferred prey during July when salmon densities were high (Cross et al. 2005), resulting in reduced growth, greater size-dependent predation, and higher mortality (Willette et al. 2001), although a bioenergetic model approach suggested prey availability may be adequate (Boldt & Haldorson 2002). Adult body size of wild PWS pink salmon also declined with greater releases of hatchery pink salmon, leading to reduced fecundity and a loss of approximately 1 million wild adult pink salmon per year (Wertheimer et al. 2004). More recently, using 60 yr of data on wild pink salmon abundances, hatchery releases, and ecological conditions in the ocean, Ohlberger et al. (2022) provided evidence that hatchery pink salmon releases into PWS (i.e. 700 million fish yr^{-1}) reduced productivity of wild pink salmon by 55%. That study also provided evidence that productivity of emigrating juvenile pink salmon declined with increasing numbers of returning pink salmon, thereby supporting the hypothesis that biennial patterns in adult pink salmon are partly related to brood interactions at sea (Ruggerone & Nielsen 2009, Krkosek et al. 2011, Irvine et al. 2014).

Analyses of scale growth of pink salmon sampled in the GOA and adult pink salmon returning to PWS hatcheries indicated significant size-selective mortality of juvenile pink salmon during and after the first growing season — slower-growing salmon experienced reduced survival (Cross et al. 2008, 2009). A potential bottleneck for growth during early to mid-July was observed, corresponding with fewer zooplankton. The authors concluded that the large influx of juvenile pink salmon into the GOA, in conjunction with the seasonal dynamics of zooplankton prey, could create localized prey depletions, density-dependent growth, and reduced survival (see Section 3.1).

Most, but not all, studies have observed density-dependent growth of pink salmon at sea. Body length and scale growth of pink salmon sampled in the central BS and in the western NPO during 1972–1998 were negatively correlated with catch per

unit effort of pink salmon in the non-selective research gillnets (Ishida et al. 1995, Azumaya & Ishida 2000), consistent with a 23% decline in pink salmon stomach fullness in odd- compared with even-years, 1991–2000 (Davis 2003). Body weight of maturing Fraser River pink salmon declined as zooplankton availability declined at Ocean Station P, 1957–1977 (odd years only, $r = -0.86$, $p < 0.001$; Peterman 1987). In BC (1951–1993) and Puget Sound, Washington (1959–1999), weight of odd-year adult pink salmon declined up to 40% with increasing pink salmon abundance (Welch & Morris 1994, Ruggerone & Nielsen 2004, Jeffrey et al. 2017). In Russia, size of pink salmon migrating through the Kuril Islands and returning to the Sea of Okhotsk region was negatively correlated with pink salmon biomass, 1991–2003 (Shuntov & Temnykh 2005). Throughout Asia and North America overall, the combined average weight of adult pink salmon declined with increasing pink salmon abundance, 1925–2015 (Ruggerone & Irvine 2018).

Density-dependent growth was not observed in other studies. For example, second-year scale growth of pink salmon sampled south of the central Aleutian Islands was positively correlated with Asian pink salmon abundance after the 1977 regime shift (1983–1995), but negative prior to the 1977 shift (Walker et al. 1998). Size of pink salmon returning to eastern Kamchatka was not related to Kamchatka pink salmon abundance, 1971–2001 (Shuntov & Temnykh 2005).

3.5. Seabirds

Most species of seabirds in the subarctic NPO fall into a functional planktivore or omnivore trophic guild (Text S2). Overlap in diet between guilds does occur, and the guilds are separated by somewhat less than one trophic level. Diets in both guilds overlap extensively with diets of pink salmon, which prey on the same species and taxa of zooplankton and fishes (Text S2). Evidence of interactions between resident seabirds and pink salmon can be found across a broad region from the western Aleutian Islands to the eastern GOA, and in 1 migrant species from the southern hemisphere that spends the austral summer primarily in the BS and Chukchi Sea.

3.5.1. Southeastern Bering Sea and Aleutian Islands

Biennial patterns in numerous elements of the diets and breeding biology of several species of seabirds in both guilds were conspicuous in the Aleutian and Pribilof Islands in the BS in 1988–2012 (Springer & van Vliet 2014; Supplement 2). Although biennial patterns in all nesting parameters of all species were not found at all colonies, among omnivores, nesting phenology (indexed by hatch date) was later in odd years compared to even years for as many as 6 species nesting at as many as 4 colonies (e.g. Fig. 13). Clutch sizes of the 2 species that lay more than 1 egg were smaller in odd years. Laying success, hatching success, fledging success, and productivity (chicks per nest attempt) of 3 or more species at up to 3 colonies were lower in odd years. The biennial differences indicated that foraging conditions for those species in late spring through summer were better in even years than in odd years. A biennial pattern in the stress hormone corticosterone in thick-billed murres *Uria lomvia* at St. George Island, which is rel-

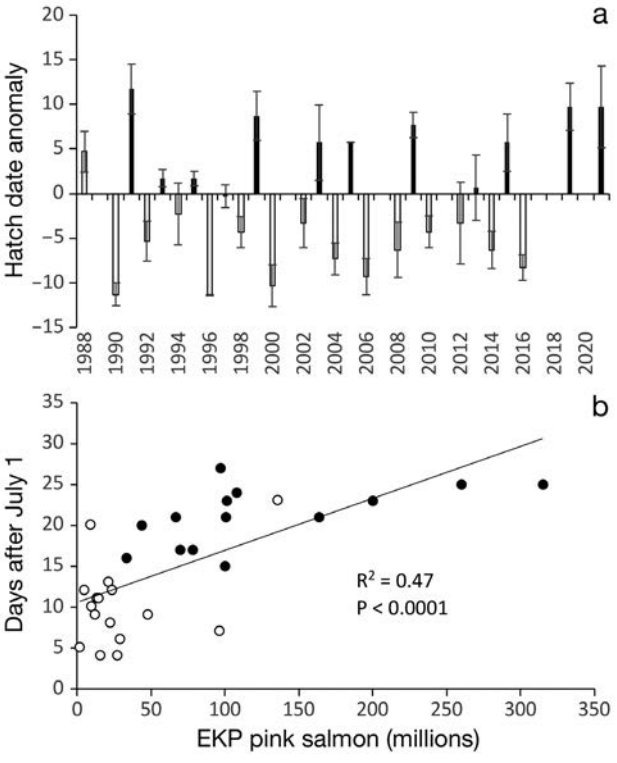


Fig. 13. (a) Phenology of tufted puffins at Buldir Island (Aleutian Islands) indexed as average hatch date each year relative to overall average hatch date across all years (no. of d relative to July 15). No data were acquired in 1989, 2017, or 2020; n = 1 nest in 2001, 2007, and 2018 and were excluded. (b) Relationship (linear regression) between eastern Kamchatka pink salmon abundance (EKP) and tufted puffin annual average hatch date (no of d after 1 July). Open bars and circles = even years; filled bars and circles = odd years. Tufted puffin data from Higgins et al. (2022); pink salmon data from Ruggerone & Irvine (2018) and Ruggerone et al. (2021)

atively high in odd years and low in even years, further supports a nutritional stress explanation for biennial variability in nesting characteristics of omnivores (Text S2).

Patterns in nesting parameters of planktivores were out of phase with those of the omnivores (Springer & van Vliet 2014). The hatching phenology of as many as 4 species at 2 locations in the Aleutian Islands and 1 species at the Pribilof Islands was earlier in odd years of higher pink salmon abundance than in even years of lower abundance. Additionally, the fledging success and productivity of 1 species at St. George Island (Pribilof Islands) were higher in odd years. Thus in contrast to omnivores, by these measures foraging conditions for planktivores apparently were better in odd years than in even years. We presently do not propose a mechanism for this observation.

In contrast, planktivorous least auklets *Aethia pusilla* at Buldir Island (western Aleutians) consumed *Neocalanus plumchrus/flemingeri*, a primary prey, in greater amounts in even years than in odd years, and consumed more of 4 out of 5 secondary prey in odd years (Springer & van Vliet 2014). Likewise, planktivorous whiskered auklets *A. pygmaea* at Buldir consumed more *N. cristatus*, a primary prey, in even years than in odd years. Those biennial dietary patterns are opposite patterns of breeding biology and suggest that even years are good relative to odd years, as in the case of the omnivorous species, and are consistent with evidence discussed above that pink salmon deplete stocks of large copepods in odd years.

Several nesting parameters of the omnivores were highly correlated with the abundance of eastern Kamchatka pink salmon (Springer & van Vliet 2014). For example, the phenology (mean hatch date of eggs) of tufted puffins *Fratercula cirrhata* at Buldir has been relatively late in odd years and early in even years since data were first acquired in 1988 (Fig. 13). In addition, annual hatch dates have been highly correlated with the abundance of eastern Kamchatka pink salmon, the dominant pink salmon population in this region. The relationship is very strong across all years, but differs between even and odd years — it is weaker in even years (linear regression, $p = 0.13$) and stronger in odd years ($p = 0.03$). As the mean abundance of pink salmon in even years since 1988 (30.4 ± 9.0 million [SE]) has been just 24 % as large as in odd years (124 ± 22 million), the implication is that for the most part, only in odd years and rare even years of uncommonly high returns are pink salmon sufficiently abundant to materially alter prey fields to the detriment of tufted puffins, and by extension other seabirds. Among prey important to both tufted puffins and pink salmon are squids (Davis et al. 2005, Higgins et al. 2022), which also have been implicated as an important variable in competition for prey between pink and other species of salmon as noted above. Nesting parameters of the planktivores in the Aleutian and Pribilof Islands were not correlated with eastern Kamchatka pink salmon. We do not understand the reason for a lack of correlation, but it may be related to the even-year bad, odd-year good pattern in breeding parameters, which is opposite that of the omnivores.

3.5.2. Prince William Sound

The productivity of black-legged kittiwakes *Rissa tridactyla* in PWS has been monitored systematically since 1985 (Irons 1996, D. B. Irons unpubl. data), and since 1990, it has been positively correlated with annual returns of PWS pink salmon (wild + hatchery, linear regression, $p = 0.032$). Overall during that time, pink salmon returns were nearly twice as large in odd years as in even years (55 ± 7.2 vs. 34 ± 3.9 [SE] million salmon; *t*-test, $p = 0.018$). Notably, the relationship to kittiwake productivity was driven primarily by hatchery stocks (linear regression, $p = 0.030$) and not wild stocks ($p = 0.31$).

That positive relationship to pink salmon is opposite the negative relationship at Chowiet Island in the western GOA (Text S2), and in the BS as discussed in Section 3.5.1 and in Text S2. For PWS, several sources of evidence lead to the hypothesis that predation on kittiwake eggs and chicks rather than competition is the primary driver of this pattern. First, a major factor in the nesting success of kittiwakes in many PWS colonies is the level of egg and chick loss to bald eagles *Haliaeetus leucocephalus*, peregrine falcons *Falco peregrinus*, common ravens *Corvus corax*, and glaucous-winged gulls *Larus glaucescens*; the presence of these aggressive predators also causes adult kittiwakes to stay away from nests for extended periods, which allows opportunistic predators such as northwestern crows *C. caurinus* and black-billed magpies *Pica pica* to prey upon nests (Suryan et al. 2006, Robbins 2009, McKnight et al. 2020). Second, kittiwakes in PWS typically lay eggs in early June on average, which hatch in early July, and chicks leave the nest in approximately mid- to late August (Suryan et al. 2006). The PWS pink salmon run begins in mid-June and extends through late July to mid-September (ADFG 2022), thus overlapping entirely with the kittiwake nesting season. Third, McKnight et al. (2020) found that kittiwake productivity at 1 colony in PWS was higher in years

of earlier pink salmon runs than in years of later runs, i.e. more salmon throughout the full nesting season in early run years diverted avian predators. We hypothesize an analogous scenario: in odd years of high pink salmon returns, the attention of avian predators is focused more on them, which provide a much higher energetic return on investment than kittiwake eggs and chicks, and PWS kittiwakes thereby achieve higher reproductive output than in even years of low pink salmon returns.

3.5.3. Southern Hemisphere

Short-tailed shearwaters *Ardenna tenuirostris*, trans-hemispheric migrant seabirds that breed in Australia and Tasmania and spend the austral winter primarily in the BS and Chukchi Sea, also have been linked to pink salmon through diet overlap and competition for prey. They are very abundant, on the order of 25–30 million, and provide terrestrial ecosystem services by aerating soils and promoting vegetation growth in nesting colonies where they burrow. They further provide cultural and societal services to Indigenous peoples who have harvested chicks for millennia.

Short-tailed shearwaters in the BS were found to be in poorer physiological condition and to die in greater numbers in odd-year summers in 1981–1990 (Lobkov 1991); and in 2002–2008, their body mass and liver mass were negatively correlated with pink salmon biomass, which was 23 times higher in odd years than in even years (Toge et al. 2011). In the southern hemisphere beginning in 2007, major mortalities of adults occurred in every odd year (but none in even years) through at least 2013 as the birds arrived on their nesting grounds after returning from the NPO (Springer et al. 2018). Shearwaters depend upon fat reserves acquired on northern feeding grounds to carry them through their 15000 km non-stop southward migration, and because the birds in the die-offs were emaciated, it appeared that those reserves were insufficient in odd years. Mean and median abundance indices of nesting short-tailed shearwaters at 2 well-studied colonies were consistently greater in even years than in odd years during 1976–2016 at one colony and between 1997 and 2015 at the other colony. The biennial differential at both colonies was most pronounced in 2005–2016, when pink salmon abundance was exceptional, especially in odd years (Fig. 1) — in this interval, the median even:odd year ratio of nests was 1.49 at Montague Island and 1.16 at Furneaux Island (Springer et al. 2018).

3.6. Humpback whales

Humpback whales *Megaptera novaeangliae* migrate to northern SEAK to feed on forage fishes and euphausiids during spring through fall, returning south to Hawaii and Mexico in winter to breed while also fasting (Gabriele et al. 2017). Using data from Neilson et al. (2022) we calculated that from 1985 to 2013, the 'crude birth rate' was 33% lower in odd years (7.5 ± 0.7% [SE]) than even years (11.3 ± 1.1%; *t*-test, df = 27, p = 0.006; Fig. 14). In 14 of 19 odd years, the crude birth rate was lower than the mean birth rate in the adjacent even years (Fig. 14). The onset of marine heat waves in 2014 may have reduced the magnitude of the biennial pattern.

The mechanism leading to this previously unreported biennial pattern is uncertain, but we hypothesize it is related to pink salmon and their effect on the prey of humpback whales in SEAK. Humpback whales feed on forage fishes, such as herring and capelin, and euphausiids (Jurasz & Jurasz 1979, Krieger 1990), all of which may be influenced by pink salmon (see Section 3). Fewer calves were observed during summer in odd than even years, based on counts reported by Neilson et al. (2022). Those whales were born the previous winter following an even-year

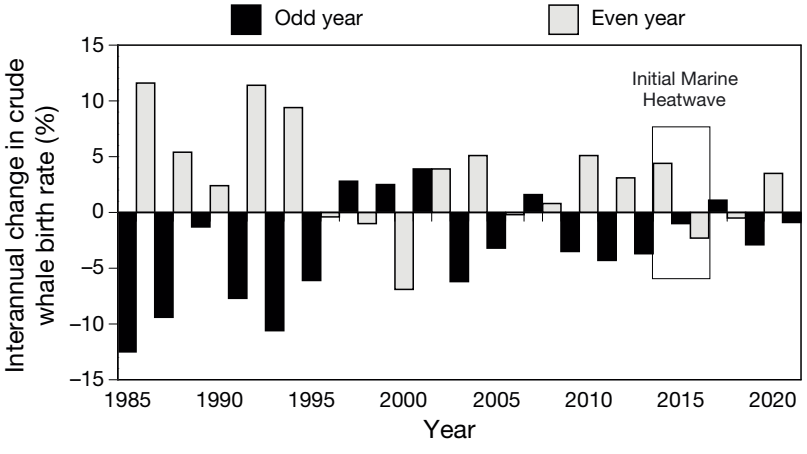


Fig. 14. Interannual change in crude birth rates of humpback whales in Southeast Alaska during even and odd years, 1985–2021. Crude birth rate is the number of unique calves divided by the total number of unique whales observed in Glacier Bay and Icy Strait from 1 June to 31 August (Gabriele et al. 2022, Neilson et al. 2022). Interannual change in birth rate (*BR*) in year i = BR_i – avg. (BR_{i-1}, BR_{i+1})

summer in which pink salmon were less abundant (see Fig. 5a). However, the parent breeding season was during the previous winter, following an odd year in which pink salmon were more abundant. Thus, the feeding rate and nutritional state at the end of odd years may have affected the mating and/or gestation of the parents, leading to fewer calves observed in SEAK during the following odd year.

3.7. Southern Resident Killer Whales

Southern resident killer whales (SRKWs) rarely eat pink salmon (Ford et al. 2016), yet this critically endangered population, which ranges from central California to mid-Vancouver Island and into the Salish Sea, exhibited a highly unusual biennial pattern in both successful births and mortality. From 1998 to 2020, mortality of newborn and older SRKWs was 3.1 times higher (65 versus 21 deaths) and successful births 42% lower (19 versus 33 calves) in even than in odd years as the population decreased from 92 to 74 animals (Fig. 15a; Ruggerone et al. 2019, CWR 2021). The biennial pattern was not apparent during the earlier period (1976–1997) when the population was stable or increasing, the primary prey (Chinook salmon) were more abundant, and pink salmon were less abundant. SRKWs feed primarily in the Salish Sea during spring through early fall on maturing Chinook salmon (Ford et al. 2016). Ruggerone et al. (2019) hypothesized that pink salmon, whose escapement to Salish Sea rivers increased 135% during the period of SRKW decline, interfered with the foraging efficiency of the animals as they attempted to capture Chinook salmon. Both returning Chinook and pink salmon concentrate along the west side of San Juan Island and into Boundary Pass from late July through early September, but pink salmon are only abundant in odd years (avg. 18 million versus 0.4 million in even years). In odd years, pink salmon are approximately 50 times more abundant than co-migrating Chinook salmon. According to the hypothesis and support from available data (Fig. 15a), reduced foraging efficiency of SRKWs in odd years when pink salmon are abundant would lower their nutritional status, which would be expressed in the following even year (increased mortality and fewer successful births) because these large mammals have a strong physiological buffering capacity (Ford et al. 2010).

Body condition measurements also support the hypothesis that prey consumption by SRKWs was reduced in odd years, potentially in response to abundant pink salmon (Stewart et al. 2021). During 2008–2019, the body condition index of the L Pod of SRKWs, which was measured in September after most pink salmon have passed through the SRKW

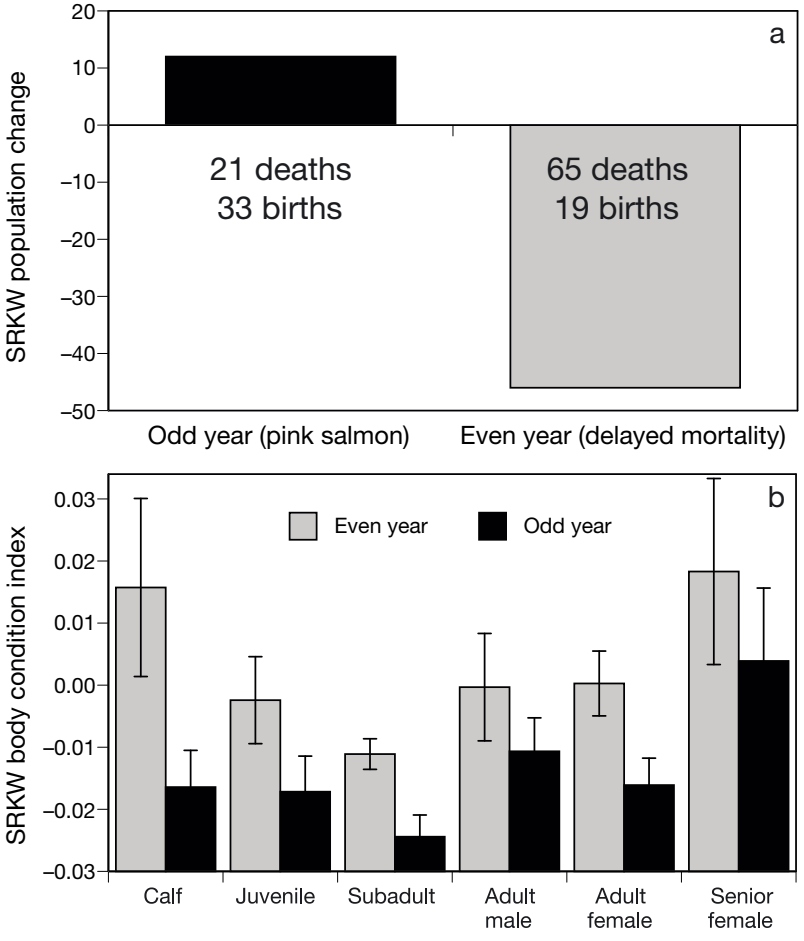


Fig. 15. (a) Southern resident killer whale (SRKW) population declined 20% from 1998 to 2020, including 46 fewer individuals in even years (19–65 animals) after interacting with abundant pink salmon in the previous odd year but increased by 12 individuals in odd years (33–21 animals) due to more successful births and fewer deaths (Ruggerone et al. 2019, CWR 2021). (b) From 2008 to 2019, annual mean (±1 SE) body condition of each age class of L Pod (SRKW) in September was lower during odd years after numerous pink salmon had migrated through the Salish Sea, the primary feeding area of SRKWs during summer. Body condition measurements were taken from Fig. S6 of Stewart et al. (2021), who recognized the biennial pattern in relation to pink salmon

foraging area, was markedly lower on average during odd versus even years in each of the 6 age categories (Fig. 15b). A biennial pattern in body condition was not readily apparent in J and K pods, populations that have declined less than the L pod since 1997. From 1998 to 2020, approximately 55% of mortality and 90% of the population decline was associated with the L Pod, which exhibited strong biennial patterns in body condition, mortality, and successful births.

Understanding the mechanism of this biennial pattern is critical to the recovery of the endangered SRKW population. For example, if births and mortality during even years had been similar to those during odd years, especially within the L Pod, then the SRKW population would have substantially increased rather than decreased during the past 20 yr (Fig. 15a). In recent years, however, SRKWs have reduced foraging time in the Salish Sea (Shields et al. 2018, Ettinger et al. 2022), a behavior that may influence the extent to which the biennial pattern holds into the future.

4. DISCUSSION

Our synthesis reveals compelling evidence for top-down effects of pink salmon on numerous pelagic species, food webs, and ecosystem function spanning broad regions of the western, central, and eastern NPO, the BS, and semi-enclosed waters including PWS and the Salish Sea (Table 1; Supplement 2). Those effects were largely, but not entirely, unknown until scientists began to notice and track biennial patterns in marine organisms that coincided with the biennial patterns of pink salmon abundance. For instance, regular large interannual differences in sockeye salmon diets were documented in the 1950s (Ito 1964), long before the spectacular rise in pink salmon abundance. Overall, pink salmon apparently have interacted strongly with other species in the NPO for many decades, playing important top-down roles in structuring pelagic ecosystems.

4.1. Conceptual model

We developed a conceptual model that synthesizes our hypotheses based on evidence discussed in Section 3 (Table 1; Supplement 2). It expands upon the 'Trophic Triangle' conceptual model presented by Aydin (2000) and Shaul & Geiger (2016), who emphasized the importance of predation by pink salmon on *Berryteuthis anonychus*. The following points highlight key dynamics implied by what we refer to as the 'Pink Salmon Impacts Model,' and are elaborated upon in Text S3 and Fig. 16.

(1) Warming in the north increases pink salmon abundance, especially odd-year adult returns (Fig. 1).

(2) Biennial variability in predation by pink salmon drives biennial fluctuations of squid abundance (*B. anonychus*), including adult squid, their progeny, and subsequent generations as a result of the 2 yr life cycle of squid (Section 3.3).

(3) Pink salmon can initiate pelagic trophic cascades through predation on large herbivorous zooplankton, lowering their abundance, which can lead to greater biomass of phytoplankton (Section 3.1).

(4) Abundant odd-year pink salmon efficiently exploit prey (zooplankton, small fishes, squid), thus reducing prey needed by other salmon species, forage fishes, and seabirds for growth, productivity, and survival, especially in odd years (Section 3). In a warming ocean, reduced prey availability, especially energy-rich squid and fishes, is particularly harmful for larger and older salmon such as Chinook salmon (Beauchamp 2009). Most salmon evidence involves interactions after their first year at sea, indicating the importance of late marine life to growth, survival, and abundance.

(5) Forage fishes, which are critical prey for many marine species, also exhibit biennial growth or abundance patterns in relation to biennial pink salmon abundance and their predation on common prey resources (Section 3.2).

(6) Humpback whales and SRKWs exhibit biennial demographic patterns that are related to pink salmon (Sections 3.6 and 3.7, respectively).

(7) The intensity of species interactions and regularity of biennial patterns varies across time and ecosystems. The strength of competition in the shared resource spaces is not expected to be equal across all species and locations, and the effects of pink salmon may interact with those of oceanographic conditions, weather, and climate. Thus, interrupted and emerging biennial patterns would not necessarily share common time frames.

Our conceptual model does not specifically address early life stages at sea of salmon in more southerly regions, such as in the Pacific Northwest or Japan, where climate warming generally leads to less favorable conditions for them during early life at sea compared with those in the north (e.g. Hare et al. 1999, Mueter et al. 2002, Mackas et al. 2007, Bi et al. 2011, Keister et al. 2011, Malick et al. 2017a). However, many southern populations of each species that migrate

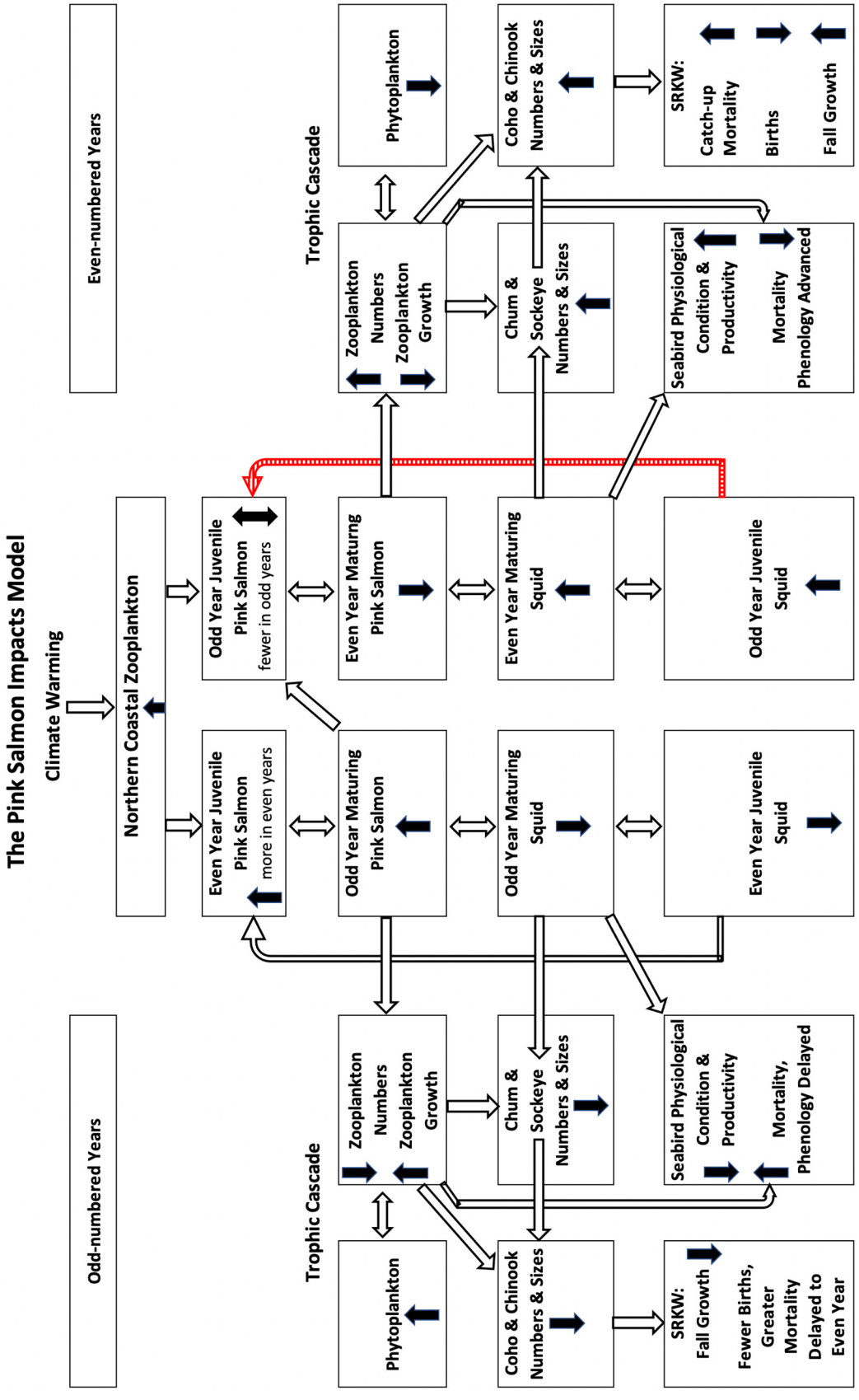


Fig. 16. The conceptual Pink Salmon Impacts Model showing how climate warming, biennial variation in pink salmon abundance, and biennial squid dynamics may influence offshore ecosystems in the North Pacific Ocean and Bering Sea. Solid arrows indicate an increase or decrease in either population abundance, growth or other variable. Hollow arrows indicate direction of influence. Red dashed arrow indicates negative competition effect of increasing juvenile squid. Although both odd and even calendar-year pink salmon abundances are currently increasing over time, odd years here reflect effects of higher pink salmon abundances relative to even years. See Section 3 for linkages to forage fishes and other species, and Text S3 for more details on the model

north into the GOA, BS, and beyond, including Chinook salmon (Larson et al. 2013), have experienced substantial declines in size, survival, and abundance (Welch et al. 2021, Buckner et al. 2023). We hypothesize that those north-migrating salmonids from the Pacific Northwest and Japan have low marine survival due to less favorable conditions during early life at sea and to reduced foraging opportunities after the first winter at sea, especially for energy-rich squid and small fishes needed to sustain larger and older Chinook salmon in a warming ocean (Section 3).

4.2. Competition exacerbated by climate warming — the case of salmon

We hypothesize that pink salmon and the warming of the NPO and adjacent seas will synergistically enhance competition between pink salmon and other marine species until continued warming leads to declines of all salmon species. Pink salmon abundance has more than doubled in the NPO since the mid-1970s ocean climate regime shift, associated warming, and increased hatchery production (Fig. 1). Pink salmon appear to have initially benefitted from increased abundance of zooplankton in northern regions (e.g. Brodeur & Ware 1992, Brodeur et al. 1996), potentially leading to faster early marine growth and improved survival compared with that prior to the mid-1970s (Ruggerone et al. 2007, Cross et al. 2009). However, warming ocean temperatures also exacerbate competition, because greater consumption of high-calorie prey is needed to offset increasing physiological demands imposed by higher temperature, especially for larger Chinook salmon (Brett 1979, Hinch et al. 1995, Beauchamp 2009, Piatt et al. 2020). Pink salmon are smaller, tend to consume prey more effectively at low densities, and more efficiently utilize food at higher temperatures than other salmon species (Davis et al. 1998), likely factors contributing to their exceptional growth in abundance in recent decades. Thus, the combined effects of greater pink salmon abundance, reduced physiological efficiency in other species at higher temperatures, and apparently fewer high-calorie prey partly in response to increasing predation by pink salmon, in addition to other oceanographic conditions (e.g. Mueter et al. 2002, 2003, Wells et al. 2008, Stachura et al. 2013, Cunningham et al. 2018, Ohlberger et al. 2019, Howard & von Biela 2023), have likely contributed to the long-term and widespread declines in growth and size of all salmon species throughout most of their range (Bigler et al. 1996, Oke et al. 2020). Furthermore, continued warming is also projected to shrink the amount of thermally suitable marine habitat available to each species (Abdul-Aziz et al. 2011, Lindley et al. 2021) and force more salmon into an increasingly crowded BS (Larson et al. 2013, Kaeriyama 2023).

Frequent marine heat waves and high pink salmon abundance are hypothesized to have led to the largest single-year collapse in salmon abundance on record (Ruggerone et al. 2021). Heat waves in the NPO were unusually frequent during 2014–2019 (Litzow et al. 2020b). In 2018 and 2019, a combined 1.34 billion adult pink salmon returned from the NPO, the highest 2 yr abundance since at least 1925 (Fig. 1). In 2020, the combined commercial harvest of all salmon species in Asia and North America declined more relative to average catch in the previous 10 yr (187 million salmon decline) than in any previous 10 yr period since 1925; escapement information indicated that low abundance rather than the COVID-19 pandemic was responsible (Ruggerone et al. 2021). Harvests of Chinook salmon in 2020 were the lowest on record since 1925, declining 54% compared with the previous 10 yr. Chum salmon harvests in 2020 declined 42%, followed by pink (–40%), coho (–27%), and sockeye salmon (–10%). Sockeye salmon harvests beyond those in Bristol Bay declined 44%. In 2021, commercial harvests of pink salmon rebounded to a record level (527 million, or 81% of all salmon), but harvests of chum (–41%), Chinook (–33%), coho (–24%), and sockeye salmon beyond Bristol Bay (–26%) remained low relative to 2010–2019. Harvest of Chinook salmon was the fourth lowest on record (NPAFC 2022a). Thus, the combined effects of both pink salmon and ocean temperatures appear to have contributed to the sharp recent decline in Pacific salmon.

4.3. Implications for salmon hatcheries and ocean carrying capacity

Annual releases of Pacific salmon from hatcheries increased 6-fold from 1970 (0.9 billion juveniles) to 1990 (5.1 billion juveniles), producing approximately 25% of all adult salmon, or 40% of the total mature and immature salmon biomass at sea (Ruggerone & Irvine 2018). This steep rise in overall hatchery production in Asia and North America occurred in part because the primary bottleneck for increased salmon abundance was thought to be in freshwater, and managers believed hatcheries would enable a rapid return to the large harvests that occurred in the early

1900s (Larkin 1974). Also, simulation models and sampling of zooplankton at sea suggested the NPO could readily support more salmon (Sanger 1972, Favorite & Laevastu 1979, Honkalehto 1984, Shuntov et al. 2017). However, some scientists suggested that the ocean could not support large-scale hatchery production without some adverse effects on wild salmon growth and survival (Peterman 1978, 1984a,b), but evidence was somewhat limited at that time (Moberly 1983, Heard 1998, Cooney & Brodeur 1998, Pearcy et al. 1999). Furthermore, Cooney & Brodeur (1998, p. 460) warned 25 yr ago that '[t]o ignore the signals manifested in diminished size of Pacific salmon is to invite potential disaster for these and other resources.' Nevertheless, from 1990 to 2020, annual juvenile salmon released from hatcheries in relatively pristine regions of Alaska and Russia increased by 50 and 75%, respectively, or by approximately 555 million juvenile salmon per year in each region (NPAFC 2022b).

Although hatchery salmon may lead to net gains in commercial harvests in local fisheries, these gains can come at the expense of local wild populations (Amoroso et al. 2017, Ohlberger et al. 2022) and distant populations that co-mingle with them, including depleted and at-risk wild populations from the Pacific Northwest and Alaska (Ruggerone et al. 2012, Larson et al. 2013, Cunningham et al. 2018, Frost et al. 2021). Furthermore, large-scale hatchery production can undermine the natural compensatory density-dependent response that would otherwise benefit wild salmon growth, maturation rate, and reproductive potential during periods of low abundance. For example, in the absence of hatchery salmon, wild salmon would potentially grow faster and thereby have higher reproductive potential (egg mass is proportional to female body mass) at a given age, mature at an earlier age, and therefore have greater survival at sea. The unique biennial patterns shown by salmon interacting with pink salmon provide strong evidence that large-scale hatchery production has unintended consequences and can lead to a tragedy of the commons. The latter topic is expanded upon by Holt et al. (2008).

Some scientists have argued that competition among salmon for prey at sea is limited, and that hatchery fish have little effect on wild populations (Favorite & Laevastu 1979, Shuntov et al. 2017, 2019, Radchenko et al. 2018, Naydenko & Somov 2019). This view is based on calculations suggesting a surplus biomass of prey is available to salmon — that consumption by salmon is only about 1–15% of prey consumed by all epipelagic nekton — and because salmon do not form dense schools that might deplete local concentrations of prey. However, those studies did not consider the nutritional value for each prey species, capture efficiency, or predation risk while foraging. Moreover, they have yet to explain widespread observations of density-dependent growth and survival of salmon, especially the unique biennial patterns of pink salmon abundance that are expressed in the growth, age, survival, and abundance of competing salmon species. Furthermore, investigators such as Shuntov et al. (2017, 2019), who argued that competition among salmon is limited, have investigated the western BS and/or western North Pacific, whereas most studies reporting evidence for competition among salmon were in other regions. Consequently, neither group of scientists has a reason to generalize too widely and deny the validity of the observations and conclusions of the other group.

Salmon typically do not form dense schools while foraging at sea, but they are often found in aggregations or groupings (Hartt & Dell 1986). Evidence collected over multiple decades of sampling salmon on the high seas indicates a significant trade-off between predation risk and foraging success in relation to group size. For sockeye, chum, coho, and pink salmon, the probability of injury (predation risk) decreased with increasing total group size (all salmon species) and conspecific group size, but the probability of consuming prey also declined for each species except pink salmon (Polyakov et al. 2022). For example, the probability of consuming prey declined approximately 20% for sockeye salmon, 6% for chum salmon, and 45% for coho salmon as total group size increased (up to about 2500 salmon per seine net). These findings suggest that salmon groups can deplete local concentrations of prey (Section 3), and that competition is exacerbated by forming groups to reduce predation risk. The decline in prey consumption was greatest for the largest and oldest salmon, which is consistent with the growth decline in older salmon such as Chinook salmon in relation to pink salmon (Section 3). In contrast, pink salmon were not adversely affected by competition, and appeared to experience greater probability of consuming prey when in larger groups.

4.4. Implications of pink salmon on other marine species, ecosystem services, and society

Most of the relationships between pink salmon and other pelagic species reported here imply direct

competition between them for common-pool prey resources or indirect food web responses to pink salmon forcing. Details of the actual mechanisms are not always known. Nonetheless, unique biennial effects have been seen in lower physiological condition, delayed nesting phenologies, lower breeding propensity, lower productivity, and higher mortality of seabirds; slower growth and lower recruitment in forage fishes; fewer births in humpback whales; and reduced body condition, higher death rate, and reduced birth rate of SRKWs (Table 1). In the case of black-legged kittiwakes in PWS, higher numbers of pink salmon appear to enhance the birds' nesting success as a result of avian predators switching from kittiwake eggs and chicks to pink salmon.

The negative effects of pink salmon on the growth, survival, and abundance of other salmon also impacts commercial, subsistence, recreational, and cultural values humans derive from them. Although climate warming has enhanced overall harvests of sockeye salmon in Bristol Bay, for example, approximately 59 million fewer sockeye salmon returned there during 1977–1997 (excluding the cyclic Kvichak population) after interacting with abundant pink salmon in odd-numbered years, and those fish would have had a value to fishermen of approximately US $310 million if they had survived (Fig. 8d; Ruggerone et al. 2003). In many regions of the Pacific Rim, especially in the Arctic–Yukon–Kuskokwim region of western Alaska, people depend on salmon for subsistence and cultural needs in addition to monetary income from commercial fisheries (Brown et al. 2022). Salmon subsistence harvests, particularly Chinook salmon, have declined over the past 25 yr, and this may partially reflect adverse interactions with pink salmon (e.g. Ruggerone et al. 2012, 2016b, Agler et al. 2013, Cunningham et al. 2018, Frost et al. 2021). Although declines in the abundance of salmon are the most obvious impact to humans, declining body size of salmon over time, which is partially linked to growing abundances of pink salmon, also has the potential to affect both humans and ecosystem services such as meals, price, eggs, and marine-derived nutrients per fish (Bigler et al. 1996, Oke et al. 2020).

Lastly, salmon are typically managed for the number of spawners or for harvest rates that rarely consider the size and fecundity of the spawning salmon and the ecosystem services they provide. Such management practices ignore the fact that decreasing body size, which is often related to increasing abundances of pink salmon, leads to fewer eggs being deposited in the spawning gravel for an equivalent number of fish (e.g. Shaul & Geiger 2016, Ohlberger et al. 2020). Declining body size and fecundity in relation to competition for prey can reduce future abundance of salmon, especially Chinook salmon, whose size, fecundity, and abundance has sharply declined over time (Section 3.4.4, Fig. 10).

5. CONCLUSIONS

The most parsimonious explanation for the many, widespread biennial patterns across the broad range of species and trophic levels in the NPO documented in this synthesis is the interaction with pink salmon. The evidence is consistent and strong that pink salmon can exert competitive dominance for common-pool prey resources shared by 4 forage fish species, all 5 species of Pacific salmon and steelhead trout, and 11 species of seabirds (Table 1; Supplement 2). It further indicates that pink salmon can have a strong influence on ecosystem structure and function by, for example, initiating pelagic trophic cascades. Whether or not it can be considered a keystone species sensu Power et al. (1996), pink salmon is clearly a very strongly interacting species in marine ecosystems of the NPO.

We cannot identify every link between pink salmon and other species. However, competing upper trophic level predators serve as proxies for the inferred direct effects pink salmon have on lower trophic level populations of food web species, including zooplankton, forage fishes, and squids. The present lack of abiotic explanations for the many biennial patterns in the natural histories of numerous species that interact with pink salmon should not be construed as evidence that physical forcing, or other biological factors, are not important to them directly or indirectly. Effects of the recent Pacific Marine Heatwave on ocean food webs and individual species are prime examples of such physical forcing (Piatt et al. 2020, Arimitsu et al. 2021).

Scientists should take advantage of the predictable biennial pattern in abundance of pink salmon, and their increasing numbers in response to ocean heating, to test these and other hypotheses about ecosystem function and species and food web interactions. Although the vast spatial scales of oceanic regions limit possibilities for true treatment–control manipulations, the biennial fluctuations fortunately create a unique natural 'experiment' that can illuminate the influence of pink salmon on their competitors and lower trophic levels. Future ecosystem models should include pink salmon as top-down drivers, in addition

to the bottom-up drivers of climate and physical oceanographic forcing. Such information is necessary for effective ecosystem-based management, especially of species harvested by humans (Malick et al. 2017b).

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Did Recent Marine Heatwaves and Record High Pink Salmon Abundance Lead to a Tipping Point that Caused Record Declines in North Pacific Salmon Abundance and Harvest in 2020?

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Total abundance of Pacific salmon returning from the North Pacific Ocean increased following the 1977 ocean regime shift, peaking in 2018 when approximately 950 million pink, chum, and sockeye salmon returned from the ocean (Fig. 1). In 2019, salmon abundance remained exceptionally high (~854 million salmon). Together the 2018/2019 period was the highest two-year period of salmon abundance on record since 1925, nearly 20% greater than the previous two-year high in 2009/2010, and more than 3.2 times higher than average abundance during relatively low salmon production years from 1960 to 1975.

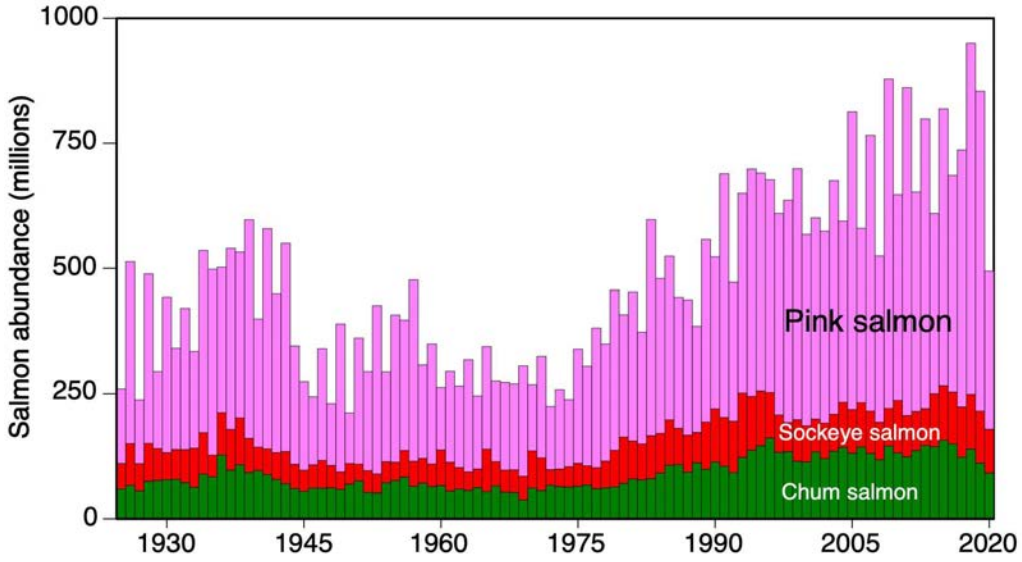


Fig. 1. Total abundance of pink, chum, and sockeye salmon (catch plus spawning escapement) returning from the North Pacific Ocean to streams in North America and Asia, 1925–2020. Updated from Ruggerone and Irvine (2018); see Irvine et al. (2021) for description of methodology for 2016–2020 values and Table 2 here.

Pink salmon continue to dominate the abundance of Pacific salmon returning from the North Pacific, reaching approximately 700 million maturing fish in 2018 and nearly 640 million fish in 2019 (Fig. 1). The exceptional return in 2018 is highly unusual because pink salmon abundance is typically highest in odd-numbered years (Irvine et al. 2014). Approximately 88% and 68% of total pink salmon returned to Asia rather than North America in 2018 and 2019, respectively (Table 1). In contrast, peak abundance of pink salmon in North America occurred in 2013 and 2015 (more than 300 million fish per year). Overall, pink salmon represented approximately 74% of total salmon abundance in 2018/2019. Most pink salmon are of natural origin, but abundance of hatchery pink salmon during 2005 to 2015 was greater than abundance of wild chum salmon and approximately equal to abundance of wild sockeye salmon. Total chum and sockeye salmon represented only 14% and 12%, respectively, of total salmon abundance in 2018/2019. These values exclude Chinook and coho salmon, whose combined reported catch was 1.5% of total salmon catch from the North Pacific during 2018/2019 and approximately 5% of total salmon catch, on average, during 1925 to 2019 (NPAFC 2020).

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Table 1. Total abundance of pink, chum, and sockeye salmon (catch plus spawning escapement) returning from the North Pacific Ocean to streams in Asia and North America, 2016 to 2020. These values extend the 1925 to 2015 salmon abundance database (Ruggerone and Irvine 2018; Irvine et al. 2021), primarily using Approach 3.

	Asia			North America			Total			
Year	Pink	Chum	Sockeye	Pink	Chum	Sockeye	Pink	Chum	Sockeye	Total
2016	335	110	24	97	39	79	432	150	104	686
2017	287	74	21	226	49	79	513	123	101	737
2018	614	98	23	87	42	86	701	140	109	950
2019	435	74	24	203	37	81	639	111	104	854
2020	205	68	17	110	23	71	315	92	87	494

Table 2. Revised abundance of sockeye salmon (millions of fish) returning to the Mainland and Islands region of Russia (M&I), as originally reported by Ruggerone and Irvine (2018). During the 2020 update of the salmon abundance database, we noticed that interceptions of sockeye salmon in the Kuril Islands that began in 2001 were not included in the database. The missing Kuril Islands sockeye catch led to very small increases in the M&I sockeye abundance values from 2001–2005 (<1%), increasing to 10% in 2006–2008, then to 60% in 2009 to 2013, and to 160% in 2014 and 2015. Inclusion of these intercepted sockeye salmon led to a maximum increase of 5% in sockeye abundance returning to Asia and 1% to North America and Asia combined (in 2015). Some of these sockeye salmon would have returned to Kamchatka, but we have assumed for simplicity that all returned to the Mainland and Islands region.

Year	M&I	Asia	North Pacific
2001	0.5	8.5	65.6
2002	0.3	13.8	70.7
2003	0.2	9.8	73.6
2004	0.1	9.1	89.8
2005	0.7	13.0	87.2
2006	0.8	12.6	89.1
2007	0.5	18.3	84.8
2008	0.4	14.5	74.8
2009	0.5	14.8	75.5
2010	0.6	15.1	105.2
2011	1.0	17.3	83.0
2012	0.8	21.1	79.0
2013	0.9	22.4	74.3
2014	0.9	18.2	106.5
2015	1.7	21.9	110.2

Unexpectedly, the high abundance of Pacific salmon came to an abrupt end in 2020. Preliminary commercial catch statistics for all salmon species indicate Pacific salmon harvests, which provide an index of abundance, declined more in 2020 than in any other period on record since 1930 (Fig. 2). Commercial salmon harvests declined by approximately 187 million fish compared with average harvest during the previous 10 years (2010–2019; Fig. 2, NPAFC 2020). Although the COVID-19 pandemic may have reduced commercial harvests to some extent in some regions, most fishery reports and preliminary escapement estimates indicate low abundance rather than harvest impacts from the COVID-19 pandemic led to unusually low harvests of Pacific salmon in 2020.

Harvests of each species of Pacific salmon declined 35%, on average, in 2020 when compared with the previous 10-year average. This decline was greater than in any previous period. Harvests of Chinook salmon in 2020 were the lowest on record since 1925, declining 54% compared with the previous ten years. Chum salmon harvests in 2020 declined 42%, followed by pink (40%), coho (27%), and sockeye (10%). Sockeye salmon harvests declined relatively little because returns to Bristol Bay in the southeastern Bering Sea remained robust and offset the exceptionally low harvests of sockeye salmon in the Gulf of Alaska, British Columbia, Washington, and the Columbia River. Pink salmon returning to the Norton Sound region in northern Alaska in 2020 continued with relatively high returns that began in 2016 (J. Menard, jim.menard@alaska.gov, personal communication), providing evidence for the beneficial effects of the warming ocean on salmon in the extreme north.

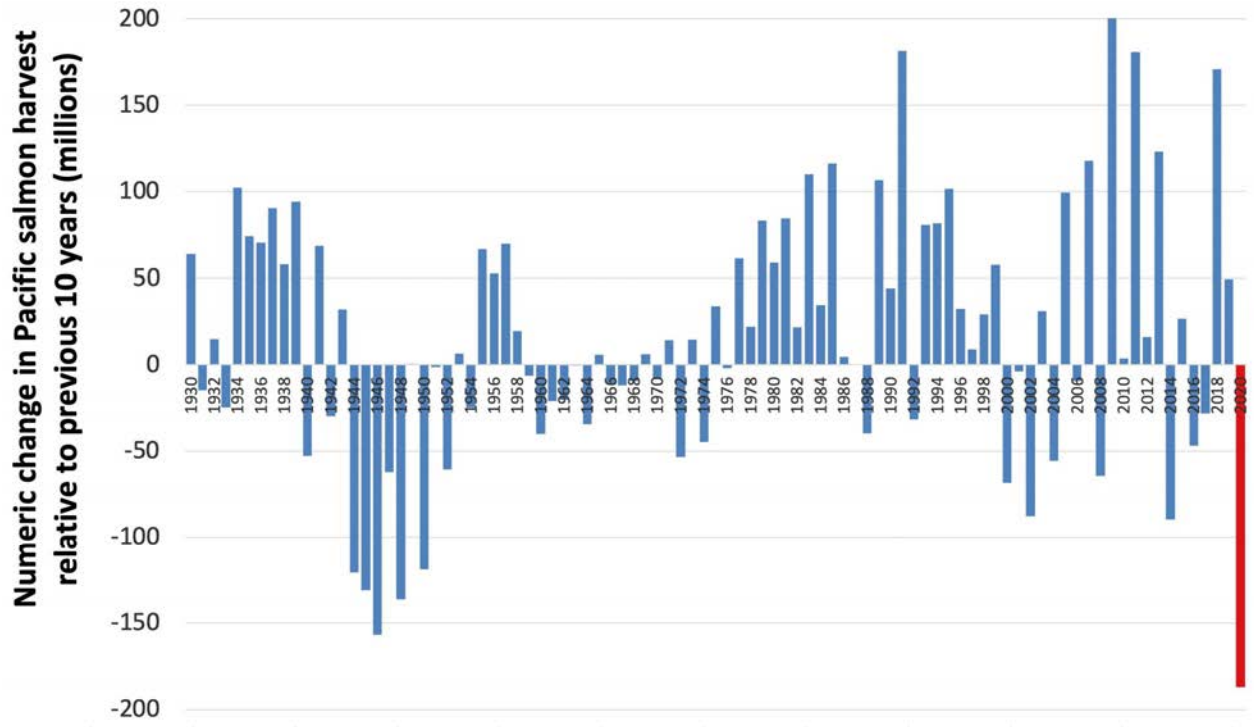


Fig. 2. Change in the commercial catch of Pacific salmon (pink, sockeye, chum, coho and Chinook) relative to the average catch during the previous ten years, 1930–2020. Catch values include both Asia and North America. Data sources: NPAFC (2020, 2021), Choi et al. (2021), Marchenko et al. (2021), Miyauchi and Saito (2021), Munro (2021), PFMC (2021), Velez-Espino et al. (2021).

We hypothesize that a tipping point was reached in the North Pacific Ocean, leading to the substantial decline of all five species of Pacific salmon in 2020. We infer that the tipping point was caused by the combined effects of unusually frequent marine heatwaves since 2014 (Krovnin et al. 2019; Gupta et al. 2020; Litzow et al. 2020) and exceptional back-to-back year abundances of pink salmon in 2018/2019 (Fig. 1). This hypothesis is partially supported by Connors et al. (2020), who reported the combined effects of sea surface temperature (SST) and pink salmon abundance on productivity (return per spawner) of 47 sockeye salmon populations (brood years 1976–2009) ranging from the Fraser River in British Columbia to Bristol Bay, Alaska. Investigators found that a 1.5°C increase in SST (1 standard deviation) was associated with a 23% increase in sockeye productivity in the Bering Sea, a 9% productivity increase in the Gulf of Alaska, but with a 12% decline in productivity in the southern region (British Columbia and Southeast Alaska). The frequent heatwaves following the period considered by Connors et al. (2020) likely contributed to the growing abundance of pink salmon in the north while also contributing to a northward shift in the adverse effects of high SST on production of other salmon species.

Connors et al. (2020), while simultaneously considering the influence of ocean warming, also reported that a 119 million increase in pink salmon abundance (i.e., 1 standard deviation) was historically associated with a 9% decline in sockeye productivity in the Bering Sea and the Gulf of Alaska, and a 21% decline in British Columbia (e.g., Fig. 3). This finding is consistent with the trophic cascade caused by abundant pink salmon (Batten et al. 2018) and other studies indicating adverse effects of pink salmon on the growth, age-at-maturation, survival, and abundance of sockeye salmon, Chinook salmon, coho salmon, chum salmon, marine fishes, seabirds, and potentially southern resident killer whales (Ruggerone and Nielsen 2004; Ruggerone et al. 2016a, 2019; Ruggerone and Irvine 2018). Support for the adverse interaction between pink salmon and other marine species is strengthened by biennial patterns in marine species that are consistent with the biennial pattern in pink salmon in most years; these biennial patterns cannot be explained by physical oceanography. The adverse effect of numerous pink salmon on vital rates of other salmon species is far-reaching because salmon are known to migrate 1,000s of kilometers at sea. For example, 11–38% of Chinook salmon sampled on the southeastern Bering Sea shelf during 2005–2010 originated from the west coast of the contiguous United States (Larson et al. 2013).

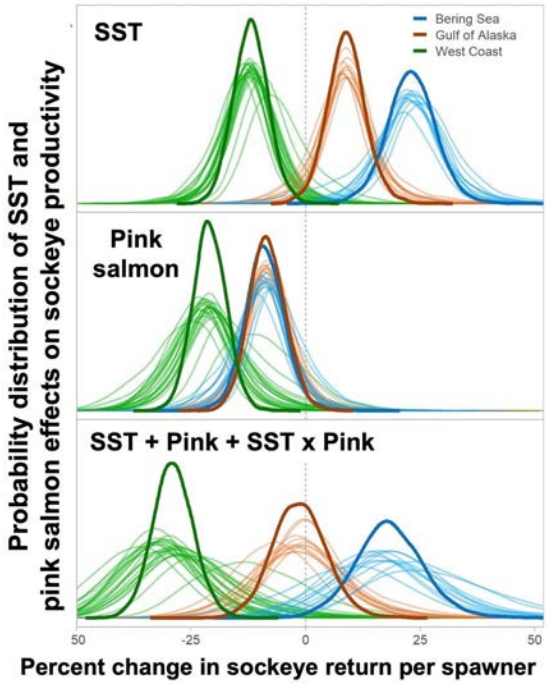


Fig. 3. Effects of a 1 standard deviation increase in both SST (1.5°C) and pink salmon abundance (119 million fish) and the combined effect of both variables on the percentage change in sockeye salmon return per spawner. Empirical model based on 47 sockeye salmon populations (1976 to 2009 brood years) spanning the Bering Sea, Gulf of Alaska, and West Coast (Southeast Alaska through British Columbia) of North America. Thin lines represent each stock; thick lines represent mean of 47 stocks. Source: Connors et al. 2020.

In summary, both pink salmon abundance and high SST were extreme leading up to the salmon decline in 2020, and more extreme than observed in the Connors et al. (2020) study, which ended with the 2009 sockeye salmon brood year. Furthermore, pink salmon abundance in 2018 did not decline as in past even-numbered years. We hypothesize that a tipping point was caused by the record-setting back-to-back-year abundances of pink salmon and unique ocean conditions leading up to the salmon decline in 2020. This hypothesis is consistent with research that has uncovered non-stationary effects of ocean temperatures on salmon catch in the Gulf of Alaska, including negative effects of recent heatwaves on catch (Litzow et al. 2020).

Preliminary 2021 commercial harvest data indicate at least some populations improved from the low numbers in 2020. Alaska and Russia pink salmon abundances appear to have rebounded to the exceptionally high values in 2019. Sockeye salmon returning to Bristol Bay, Alaska, set a new record high in 2021 (66 million fish (catch and escapement); T. Sands, ADF&G, personal communication), apparently in response to favorable early marine growth in the Bering Sea (e.g., Ruggerone et al. 2007) and relatively few maturing pink salmon in 2020 (Ruggerone et al. 2016b). In contrast, commercial harvests of Chinook, coho, chum, and sockeye salmon remain somewhat low in many regions of Alaska and Russia. Further evaluation of 2021 and 2022 harvests and returns of Chinook, coho, chum, pink, and sockeye salmon are needed to evaluate the validity of our tipping point hypothesis.

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Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea

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Climate change in the last century was associated with spectacular growth of many wild Pacific salmon stocks in the North Pacific Ocean and Bering Sea, apparently through bottom-up forcing linking meteorology to ocean physics, water temperature, and plankton production. One species in particular, pink salmon, became so numerous by the 1990s that they began to dominate other species of salmon for prey resources and to exert top-down control in the open ocean ecosystem. Information from long-term monitoring of seabirds in the Aleutian Islands and Bering Sea reveals that the sphere of influence of pink salmon is much larger than previously known. Seabirds, pink salmon, other species of salmon, and by extension other higher-order predators, are tightly linked ecologically and must be included in international management and conservation policies for sustaining all species that compete for common, finite resource pools. These data further emphasize that the unique 2-y cycle in abundance of pink salmon drives interannual shifts between two alternate states of a complex marine ecosystem.

ocean ecology | exploitative competition | consumer front | interaction strength | carrying capacity

Predator control of community structure and ecosystem function became a tenet of intertidal and nearshore marine ecology following early studies of Paine and others (1–3), yet with few exceptions (4, 5), until more recent times the idea has been less well appreciated for open oceans. Growing attention now is being paid to the overexploitation of pelagic species, particularly those at higher trophic levels currently and in the past, and effects on ocean ecosystems of the loss, or development, of top-down forcing (6–12).

The prevailing view has long held that most biological change in ocean ecosystems, apart from human exploitation, is driven from the bottom up (13–16). One striking example that has been linked to bottom-up processes driven by climate change is the burgeoning abundance of wild Pacific salmon (*Oncorhynchus* spp.), and in particular pink salmon (*Oncorhynchus gorbuscha*), in the subarctic North Pacific Ocean and Bering Sea (SNPO/BS). Underpinning the notion initially were studies that found (*i*) strong coherence between decadal patterns in the Aleutian Low pressure system, which exerts a large influence over climate in the North Pacific Ocean, and patterns in salmon production across a broad region of the SNPO/BS (17, 18); (*ii*) decadal patterns in primary production that could be explained by the effect of the Aleutian Low pressure system on basin scale wind fields (19); and (*iii*) decadal patterns in zooplankton, squid, and pelagic fish production that also were correlated with meteorological forcing over the North Pacific Ocean and consistent with patterns in primary production (20). Thus, the general explanation for waxing and waning abundances of salmon over the record in the 20th century was that physical forcing by shifts in the strength and position of the Aleutian Low altered winds, ocean temperatures, and primary and secondary production to the benefit or detriment of salmon. A decadal scale oscillation in the Aleutian Low, now often referred to as the Pacific Decadal Oscillation (PDO) (21), has been linked to numerous physical and biological variability in the SNPO/BS in addition to salmon abundance (21–23).

It was subsequently shown that salmon population responses and their relation to the PDO were out of phase between Alaska and the northwest coast of North America during much of the 20th century (24); that warm anomalies in coastal temperatures were associated with increased survival of salmon in Alaska; and that regional-scale variability in ocean temperature was a better predictor of salmon survival than large, basin-scale variability characterized by the PDO (25). A recent analysis from around the rim of the North Pacific Ocean found regional covariance in abundance of pink salmon, chum salmon (*Oncorhynchus keta*), and sockeye salmon (*Oncorhynchus nerka*) associated with the Aleutian Low, and with smaller scale spatially coherent, but regionally distinct, patterns in climate (26).

Water temperature can be important to the early growth and survival of pink salmon fry directly by its effect on physiology and indirectly by its effect on the timing and development of zooplankton prey stocks in nursery areas, which commonly is advanced and greater in warmer years than in cooler years. In cooler springs, fry grow more slowly and a greater number die both from lack of food and from an increased susceptibility to predators (27, 28). For example, a conceptual model for Prince William Sound, Alaska, holds that, in years of abundant spring zooplankton, fry grow faster and remain longer in the shelter of inshore nurseries where they are protected from walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasii*), two chief predators that remain offshore feeding primarily on swarms of large calanoid copepods and other macrozooplankton.

Significance

Wild salmon in the North Pacific Ocean, particularly pink salmon, have grown greatly since the mid-1970s apparently due to bottom-up effects of climate change on ocean physics and production processes. Pink salmon spend less than 2 y at sea and most stocks alternate between high and low levels of abundance every other year. In years of high abundance, they now constitute a pelagic consumer front as they return to their spawning rivers, exert top-down control over the open ocean ecosystem by outcompeting other species for shared prey resources, and drive major ecological shifts between years of high and low abundance. Their effect on competing species must be considered in international conservation policies and when developing informed ecosystem-based management strategies.

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See Commentary on page 6534.

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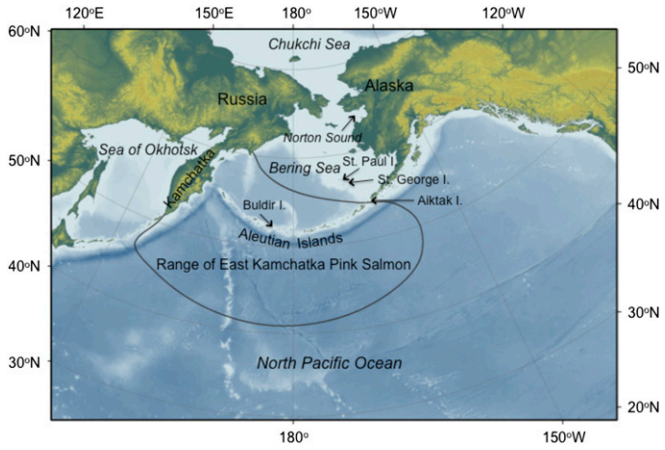


Fig. 1. The northern North Pacific Ocean and Bering Sea and locations of places discussed in the text. Salmon distribution is adapted from ref. 37.

In cooler years of lower zooplankton biomass inshore, fry grow more slowly, move offshore earlier, and suffer higher predation by pollock and herring due to spatial overlap, smaller size, and less alternative prey for those two predators (28).

Although the relationship between climate and pink salmon survival is likely complex, fluctuations in abundance appear to be modulated in large measure directly and indirectly by the thermal environment in which a stock lives. Such a fundamentally bottom-up explanation is bolstered by observations of high growth and survival rates of pink salmon during the period of warmer ocean temperatures and population increase (29, 30), and at this time provides a more parsimonious explanation for population dynamics than would explanations invoking strictly top-down control across such a broad region. Now, however, several lines of evidence indicate that pink salmon themselves are having a large top-down influence on other salmon species, other upper trophic level pelagic species, plankton standing stocks, and by inference, the functioning of the open-ocean ecosystem in the SNPO/BS.

Pink Salmon in an Ecosystem Context

Pink salmon are the most abundant of the wild Pacific salmon, representing about 70% of all returning fish each year across their range (31). They have several early life history characteristics that seem to explain their relatively great abundance, and a short 2-y life cycle from egg to spawning adult (30). Most stocks have interannually alternating weak and strong runs and strong runs can be in either even years or odd years: shifts between strong runs in odd years to strong runs in even years (and visa versa) have been documented in some stocks, even-year and odd-year brood lines are reproductively isolated, and the abundance of fish in strong runs is commonly far greater than in weak runs (32–36). The cause of this phenomenon is not known.

The majority of pink salmon in the northwestern and central SNPO/BS are of Asian origin, especially fish that spawn in rivers of the eastern Kamchatka Peninsula and western Bering Sea (Fig. 1) that are odd-year–dominant stocks (34). Although data are reported as "eastern Kamchatka," more than 90% of those fish spawn in river tributaries of the western Bering Sea (38). The total run size (catch plus escapement) has been steady in even years for the past several decades, averaging about 17 ± 2 (SEM) × 10^6 fish per y from 1972 through 2012, whereas runs in odd years rose from an average of about 47 ± 6 × 10^6 fish per y in 1971–1987, to 83 ± 7 × 10^6 fish per y in 1989–2007, and to 173 × 10^6 fish in 2009 and 225 × 10^6 fish in 2011 (34, 39) (Table S1). The increases were not augmented by hatchery releases (34). A smaller stock of even-year–dominant pink salmon spawns in the eastern Bering Sea, primarily in Norton Sound, with run sizes there averaging 3.3 × 10^6 fish in even years and 0.56 × 10^6 fish in odd years between 1997 and 2012 (40).

Questions concerning the carrying capacity of the North Pacific Ocean in regard to salmon emerged in the early 1990s with increasing overall numbers of fish (41, 42). Differences in diets, growth, condition, distribution, and catch of three competing species—pink salmon, sockeye salmon, and chum salmon—in even years compared with odd years suggested that pink salmon were placing a disproportionately high demand on pelagic production (43–48). It was further suggested that biennial oscillations in standing stocks of phytoplankton and zooplankton in the central SNPO/BS, apparent by 1990 and out of phase with each other, represented a trophic cascade initiated in odd years by prey demand of pink salmon—during odd years, relaxed grazing pressure by depressed numbers of macrozooplankton, among the primary prey of pink salmon, led to an elevated standing stock of phytoplankton in summer (49, 50). This conclusion was reached after considering variability in physical indices and forcing factors, including the Northern Hemisphere Zonal Index, solar radiation flux, surface wind speed, sea surface temperature, salinity, density, and nutrient levels that were associated with interannual and decadal patterns in production at lower trophic levels, but not systematic biennial oscillations.

Such a relationship between zooplankton and phytoplankton abundance would explain a conspicuous biennial alternation in body size of *Neocalanus* copepods in the central North Pacific Ocean, during a study spanning the 1980s and 1990s, that generally was poorly correlated with climatological and environmental variables as well (integrated mean water column temperature from surface to 150 m, vertical stability index, North Pacific Index, and Southern Oscillation Index) (51). The authors found that individuals were larger in odd years, when competition for phytoplankton would have been less, than in even years when competition would have risen. The one significant correlation they did report was a positive one between body size of *Neocalanus cristatus* and chlorophyll *a* concentration, which would be expected in this scenario.

Seabirds in a Pink Salmon Context

Observations in the Bering Sea in odd years of lower body mass and liver mass of short-tailed shearwaters (*Puffinus tenuirostris*), a Southern Hemisphere seabird that spends the austral winter in the SNPO/BS and Chukchi Sea (52), and two to five times higher

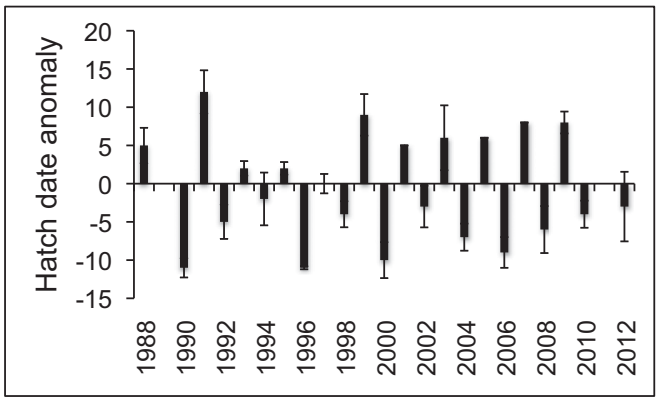


Fig. 2. Nesting phenology (mean hatch date anomaly, days) using the example of tufted puffins at Buldir Island. Positive values are late, and negative values are early: no data for 1989 or 2011. Error bars denote ±1 SEM. Data are from ref. 67. See Tables S2 and S3 for phenology data for all species tested.

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Table 1. Comparisons of seabird nesting parameters in even years versus odd years

Parameter	No. of tests	No. rejections (%)	No. expected
Clutch size	9	4 (44)	1
Hatch date	25	21 (84)	3
Laying success	8	6 (75)	1
Hatching success	27	9 (33)	3
Fledging success	21	6 (29)	2
Productivity	21	9 (43)	2
Overall	111	55 (50)	11

Number of tests of the null hypothesis of no difference between mean values of seabird nesting parameters in even years versus odd years, the number (percentage) of hypotheses that were rejected at $\alpha = 0.10$, and the number that would be expected to be rejected at $\alpha = 0.10$ due to chance alone.

strandings of shearwaters on the coast of eastern Kamchatka (53), provided the first evidence (to the authors' knowledge) of the influence of pink salmon over a competing species besides other salmon (and see ref. 54). Among the important prey of pink salmon (29, 55, 56), copepods (*Neocalanus* spp.), euphausiids (*Thysanoessa* spp.), squids (Gonatidae), myctophids (Myctophidae), and Atka mackerel (*Pleurogrammus monopterygius*) are at times also important prey of shearwaters and of resident seabirds wintering in the subarctic North Pacific Ocean and nesting in the Aleutian Islands and Bering Sea (52, 57–66).

Systematic annual monitoring of nesting seabirds at four major colonies in the southern Bering Sea and Aleutian Islands (Fig. 1) began in 1984 at St. George Island and St. Paul Island (Pribilof Islands), 1988 at Buldir Island (western Aleutian Islands), and 1995 at Aiktak Island (eastern Aleutians) (67–70). One of the most conspicuous patterns over the years, and the one that first alerted us to the possibility of a connection between the birds and pink salmon, is the alternating early (even year)–late (odd year) nesting phenology of tufted puffins (*Fratercula cirrhata*) at Buldir (Fig. 2). This led us to examine phenology and up to five additional elements of the breeding biology of tufted puffins and as many as 15 other seabird species of two feeding guilds—omnivores (12 species that consume a mixture of fishes, squids, zooplankton, and other invertebrates) and planktivores (4 species that consume primarily zooplankton)—at those islands for

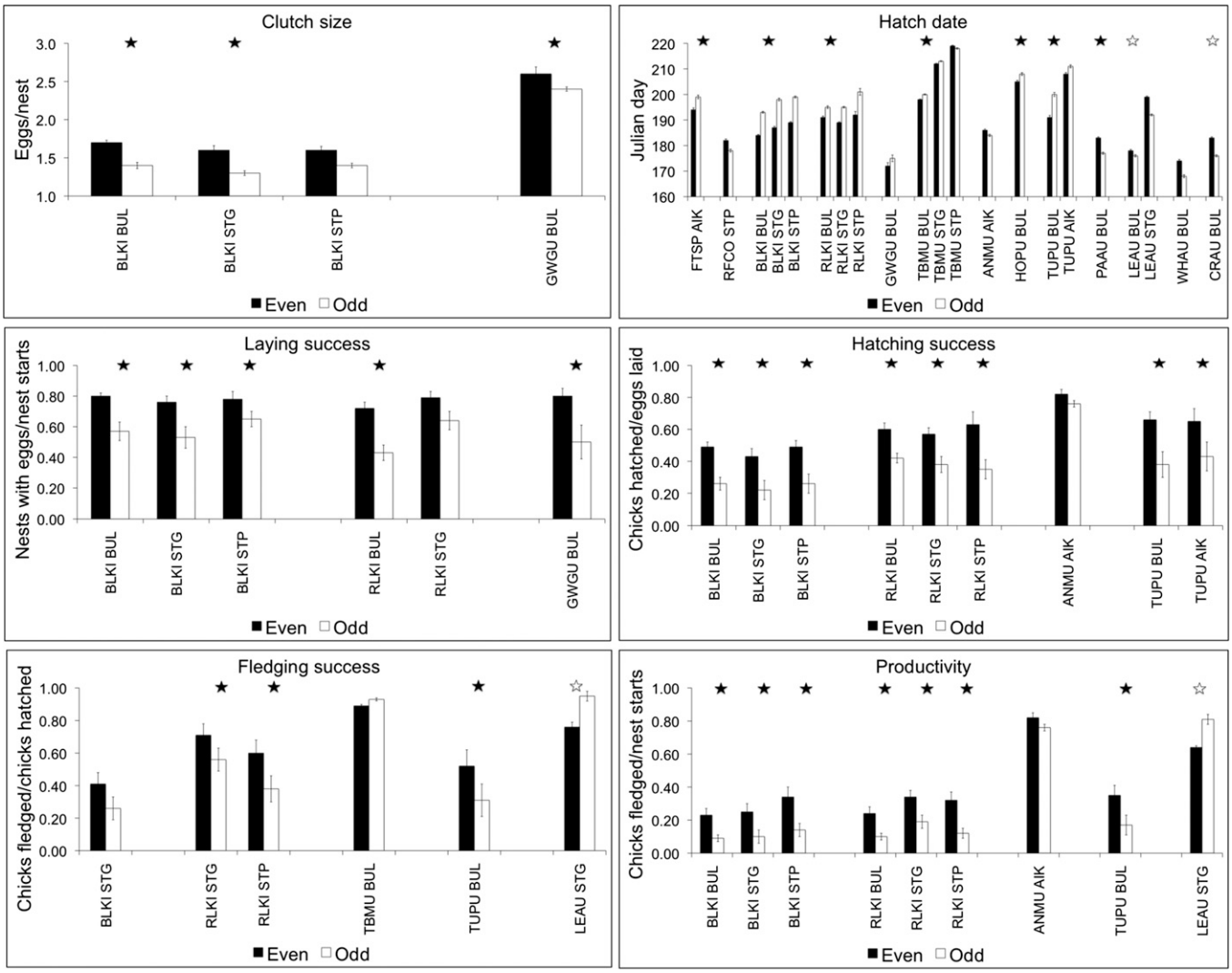


Fig. 3. Mean values of seabird breeding parameters that exhibited differences between even years and odd years at $\alpha = 0.10$. See Tables S2 and S3 for all parameter tests in all species and sample sizes. Error bars denote ±1 SEM. Filled stars indicate relationships to eastern Kamchatka pink salmon abundance (linear regression, $\alpha = 0.10$); open stars indicate relationships to western Alaska pink salmon abundance at $\alpha = 0.10$ (Table S4). See Table S2 for species abbreviations. BUL, Buldir Island; STG, St. George Island; STP, St. Paul Island. Data are from refs. 67–70.

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similar even-year–odd-year patterns. We further examined the possible connection between seabirds and salmon by comparing seabird nesting parameters to the annual run size of eastern Kamchatka pink salmon, and in particular cases to the annual run size of pink salmon in western Alaska. Using these approaches, we found compelling evidence that pink salmon have a major influence on diets, numbers, phenology, fecundity, and/or productivity of one or more species (in the order of 10^7 individuals) at one or more of these islands.

Results

We ran 111 tests of the null hypothesis that there was no difference in mean values of six nesting parameters of 16 species at four islands between even and odd years (Table 1 and Tables S2 and S3). Rejection of the null hypothesis for the individual parameters at $\alpha = 0.10$ ranged from 29% to 84% and was 50% overall. These rates exceeded in all cases the number that would be expected by chance alone and demonstrated strong directionality and the large magnitude of effect that we hypothesize pink salmon have on seabirds, and the ecosystem, of the SNPO/BS.

Omnivorous Seabirds. Phenology, as indexed by mean hatch date, was later (at $\alpha = 0.10$) in odd years than in even years for 13 of the 20 species/island samples and was seen on all islands: the difference was particularly pronounced in black-legged kittiwakes (*Rissa tridactyla*), which had mean hatch dates that were 9–12 d later in odd years (Fig. 3 and Tables S2 and S3). It was earlier by 4 d for red-faced cormorants (*Phalacrocorax urile*) at St. Paul, and earlier for ancient murrelets (*Synthliboramphus antiquus*) at Aiktak and for common murres (*Uria aalge*) and thick-billed murres (*Uria lomvia*) at St. Paul by 2, 4, and 1 d, respectively. Clutch size was smaller in odd years than in even years for black-legged kittiwakes at all three islands and for glaucous-winged gulls (*Larus glaucescens*) at Buldir. Laying success (number of nests with eggs per number of nest starts) was lower in odd years for black-legged kittiwakes at all three islands, for red-legged kittiwakes (*Rissa brevirostris*) at Buldir and St. George (and by 15% at St. Paul, although it missed the $\alpha = 0.10$ criterion), and for glaucous-winged gulls at Buldir. Hatching success (number of eggs hatching per number of eggs laid) was lower in odd years for both species of kittiwakes at all three islands, for tufted puffins at Buldir and Aiktak, and for ancient murrelets at Aiktak. Fledging success (number of chicks fledged per number of eggs hatched) was lower in odd years for tufted puffins at Buldir, both species of kittiwakes at St. George, and red-legged kittiwakes at St. Paul (and black-legged kittiwakes by 12%, although it too missed the $\alpha = 0.10$ criterion), but was higher in odd years for thick-billed murres at Buldir. Productivity (number of chicks fledged per number of nest starts) was lower in odd years for both species of kittiwake at all three islands, for ancient murrelets at Aiktak, and for tufted puffins at Buldir.

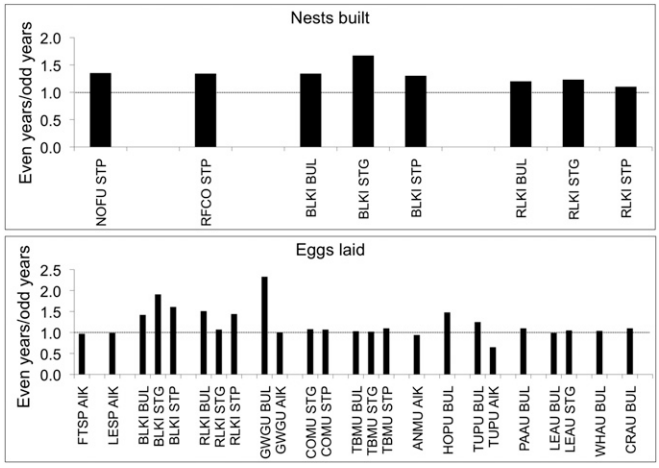


Fig. 4. Ratios of the numbers of nests built and eggs laid in even years compared with odd years across all years. See Table S2 for species abbreviations. AIK, Aiktak Island; BUL, Buldir Island; STG, St. George Island; STP, St. Paul Island. Data are from refs. 67–70.

Counts of nests of some species that build nests (not all species of seabirds do) at Buldir and the Pribilofs were made in sufficient numbers of even and odd years to compare differences, and in all cases more nests were built in even years than in odd years (Fig. 4). Although these are small sample sizes and not all differences had high significance levels (Table S5), they strongly support the other even-year–odd-year evidence of an effect of pink salmon on these birds. In addition, finally, black-legged kittiwakes at all three islands, red-legged kittiwakes at Buldir and St. Paul, and glaucous-winged gulls, horned puffins (*Fratercula corniculata*), and tufted puffins at Buldir laid conspicuously more eggs in even years than in odd years (Fig. 4).

Nesting parameters of several of the omnivores also exhibited negative correlations with the run size of eastern Kamchatka pink salmon (Fig. 3 and Table S4). Clutch size of black-legged kittiwakes at Buldir and St. George was well correlated with salmon abundance, and of glaucous-winged gulls at Buldir. The hatch date for five of six species at Buldir was highly correlated with salmon abundance, although not correlated at either of the Pribilof islands despite large differences in mean hatch dates between even and odd years. Laying success of black-legged kittiwakes at all three islands and of red-legged kittiwakes and glaucous-winged gulls at Buldir was correlated with salmon abundance. Hatching success of both species of kittiwakes at all three islands and of tufted puffins at Buldir and Aiktak was also correlated with salmon abundance. Fledging success was generally less well correlated with salmon abundance, reflecting the smaller, or lack of, differences between mean values in even and odd years, but still was correlated for black-legged kittiwakes at St. Paul, for red-legged kittiwakes at St. George and St. Paul, and for tufted puffins at Buldir. Productivity was strongly correlated with pink salmon abundance for both species of kittiwakes at all islands and for horned and tufted puffins at Buldir.

There were no consistent geographic patterns in the magnitude of differences between mean values of parameters in even and odd years for the three species that were sampled at Buldir, St. George, and St. Paul (Table 2), nor were there consistent geographic patterns in the strength of relationships of nesting parameters to eastern Kamchatka pink salmon run size (Table S4).

Planktivorous Seabirds. The limited data on breeding parameters of planktivores—four species at Buldir and one species at St. George—revealed either an opposite pattern to that of omnivores, or no pattern at all (Fig. 3 and Tables S2 and S3). Only the hatch date was very different between even years and odd years at Buldir, and in all cases it was earlier (by up to 7 d) in odd years. The hatch date for least auklets (*Aethia pusilla*) at St. George also was much earlier in odd years, and fledging success and productivity were higher. The hatch dates of least auklets and crested auklets (*Aethia cristatella*) at Buldir were well correlated with Norton Sound pink salmon abundance, as were fledging success and productivity of least auklets at St. George (Fig. 3 and Table S4).

Diets of least auklets at Buldir during the chick period (mid-June to mid-July) differed between even years and odd years (Fig. 5). In 1994–2009, the dominant prey of least auklets, the large calanoid copepod taxon *Neocalanus plumchrus/flemingeri* (the two species are difficult to differentiate), had a mean frequency of occurrence of 97 ± 2% and there was no difference between

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Table 2. Values of nesting parameters in even years divided by values in odd years for omnivorous species that were each measured at Buldir (BUL), St. George (STG), and St. Paul (STP)

Species location	Clutch size	Hatch date	Laying success	Hatching success	Fledging success	Productivity
BLKI BUL	1.21	0.95	1.40	1.88	1.00	2.56
BLKI STG	1.23	0.94	1.43	1.95	1.58	2.50
BLKI STP	1.14	0.94	1.20	1.88	1.34	2.43
RLKI BUL	na	0.98	1.67	1.43	0.96	2.60
RLKI STG	na	0.97	1.23	1.50	1.28	1.74
RLKI STP	na	0.96	1.35	1.75	1.58	2.67
TBMU BUL	na	0.99	na	1.03	0.96	1.00
TBMU STG	na	1.00	na	0.98	1.00	1.00
TBMU STP	na	1.00	na	0.91	0.99	0.89

BLKI, black-legged kittiwake; RLKI, red-legged kittiwake; TBMU, thick-billed murre; na, not applicable. Data are from refs. 67, 69, and 70.

even and odd years. In 1994–2006, it made up an estimated 65 ± 7% of the biomass of prey brought to chicks; however, the proportion in even years (excepting 2000 when it was anomalously low at just 12%) was 77 ± 6%, but 62 ± 9% in odd years ($P = 0.18$). Although the apparent difference did not have high statistical significance, it is consistent with even-year–odd-year differences found in the consumption of principal secondary prey—that is, with the exception of euphausiids, consumption of *N. cristatus*, decapods, hyperiids, and pteropods was generally higher in odd years than in even years. The lower consumption of euphausiids in odd years may have been proportional to a lower abundance of euphausiids in odd years due to pink salmon predation.

Likewise, whiskered auklets (*Aethia pygmaea*) at Buldir (67) consumed more *Neocalanus cristatus*, their dominant prey, during the chick rearing period in even years than in odd years (52 ± 8% versus 32 ± 11%; $P = 0.18$). Although this difference also was not highly significant, it and the differences in least auklet diets

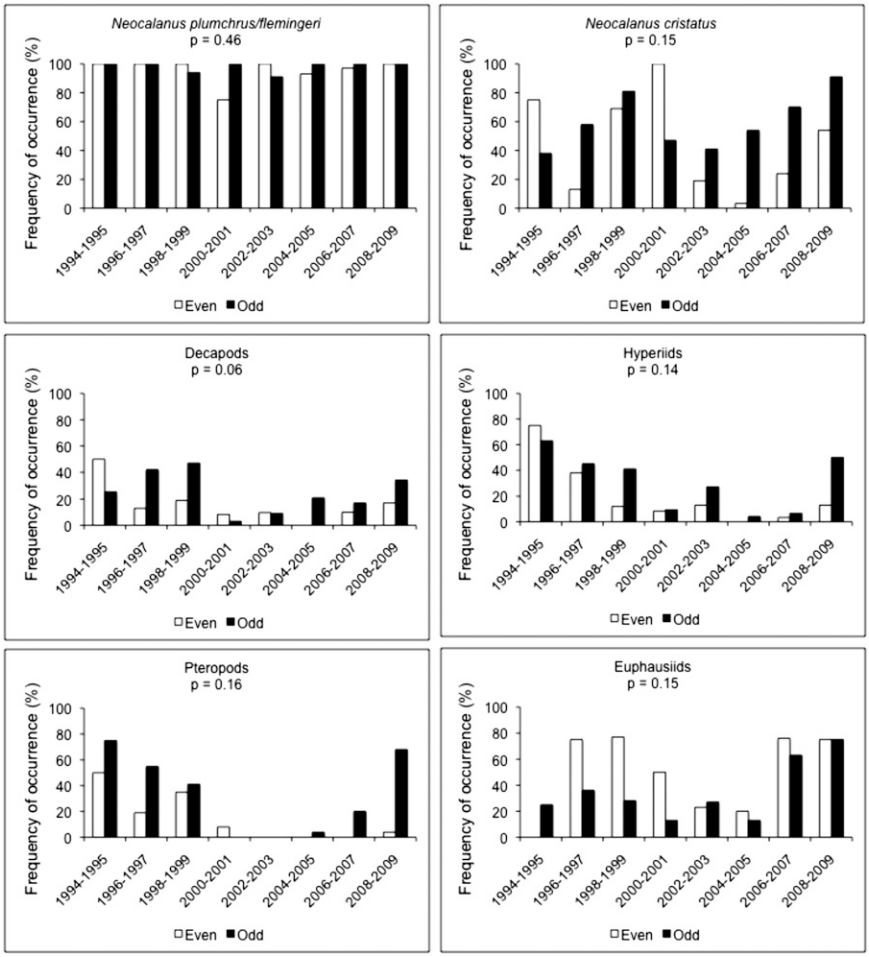


Fig. 5. Frequency of occurrence (percentage) of principal prey in diets of least auklets at Buldir Island. Significance levels (*P*, Student *t* test; $n = 16$ y) are for differences between mean values in even years and odd years across all years. Data are from ref. 67.

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between even and odd years are likely biologically significant. Such a conclusion is supported by continuous plankton recorder data primarily from the southern Bering Sea (173 W × 173 E, 52 N × 54 N; appendix 5 in ref. 66) that show large differences in the abundance of *N. cristatus* and *N. plumchrus/flemingeri* across even and odd years—4.8 ± 2.3 g versus 0.06 ± 0.01 g, $P = 0.14$; and 3.9 ± 0.6 g versus 0.6 ± 0.3 g, $P = 0.0071$, respectively (Fig. 6).

Discussion

The great interaction strength of pink salmon during years of high abundance apparently derives from voracious consumption to fuel exceptionally rapid growth in spring–summer of their second year—the mass of maturing fish increases by some 500%, from about 300 to 1,500 g, in just 4 mo between March and July when they spawn (29). Prominent among their prey are species important to the structure of the plankton community of the SNPO/BS and to other consumers, such as seabirds, both directly and indirectly as trophic links. Exploitative competition is common within many trophic levels in many ecosystems, but there are few cases where it has been identified or suspected among lower and higher trophic levels in the open ocean (e.g., refs. 71–74). Now we show evidence of strong exploitative competition by pink salmon visited upon pelagic species, besides other species of salmon, in the SNPO/BS: in years of high abundance pink salmon consume zooplankton and micronekton in sufficient amounts to compromise a variety of nesting parameters of resident seabirds, as well as the survival of migratory seabirds.

Most of the omnivorous seabirds considered here winter in the northern North Pacific Ocean and southern Bering Sea (59, 60, 75, 76). Thus, most species are exposed to competition with pink salmon during much of the year, and competition would intensify rapidly in late spring and early summer when fish move back into the Bering Sea from the North Pacific Ocean. Any carryover effects of prebreeding food stress on nesting success (77) would exacerbate the effect of continuing competition through the early to mid stages of nesting.

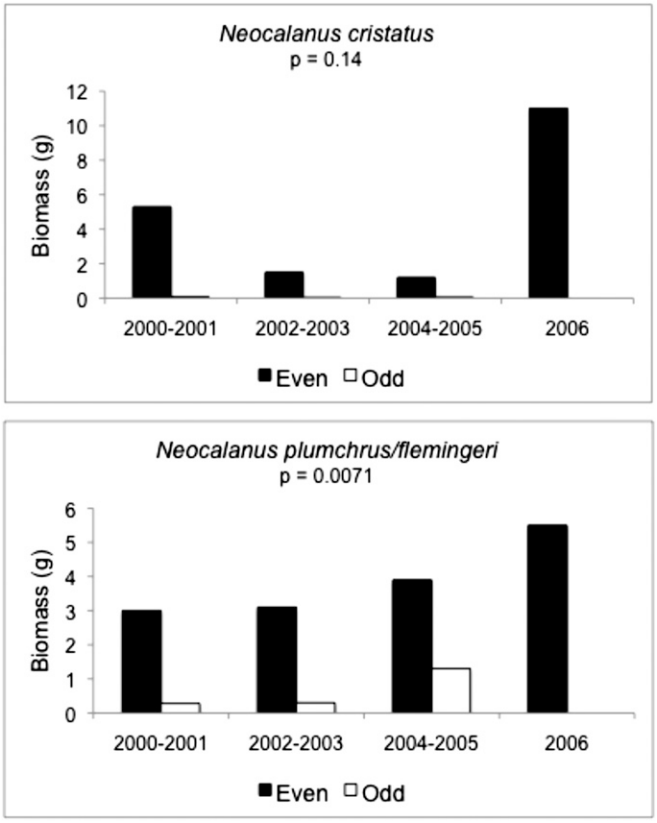


Fig. 6. Biomass of *Neocalanus* copepods in continuous plankton recorder standardized tows in the southern Bering Sea. Significance levels (*P*, Student *t* test; $n = 7$ y) are for differences between mean values in even years and odd years across all years. Data are from ref. 66.

This comports reasonably well with the timing of the migration of eastern Kamchatka pink salmon (78). Most fish are in the northern North Pacific Ocean through May (coincident with prelaying), which would explain the strong relationships of phenology and laying success with salmon abundance. The fish begin moving back into the Bering Sea through the Aleutian Islands and Bering Sea basin in June (coincident with laying and incubation), and by July (coincident with peak hatch) they are moving into the central and western Bering Sea. Thus, by the chick period (July–August) the bulk of the fish are in or approaching their spawning rivers and their influence is apparently diminished. Their distribution and the timing of migration vary between years depending on oceanographic conditions, particularly temperature (79), which would be expected to lead to interannual variability in the strengths of relationships with various elements of seabird breeding biology.

There is the question of why planktivorous seabirds exhibit the opposite pattern in phenology—that it is advanced in odd years and delayed in even years and why least auklets on St. George have higher fledging success and productivity in odd years. However, the consistent differences between mean values in even years and odd years also suggest a connection to pink salmon. One possibility is that the differences are due not to effects of eastern Kamchatka pink salmon, but to effects of pink salmon from western Alaska that spawn in rivers emptying into the eastern Bering Sea and that have strong runs in even years (34). These fish appear to move out of the Bering Sea and into the northeastern North Pacific in winter, and maturing fish return in spring through the central and eastern Aleutian Islands and southeastern Bering Sea (78, 79). Although the western Alaska stock is smaller than the eastern Kamchatka stock, as they return in spring and early summer their numbers are concentrated in a comparatively smaller geographic region, which would concentrate possible effects on resource pools shared with auklets and other species. Thus, least auklets on St. George would compete with them from prelaying through much of the breeding season, which would explain the correlations between their breeding parameters and western Alaska pink salmon abundance. Auklets from elsewhere that winter in the eastern Aleutian Islands, for example, whiskered auklets (80, 81), would be exposed to competition with western Alaska pink salmon in winter–spring, but likely not in summer, which would explain why only phenology differs between even and odd years and why it is delayed in even years. Alternatively, auklets from the western Aleutian Islands, if they winter in the western North Pacific Ocean off Japan and the Kurile Islands (82), might be exposed to competition with Sea of Okhotsk pink salmon, which also are dominant in even years and highly abundant (34).

Neocalanus plumchrus/flemingeri and *N. cristatus* commonly dominate the biomass of zooplankton in the SNPO/BS and are major conduits of energy between phytoplankton and higher trophic levels, in large measure because they accumulate a high lipid content in summer in preparation for overwinter diapause (83). They are thus high-quality prey for planktivores including least auklets, whiskered auklets, pink salmon, and others. Although some of the secondary prey of least auklets and whiskered auklets also have comparatively high lipid concentrations, e.g., euphausiids, many are of much lower energy density (84). The rise in occurrence of secondary prey in auklet diets in odd years is presumably related to the same phenomenon in chum salmon in the SNPO/BS—in even years chum salmon diets include high lipid copepods, euphausiids, and other crustaceans,

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but in odd years their diets are dominated by lower lipid prey, primarily gelatinous taxa such as pteropods, appendicularia, and coelenterates, due apparently to the depressing effect on crustacean biomass of pink salmon predation (43). Similarly, diets of pink, chum, and sockeye salmon in the northeastern North Pacific Ocean and Bering Sea contain different levels of important prey in even and odd years (46, 56).

Depression of seabird productivity cannot be tied to long-term trends in the abundance of any of the species, trends that vary among species and islands (67–70, 85). However, the combination of fewer birds attempting to nest in odd years; fewer eggs being laid, and later, by those that do attempt to nest; and poorer reproductive success by some species raises questions for the future. Seabirds are long-lived, K-selected animals, a strategy that dampens effects of interannual variability in productivity on abundance, but increases the sensitivity of populations to adult mortality. However, over the long term they do depend on reproduction, and the combination of depressed productivity every other year, by as much as 62% for both species of kittiwake, coupled with possible deleterious effects of physiological stress on developing chicks and reproductive life spans of adults experiencing biennial physiological stress (86) could lead to declines in the abundance of the more sensitive species if pink salmon numbers remain at high levels and seabird mortality begins to outpace recruitment. That not all seabird species were affected equally likely reflects differing degrees of ecological separation from pink salmon, which could include the extent of dietary overlap and spatial and temporal physical overlap, and the behavioral ability of some (e.g., murres in particular) to buffer effects of variability in prey quantity and quality on breeding success (87).

Ocean temperature has steadily risen in the western Bering Sea since the middle of the last century, with a pronounced increase in the 2000s that corresponded to the most recent increase in pink salmon abundance (39). One would expect that there is an optimum thermal window above and below which salmon populations cease to prosper (88–91), although the unusually large aerobic scope and cardiorespiratory capacity of pink salmon significantly broadens their range of thermal tolerance (92). However, even if pink salmon abundance experienced no further growth, important questions remain concerning their impact on ecosystem function in the SNPO/BS and the capacity of ocean production processes to support the current biomass of many higher trophic level species including salmon, other fishes, seabirds, and recovering populations of great whales. The potential problem may grow over the course of this century if habitat shrinks due to projected ocean warming and competitive dominance of pink salmon increases if they and other species become more tightly crowded (91).

The resource vacuum and altered community composition left behind as pink salmon migrate back through the SNPO/BS in spring–summer are functionally equivalent to effects of consumer fronts described in a variety of terrestrial and marine ecosystems (93). Although consumer (fish) density would not be as high per square meter as in other ecosystem types, at the geographic scale over which the process occurs (about 1.3×10^6 km^2 in the Bering Sea basin alone) it bears a resemblance, particularly if pink salmon tend to coalesce as their migration progresses. In this case, the movement of the consumers is not necessarily driven by serial depletion of resources at the "front," but by the biological imperative to return to their natal streams to reproduce. Consumer fronts in open ocean ecosystems previously have not been described (93), and the indication that the return migration of eastern Kamchatka pink salmon now effectively constitutes one in odd years apparently derives from the role that climate change has played in the growth in their abundance. In aggregate, the direct, indirect, and cascading effects of pink salmon suggest that they have a destabilizing effect on the ecosystem of the SNPO/BS.

Additional pressure in the North Pacific comes from the growing number of hatchery produced pink and chum salmon—e.g., some 3×10^9 chum smolts are released each year in Japan and the annual run size has been in the order of $50–80 \times 10^6$ fish since the 1980s, plus there are many more in the ocean given their multiyear life history strategy, and most of them spend the summer–fall feeding period in the Bering Sea (31, 37, 45). A recommendation has been made to increase Russian hatchery production of chum salmon (94), which currently is negligible. In the northeastern North Pacific, hatchery production of pink salmon in Prince William Sound began in the mid-1970s and has grown to annual runs as high as nearly 70×10^6 fish (34). Record-breaking runs of wild pink salmon in summer 2013 from Washington State to the Gulf of Alaska (95–97) highlight the continuing trend.

Interannual switching between alternate ecosystem states of the SNPO/BS driven by pink salmon must be accounted for when attempting to explain patterns of change in populations of species at lower and higher trophic levels and when building ocean ecosystem models. Key forcing from the salmon is additive to, perhaps dominant to in some cases, whatever other drivers are important in the environment. The abundance of pink salmon, owing to their life history strategy, is an uncommon case of too many fish in the sea, and the ecosystem-scale effect they have needs to become part of international resource common-pool policy discussions that include seabirds, and by extension additional competing species (98). The response of wild salmon, and other commercially targeted fishes, to climate change has important management implications (98–102) and conservation implications as revealed by this study. The large and growing number of hatchery-reared salmon raises additional concern about the carrying capacity of the SNPO/BS, although such concern is not universally embraced (103).

Pacific salmon has considerable societal importance, as the commercial fishery is a multibillion dollar industry employing tens of thousands of people (104) and feeding millions of people. There is an obvious strategy in using the oceans as unattended feedlots, but we know that the feed troughs will not be perpetually full, and despite the nutritious protein and fatty acids of free-range salmon, it is time to consider additional issues as well. The need to sustainably accommodate not only salmon but other denizens of the sea could potentially turn salmon fishery management in certain cases from the now common practice of imposing catch limits and raising hatchery production to enhance stocks, to relaxing catch limits and encouraging larger harvests and smaller hatchery releases to help maintain equity among all of the trophically linked consumers—in other words, to devise a broad-scale ecosystem-based management strategy.

Materials and Methods

Values of seabird breeding parameters at the four monitoring colonies are reported annually by the US Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge (67–70). Unless otherwise noted, all seabird data were from these sources—additional data were available in ref. 66 as cited. We used the data as reported for all parameters except number of eggs laid, which we calculated by adjusting the reported number of chicks hatched annually on phenology monitoring plots by the average hatching success of eggs in even and odd years. We compared mean values of nesting parameters in even years to those in odd years using Student *t* test.

Annual run sizes (catch plus escapement, millions of fish) of wild eastern Kamchatka pink salmon were reported for 1952–2005 in ref. 34, and catch only (tonnes) for 1971–2009 in ref. 39 and 2010–2012 (as shown in Table S1). We estimated the run size in 2006–2012 using the relationship between run size and catch in 1971–2005 ($r^2 = 0.90$, $P < 0.0001$). We used the annual run size of wild pink salmon in Norton Sound from 1997 to 2012 (40) as an index of run size in western Alaska. There are no hatchery programs in eastern Kamchatka or western Alaska. Run sizes were log normal transformed to compute values of linear regressions against nesting parameters.

We used $\alpha = 0.10$ to parse the full dataset for discussion and clarity in presentation in figures—it does not imply a firm judgment about the statistical or biological significance of differences between mean values in even and odd years or the slopes of regressions of nesting parameter values against salmon abundance. Significance levels of all tests of null hypotheses are reported in Tables S2–S5.

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Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem

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Pink salmon (*Oncorhynchus gorbuscha*) in the North Pacific Ocean have flourished since the 1970s, with growth in wild populations augmented by rising hatchery production. As their abundance has grown, so too has evidence that they are having important effects on other species and on ocean ecosystems. In alternating years of high abundance, they can initiate pelagic trophic cascades in the northern North Pacific Ocean and Bering Sea and depress the availability of common prey resources of other species of salmon, resident seabirds, and other pelagic species. We now propose that the geographic scale of ecosystem disservices of pink salmon is far greater due to a 15,000-kilometer transhemispheric teleconnection in a Pacific Ocean macrosystem maintained by short-tailed shearwaters (*Ardenna tenuirostris*), seabirds that migrate annually between their nesting grounds in the South Pacific Ocean and wintering grounds in the North Pacific Ocean. Over this century, the frequency and magnitude of mass mortalities of shearwaters as they arrive in Australia, and their abundance and productivity, have been related to the abundance of pink salmon. This has influenced human social, economic, and cultural traditions there, and has the potential to alter the role shearwaters play in insular terrestrial ecology. We can view the unique biennial pulses of pink salmon as a large, replicated, natural experiment that offers basin-scale opportunities to better learn how these ecosystems function. By exploring trophic interaction chains driven by pink salmon, we may achieve a deeper conservation conscientiousness for these northern open oceans.

teleconnection | short-tailed shearwater | carryover effect | interaction chain | ecosystem management

Linkages between ecosystems and the importance to animal and plant populations, production processes, and community characteristics within and between them are known from a variety of examples at regional geographic scales (e.g., refs. 1–4). On larger scales, linkages, or teleconnections, across broadly separated regions of Earth have been described in numerous fields, including atmospheric sciences, marine and terrestrial ecology, social-ecological systems, and economic markets (e.g., refs. 5–15), and are a foundational element of the emerging subdiscipline of macrosystem ecology (e.g., refs. 16–17, and references therein). Macrosystem ecology draws attention to interactions spanning spatially distant regions that, taken together, have ecosystem characteristics, and indirectly addresses the difficulty in defining ecosystem space. Here we describe a remarkable example of a transhemispheric macrosystem that integrates processes at five geographic scales and six trophic levels spanning some 15,000 km of the Pacific Ocean, with links between meteorology and marine climate in the Northern Hemisphere; the abundance of pink salmon (*Oncorhynchus gorbuscha*) and marine ecology in the northern North Pacific Ocean and Bering Sea (NP/BS); the ecology of a transhemispheric migrant seabird, the short-tailed shearwater (*Ardenna tenuirostris*); and terrestrial ecology and social systems in the Tasman Sea in the South Pacific Ocean (SP/TS). Interesting in its own right, this macrosystem is important because it further exposes concern over the growing abundance of wild and hatchery produced salmon, competition for finite common prey resource pools in the NP/BS, and international management and conservation responsibilities for these little-known pelagic ecosystems.

Wild pink salmon stocks began to increase in the 1970s across much of their range in the North Pacific Ocean in association with a shift in the mean state of the Aleutian Low pressure system, the dominant meteorological feature affecting ocean climate over this broad region (e.g., ref. 18). The ensuing regime was favorable for pink salmon (19, 20), and despite subsequent meteorological state shifts (21), their abundance continued to grow. Two other species of Pacific salmon also increased during this time, sockeye (*Oncorhynchus nerka*) and chum (*Oncorhynchus keta*), but to far lesser degrees (22). These increasing trends contrast with widespread declines in the abundance of coho salmon (*Oncorhynchus kisutch*) and the iconic Chinook, or king, salmon (*Oncorhynchus tshawytscha*) that are of great concern in many ways (e.g., refs. 22–25).

Returns of wild stocks of pink salmon have been augmented 10–20% by hatchery production since the 1980s, primarily in Russia and the United States (22). Pink salmon now constitute ∼70% of the total of all species of Pacific salmon combined and have annual returns in recent years of up to 650×10^6 fish (22).

Significance

Ecological processes at regional geographic scales can be connected to those in far distant locations by teleconnections, or interactions between species and systems far removed from one another. Macrosystem ecology views such interactions as elements of much larger ecosystems than either component. We have identified a remarkable example of a transhemispheric macrosystem spanning 15,000 kilometers of the Pacific Ocean maintained by a migratory species of seabird that nests in the South Pacific and winters in the North Pacific. It highlights another example in a growing list of ecosystem disservices of an abundant species of North Pacific salmon, and the need to include ecosystem processes at such geographic scales in conservation and management considerations for this northern open ocean.

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The mechanisms linking pink salmon population dynamics to meteorology and ocean climate are not fully known, but the principal hypotheses focus on early marine survival that is determined in large measure by seawater temperature, the abundance of zooplanktonic prey, and the abundance of piscine predators (e.g., refs. 26 and 27).

Among the Pacific salmon, pink salmon have a unique 2-y life cycle between egg and spawning adult, and most stocks alternate in abundance between years; the majority are much more abundant in odd years than in even years (22, 28). Overall, odd-year stocks are now over twice as abundant as they were in the 1970s (22, 29). It has been argued since the mid-1990s that pink salmon have been having important negative effects on other resident species in the NP/BS through exploitative competition for common prey resources, on the structure of pelagic food webs, and on ecosystem function (30–39).

Pink salmon also have been reported to be an important factor in the ecology of short-tailed shearwaters, seabirds that breed in the SP/TS, specifically southeastern Australia, Bass Strait, and Tasmania (*SI Appendix*, Fig. S1), and spend the austral winter primarily in the NP/BS, although some continue north into the Chukchi Sea (Fig. 1). Roughly 23×10^6 short-tailed shearwaters (45), one of the most abundant species of seabirds in the world, undertake annual migrations of some 30,000-km round trip between the Southern and Northern Hemispheres. Short-tailed shearwaters were shown to be in poorer physical condition and to succumb in greater numbers in the northwestern North Pacific Ocean and central Bering Sea in odd years than in even years (46, 47). Numbers of dead shearwaters encountered on St. Paul Island (Pribilof Islands, eastern Bering Sea) were more than an order-of-magnitude greater in odd years than in even years between 2006 and 2010: odd-year average of 0.57 versus even-year average of 0.022 birds per standardized beach survey (from data reported in ref. 48). Diets of pink salmon and short-tailed shearwaters overlap (49–54), and the biennial pattern in shearwater body condition has been linked to competition with pink salmon for common prey (47). These patterns are distinct from occasional mass mortalities (wrecks), which are comprised primarily of immature birds that occur off Japan in spring as they arrive from the Southern Hemisphere (55), and in the Bering Sea, where wrecks have occurred at least twice in late summer, in 1983 and 1997 (56, 57). Both years were odd years but were further beset by strong El Niño conditions. Birds found in wrecks off Japan and in the Bering Sea appeared to have starved to death. The return migration from the NP/BS to the SP/TS takes about 18 d in September to October (42), and is fueled by fat stores accumulated on the wintering grounds. Because both fall and spring migrations are nonstop, short-tailed shearwaters would not be a factor in, or be affected by, food web processes in the intervening ocean.

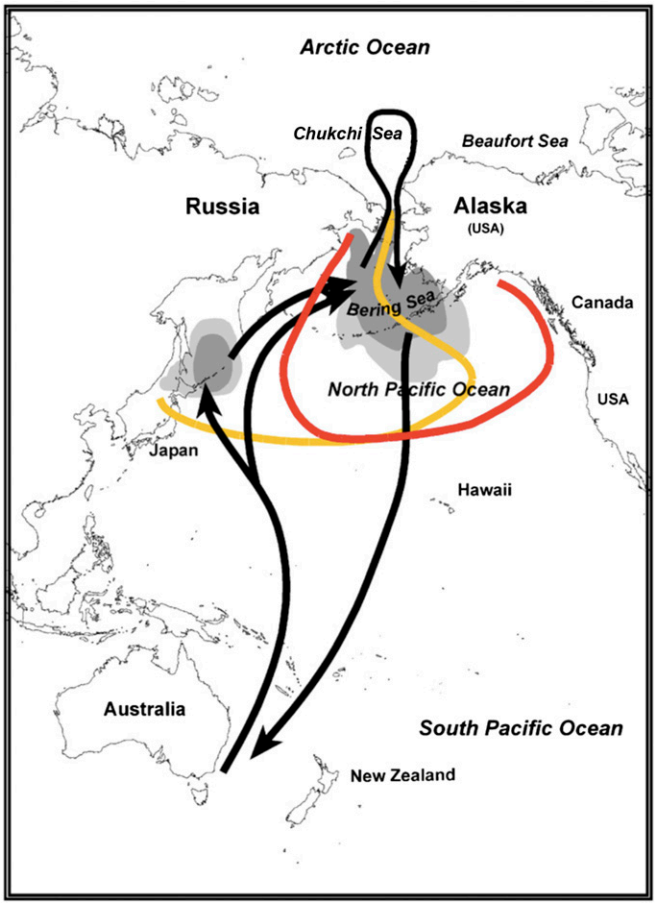


Fig. 1. Generalized open ocean ranges of pink salmon from Japan and Russia (yellow) and Alaska (red) as depicted by refs. 40 and 41, and generalized migration routes of short-tailed shearwaters (arrows) and distribution in the northern North Pacific Ocean, Bering Sea, and Chukchi Sea (after refs. 42 and 43, and information presented in ref. 44). Shearwater distribution depicted in gray, with higher concentrations in darker shades.

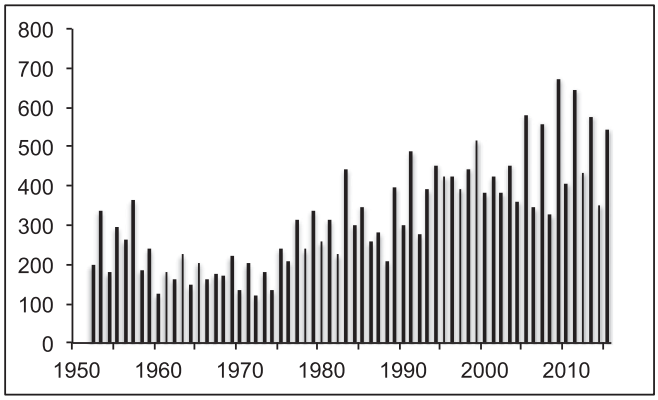


Fig. 2. Returns (catch plus escapement, millions) of pink salmon in the North Pacific Ocean, 1952–2015. Data from ref. 22.

Results

Trends in Pink Salmon Abundance. The overall abundance of pink salmon varied over a comparatively small, low range from the early 1950s to the mid-1970s, then increased markedly through about 1990 (Fig. 2). That increase was followed by a second period of relative stability to about 2004. Beginning in 2005, odd-year stocks increased substantially, whereas even-year stocks remained about the same as in the previous interval: the odd-year mean in 2005–2015 increased by 35% over the odd-year mean for 1990–2004 (from 440×10^6 to 595×10^6 fish, $P = 0.0001$), with odd-year stocks averaging 60% greater than even year stocks (595×10^6 fish vs. 372×10^6 fish, $P = 0.0001$).

Long-term trends in abundance of the four groups of salmon we used in our analyses (*Methods*) were generally similar (*SI Appendix*, Fig. S2). The greatest difference from the overall pattern was for salmon from the Western Kamchatka Peninsula.

Trends in Shearwater Abundance. The abundance of short-tailed shearwaters at Montagu Island fell by about 50% during the 1980s (Fig. 3 and *SI Appendix*); Montagu Island is one of the longest systematic annual monitoring sites for the species. There was no trend in the interval 1990–2016 ($R^2 = 0.043$, $P = 0.86$),

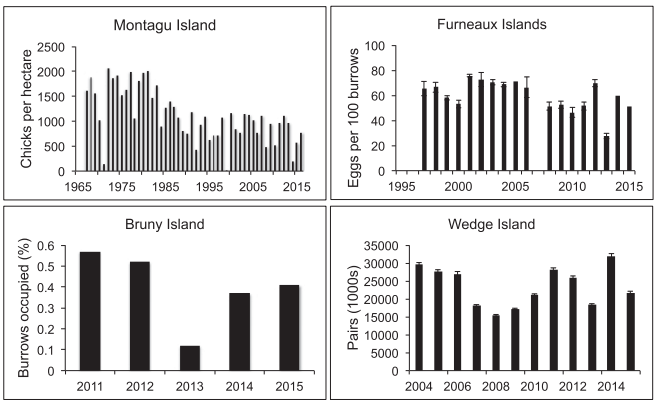


Fig. 3. Trends in abundance of short-tailed shearwaters at four breeding locations in southeastern Australia: Montagu Island, the Furneaux Islands, Wedge Island, and Bruny Island. See *Methods* for data sources and metrics for abundance estimates.

but abundance declined at about −4% y^{-1} during 2000–2015 ($R^2 = 0.21$, $P = 0.063$). The slope of the regression for the most recent interval 2005–2016 indicated a decline in abundance of −4.7% y^{-1}, but had little predictive power ($R^2 = 0.11$, $P = 0.29$), perhaps because of the short time series. Abundance at colonies monitored in the Furneaux Islands declined by −2.1% y^{-1} across the full sampling interval of 1997–2015 ($R^2 = 0.26$, $P = 0.032$). Although the slope of the regression was greater after 2005 (−3.4% y^{-1}), it too had little predictive power ($R^2 = 0.17$, $P = 0.23$). Numbers at Wedge Island fell from ∼30,000 pairs in 2004, when systematic censusing began, to 15,000 pairs in 2008. Since then population estimates have been variable and there was no trend across the full interval ($R^2 = 0.002$, $P = 0.88$). A short time series of population estimates in 2011–2015 at the main colony on Bruny Island showed no overall trend in abundance ($R^2 = 0.064$, $P = 0.68$), even though the slope of the regression was −10% y^{-1}, but did reveal a sharp drop in 2013 that was apparent at all of the other locations where data were available.

Interannual Variability in Shearwater Abundance. The mean and median abundances of short-tailed shearwaters in even years and odd years at Montagu Island were not different in the full interval 1967–2016 (Table 1). However, as the intervals became shorter and more recent, the difference between even- and odd-year abundances grew such that by 2005–2016, when odd year pink salmon stocks were largest, ∼40–50% more shearwaters nested in even years than in odd years.

There was no evidence of differences in mean values of even years and odd years in 1997–2015 or 2005–2015 at the Furneaux Islands based on *P* values, although the mean and median values in even years in 2005–2015 were 16% greater than in odd years (Table 2). Similarly, means and medians in the single interval at Wedge Island, 2004–2015, were 15% and 32%, respectively, higher in even years than in odd years, but the significance level of the difference between mean values also was low (Table 3). The time series at Bruny Island was too short for meaningful analysis.

Shearwater–Pink Salmon Correlations. The small number of years in our time series, in the two most recent intervals in particular, limited the power to make inferences about the importance of local summer rainfall (*Methods*) and salmon to shearwater abundance. With that in mind, rainfall and pink salmon abundance explained from 50% to over 70% of the variability in the abundance of short-tailed shearwaters on Montagu Island in four of the five intervals we analyzed (Table 4). The relationship was weaker in the interval 2000–2016. Rainfall and Alaska salmon were both important predictors of shearwater abundance in the first three intervals, as was Eastern Kamchatka Peninsula salmon in the last three intervals. The importance of December to February rainfall and Alaska salmon declined in 2000–2016 and 2005–2016. In the most recent interval (2005–2016), when pink salmon abundance was highest, 73% of the variability in shearwater abundance at Montagu Island was explained, primarily by rainfall, Eastern Kamchatka Peninsula salmon, and Alaska salmon. Japan + Sea of Okhotsk salmon were marginally significant only in 1990–2016, and Western Kamchatka Peninsula salmon only in 2005–2016.

The positive relationship between Eastern Kamchatka Peninsula salmon and shearwaters in all intervals, particularly the apparently highly significant ones in the most recent three intervals, was not expected. Because of this, and because Japan + Sea of Okhotsk and Western Kamchatka Peninsula stocks did not contribute importantly in any intervals, we reran the model using only December to February rainfall and Eastern Kamchatka Peninsula and Alaska salmon (Table 5). The adjusted R^2 value for 2005–2016 fell somewhat but remained strongly significant, while all other interval values were similar to those in the original model. The importance of December to February rainfall remained about the same, and Alaska salmon tended to be more important. In contrast, the importance of Eastern Kamchatka Peninsula salmon declined markedly in the two most recent intervals, although it remained important in the single interval 1990–2016. When shearwater abundance in the five time intervals was regressed against Eastern Kamchatka Peninsula pink salmon alone, the only marginally significant relationship was for the full interval (1967–2016, $P = 0.08$), but it explained very little of the variability in shearwater abundance ($R^2 = 0.06$). There were no relationships for the other four intervals: all $R^2 \leq 0.03$ and all $P \geq 0.33$.

There was no relationship between shearwater abundance at the Furneaux Islands and rainfall and salmon in 1997–2015 (adjusted $R^2 = -0.02$, $P = 0.49$) or 2005–2015 (adjusted $R^2 = -0.40$, $P = 0.77$). Similarly, there was no relationship between shearwaters and rainfall and salmon at Wedge Island in 2004–2015 (adjusted $R^2 = -0.17$, $P = 0.64$).

Shearwater Wrecks in Australia. Wrecks of short-tailed shearwaters shortly after they returned to nesting colonies in Australia and Tasmania have been reported occasionally since the mid-1800s, and dead birds were typically emaciated (e.g., refs. 58 and 59).

Table 1. Mean and median abundances of short-tailed shearwaters at Montagu Island in even years and odd years

Interval	Mean (±SE) even	Mean (±SE) odd	*P*	Median even	Median odd	Mean ratio	Median ratio
1967–2016	1,237 (92)	1,092 (101)	0.30	1,144	1,066	1.13	1.07
1980–2016	1,064 (89)	876 (80)	0.12	966	831	1.22	1.16
1990–2016	916 (57)	783 (87)	0.22	952	769	1.17	1.24
2000–2016	942 (64)	716 (111)	0.10	962	764	1.31	1.26
2005–2016	907 (91)	639 (127)	0.13	957	641	1.42	1.49

Chicks per hectare. First series without 1967 and 1999. Second two series without 1999, as explained in *Methods*.

Table 2. Mean and median values of short-tailed shearwater abundance at the Furneaux Islands in even years and odd years (eggs per 100 burrows)

Interval	Mean (±SE) even	Mean (±SE) odd	*P*	Median even	Median odd	Mean ratio	Median ratio
1997–2015	61.7 (3.1)	58.1 (4.9)	0.55	66.4	58.0	1.06	1.14
2005–2015	58.9 (4.4)	50.1 (8.9)	0.41	60.1	51.6	1.16	1.16

Environmental conditions in the broader marine region of the Tasman Sea as the birds return from the Northern Hemisphere may at times be responsible: for example, anomalously warm sea surface temperatures in October 2000 may have reduced the availability of important prey at a critical time that caused a major wreck that year (59).

However, beginning in 2007 and coinciding with the increasing abundance of odd-year pink salmon, wrecks occurred in every odd year to at least 2013. The wreck in 2013 was extreme, when very high numbers of birds were stranded in Australia and Tasmania, and even in New Zealand, where they do not nest (60), and corresponded with extremely high abundances of pink salmon returning to United States waters (ref. 22 and www.npafc.org/new/science_statistics.html). Birds in those wrecks also were emaciated, suggesting that they failed to accumulate sufficient fat before departure on their southward migration to sustain them until they could refuel upon their return. Because the wrecks have been occurring in odd years, pink salmon may be implicated as the cause. Negative carryover effects of poor nutrition, apparently due to competition with pink salmon in odd years, also have been seen in resident seabirds that nest in the Aleutian Islands and Bering Sea (37).

Discussion

Short-tailed shearwaters depart their wintering areas beginning in mid to late September (42, 43), about 1 to 2 mo after the peak spawning runs of pink salmon (61, 62). However, their distributions broadly overlap during the time in summer when salmon are feeding voraciously and growing rapidly as they return to their spawning rivers. We believe correlations between the abundance of short-tailed shearwaters and pink salmon in this study provide strong support for the hypothesis that exploitative competition by the fish is having negative effects on the birds, with carryover effects on them at their nesting colonies in the SP/TS. The evidence includes observations of poor physical condition and elevated mortality in the western and eastern Bering Sea in odd years that have been noted previously and that we report here, and in recent years: (*i*) the wrecks in odd years in southeastern Australia as birds return to their nesting grounds; (*ii*) the tendency for greater numbers of shearwaters to nest in even years than in odd years, with the biennial difference growing as pink salmon abundance has increased in odd years; (*iii*) the negative trends in shearwater abundance at Montagu Island and the Furneaux Islands; and (*iv*) after accounting for the important effect of rainfall, the strong inverse relationship between the abundance of nesting shearwaters at Montagu Island and the abundance of Alaska pink salmon in all five time intervals we examined. That Alaska pink salmon, and not Asian pink salmon, explained most of the variability in shearwater abundance at Montagu Island is perhaps not surprising, since the range of Alaska pink salmon at sea appears to overlap most with the wintering range of the birds. We do not know why Eastern Kamchatka Peninsula salmon were positively related to shearwater abundance at Montagu Island in the full model, but the strength of the relationship was weak or absent after removing Japan + Sea of Okhotsk and Western Kamchatka Peninsula from our analysis. Moreover, there was no evidence of a relationship of the birds to Eastern Kamchatka Peninsula pink salmon in the latter four time intervals when only those fish were considered.

Nor do we know why correlations between pink salmon and shearwaters nesting at the Furneaux Islands and Wedge Island were not identified in our analysis, and refrain here from speculating about possible reasons. However, we believe that this does not materially controvert our hypothesis, based on the totality of evidence, that competition by pink salmon leads to negative effects on overwintering and nesting short-tailed shearwaters.

Our hypothesis is bolstered by compelling correlations between pink salmon abundance and the phenologies, productivity, and diets of several species of resident seabirds in the Bering Sea (37). The weaker strength of correlations between shearwaters and salmon compared with resident seabirds and salmon may be explained by the broad distribution of shearwaters during their nonbreeding season and the smaller spatial, and briefer temporal, overlap with foraging areas occupied by pink salmon. Interannual variability in shearwater distribution in the Bering Sea due to changing sea ice conditions (63) may further mask the appearance of relationships to pink salmon.

The proposed role of pink salmon in the ecology of short-tailed shearwaters does not preclude other negative or positive impacts on the abundance or productivity of the birds that may derive from seasonal or annual vagaries in ocean climate or longer-term changes in the marine environment of the Tasman Sea or the Southern Ocean due to ocean warming or other causes (e.g., refs. 64–66).

Shearwaters and Terrestrial Ecology. The putative negative effects of pink salmon on short-tailed shearwaters carry beyond just the birds. Many species of seabirds can be important to terrestrial ecology on islands where they nest, chiefly by the transport of marine-derived nitrogen and phosphorus that fertilize soils and streams, and by bioturbation by burrowing species, such as shearwaters, which mixes and aerates soils, all of which alter the composition and productivity of floral communities (e.g., refs. 3 and 67–69). The effects of guano deposition and bioturbation by short-tailed shearwaters on physical and chemical soil properties and on terrestrial vegetation are well documented, as they are for two closely related species, wedge-tailed shearwaters (*Ardenna pacifica*) in Western Australia and sooty shearwaters (*Ardenna grisea*) in New Zealand, and are important influences on island ecology (69–73). At Bruny Island, for example, changes in abundances of short-tailed shearwaters between 1977 and 1992 led to marked changes in the composition of the floral community (71).

Shearwaters and Society. Short-tailed shearwaters also are important to cultural, social, and economic systems in Tasmania, as are other species of shearwaters and petrels there and in New

Table 3. Mean and median abundances of short-tailed shearwaters at Wedge Island in even years and odd years (adults)

Interval	Mean (±SE) even	Mean (±SE) odd	*P*	Median even	Median odd	Mean ratio	Median ratio
2004–2015	25,154 (2,462)	21,903 (2,008)	0.33	26,498	20,074	1.15	1.32

Table 4. Results of multiple regression analysis of short-tailed shearwater abundance at Montagu Island versus summer (December to February) rainfall at Montagu Island and pink salmon abundance in four regions of the North Pacific Ocean

Interval	Adjusted R^2 (P)	December to February rain, t (P)	A*, t (P)	B†, t (P)	C‡, t (P)	D§, t (P)
1967–2016	0.61 (<0.0001)	−5.5 (<0.0001)	−1.2 (0.24)	−1.3 (0.21)	0.63 (0.53)	−5.1 (<0.0001)
1980–2016	0.50 (0.0001)	−3.7 (0.001)	−1.4 (0.17)	−0.77 (0.44)	1.2 (0.24)	−3.7 (0.0009)
1990–2016	0.65 (0.0001)	−5.6 (<0.0001)	−1.8 (0.08)	0.028 (0.98)	2.8 (0.013)	−4.2 (0.0006)
2000–2016	0.33 (0.11)	−1.6 (0.14)	−1.5 (0.15)	0.28 (0.79)	2.1 (0.064)	−2.2 (0.053)
2005–2016	0.73 (0.031)	−1.7 (0.14)	−1.4 (0.21)	2.0 (0.10)	3.5 (0.017)	−2.9 (0.033)

*Japan + Sea of Okhotsk, excluding Western Kamchatka Peninsula.
†Western Kamchatka Peninsula.
‡Eastern Kamchatka Peninsula.
§Alaska.

Zealand (74, 75). A commercial harvest of short-tailed shearwater chicks by Aboriginal residents averaged about 72,000 ± 8,800 birds each season in 2007–2017 (76). Chicks also are harvested under recreational licenses available to the public: for example, an average of 884 ± 44 licenses were sold annually in 2011–2016 that resulted in an average annual harvest of about 34,500 ± 5,300 chicks (77).

As a consequence of the massive wreck in 2013 and the dramatic drop in abundance of nesting adults, only 3,300 chicks were taken in the commercial harvest and only 10,913 in the recreational harvest during the ensuing season in 2014 (76, 77).

Teleconnections. The conceptual model of the macrosystem we propose integrates processes at five geographic scales: local, regional, basin, hemispheric, and transhemispheric. At local scales, individual stocks of pink salmon prosper or not depending on factors that influence early marine survival: that is, prey and predator fields that are in turn determined by local and regional ocean climate (26, 27). At basin scales, atmospheric forcing sets up regional and local ocean climate conditions (78) that influence trends in pink salmon abundance (79) and the effect salmon have on basin-scale prey fields as they mature and migrate in a consumer front back to their spawning rivers. At hemispheric scales, teleconnections between atmospheric systems over the Pacific Ocean, North America, and the Arctic drive basin-scale physical forcing in the NP/BS that condition local-, regional-, and basin-scale ocean climate (refs. 18 and 80, and references therein). At transhemispheric scales, shearwaters migrate 15,000 km from wintering grounds in the NP/BS to nesting colonies in the SP/TS, where in odd years they arrive in poorer physical condition, may experience wrecks, and tend to nest in fewer numbers than in even years. And back to local and regional scales, where wrecks and an apparent decline in shearwater abundance is of concern to Aboriginal residents in regard to their subsistence economy, cultural identity, and recreational and commercial harvests, and stand to impact ecosystem services in the form of soil fertilization and aeration that are important to vegetation community structure on islands where they nest.

The model also integrates interactions across at least six trophic levels in the NP/BS and three in the SP/TS. In the NP/BS pink salmon apparently can initiate pelagic trophic cascades by depleting the abundance of herbivorous zooplankton that leads to elevated standing stocks of phytoplankton. In the other trophic direction, reductions of zooplankton stocks impact predatory micronekton and mesonekton, including other species of salmon that prey upon them. Many species of zooplankton and micronekton are important prey of resident NP/BS seabirds and migratory short-tailed shearwaters. In the SP/TS, shearwaters are important in several ways to indigenous residents and to terrestrial vegetation patterns and ecology.

Conservation of Ecosystems. Competition among wild pink salmon and numerous other species for finite, common prey resources in the NP/BS appears to have been increasing as salmon abundance has grown. The addition of hatchery-produced salmon that are further filling the ocean is becoming a particular cause for concern; for example, since 1990 in the order of $1.2–1.5 \times 10^9$ juvenile pink salmon have been released annually into the northern North Pacific Ocean (22). In 2016 $\sim 0.64 \times 10^9$ smolts were released into Prince William Sound, Alaska alone, where they appear to be having negative impacts on wild pink salmon, sockeye salmon (*O. nerka*), and Pacific herring (*Clupea pallasi*) (81–83). In 2013 an estimated 103×10^6 adult pink salmon returned to Prince William Sound, of which ~30% were wild and 70% were hatchery fish (84).

Salmon and seabirds are conspicuous and have high ecological, economic, cultural, and societal values, thus a great amount of research is devoted to them. But there are other crucial species in the oceanic ecosystems of the NP/BS, including mesopelagic squids, myctophids (Myctophidae), and deep-sea smelts (Bathylagidae) that also compete for the same prey (85–89). They are of particular ecological value in a variety of ways, from sustaining numerous species of salmon, seabirds, and marine mammals (90–96), to being important engines in the oceanic

Table 5. Results of multiple regression analysis of short-tailed shearwater abundance at Montagu Island versus summer (December to February) rainfall at Montagu Island and pink salmon abundance in two regions of the North Pacific Ocean

Interval	Adjusted R^2 (P)	December to February rain, t (P)	C*, t (P)	D†, t (P)
1967–2016	0.60 (<0.0001)	−5.6 (<0.0001)	0.76 (0.45)	−6.3 (<0.0001)
1980–2016	0.50 (<0.0001)	−4.2 (0.0002)	1.2 (0.23)	−4.4 (0.0001)
1990–2016	0.62 (<0.0001)	−5.4 (<0.0001)	2.5 (0.019)	−4.1 (0.0005)
2000–2016	0.29 (0.069)	−1.7 (0.10)	1.7 (0.11)	−2.9 (0.012)
2005–2016	0.53 (0.040)	−1.5 (0.18)	1.9 (0.10)	−3.8 (0.007)

*Eastern Kamchatka Peninsula.
†Alaska.

biological pump as vertically migrating predators (97). The biomass of myctophids and bathylagids in the eastern Bering Sea basin alone has been placed in the order of 1–8 × 10^6 tons each (97, 98), but nothing is known about trends in abundance and other fundamental elements of their ecology because they have no direct economic value.

The desire to continue to raise production levels of wild and hatchery salmon is understandable; the overall annual multinational economic value of Pacific salmon is in the order of 10^9 US $ and the industry employs tens of thousands of people (99). But it is now time to take stock of the consequences—the ecosystem disservices of salmon—of doing so on other economic, social, cultural, and ecological values in the NP/BS (100, 101) and, because of the teleconnection described here, in the SP/TS as well.

The short-tailed shearwater is not a species in peril, but the apparent response of these birds, as well as responses of humans, resident NP/BS seabirds, other salmon, herring, and likely species yet to be identified, to ecological forcing by pink salmon suggests that pink salmon are altering the distribution of wealth stored in this macrosystem (in the sense of ref. 102). Together, these responses emphasize that we must develop a deeper conservation conscientiousness for this entire oceanic system and more informed approaches for the management of the whole.

This large, replicated, natural experiment is not strictly a replicated natural experiment, since conditions in the NP/BS vary on annual and multiyear timescales for reasons other than pink salmon, for example weather and climate have large influences over patterns of annual production, including those of pink salmon. However, it is perhaps as near as we can come to experimental replication at ocean basin scales, and we should therefore use this unique opportunity to delve into trophic interaction chains driven by pink salmon and help remedy the conspicuous and unfortunate lack of knowledge about marine ecology in these important realms.

Methods

Shearwater Abundance. The abundance of adult shearwaters arriving at the nesting colonies and the numbers that lay eggs are most meaningful to address correlations with pink salmon abundance. However, this information is very difficult to acquire and is lacking for most sites. Thus, we used proxies of abundance for Montagu Island, the Furneaux Islands, and Bruny Island (*SI Appendix*, Fig. S1). The proxy at Montagu Island (1967–2016) was the density of chicks on three representative study plots in late March, just before fledging of chicks, as reported by refs. 103–107 for 1967–2003, and by ref. 108 for 2004–2015; P.F. provided data for 2016. Single annual values were derived by summing the numbers of chicks on the plots, calculating the density by dividing that number by the total area of the three plots (1,014 m^2), and converting that value to chicks per hectare. Burrow searches were thorough and counts were made only once each year to reduce disturbance and the possibility of desertion by adults.

The proxy of abundance at the Furneaux Islands (1997–2015) was the mean number of eggs per 100 burrows on standardized survey transects on four islands in the island group (East Kangaroo, Little Green, Little Dog, and Big Green) provided by R.M. Counts were made in all but 1 y at East Kangaroo and Big Green, and in 14 of 19 y at Little Green and Little Dog. The proxy at Bruny Island was the number of burrows occupied by nesting birds per total number of burrows examined. Data from 2011 were provided by B. Edwards, Bruny Island, Parks and Wildlife Service, Hobart, Tasmania, Australia; data from 2012 and 2013 were provided by N.B.; and data from 2015 were provided by P. Vertigan, BirdLife Tasmania, Hobart, Tasmania, Australia. We used the actual number of breeding pairs on Wedge Island (2004–2015) as reported by (109) for 2004–2010 and provided by N.B. for 2011–2015. All census data used here for the Furneaux Islands, Wedge Island, and Bruny Island were collected in December. As at Montagu Island, burrow searches at those locations were thorough and were made only once each year.

We compared shearwater abundance between even years and odd years at Montagu Island during five intervals: (*i*) 1967–2016, (*ii*) 1980–2016, (*iii*) 1990–2016, (*iv*) 2000–2016, and (*v*) 2005–2016. The intervals correspond to: (*i*) the full sampling interval, (*ii*) the approximate beginning of the decline in abundance in 1980, (*iii*) the approximate end of the decline in 1990 and ensuing period of markedly higher salmon abundance, (*iv*) a period of relative stability in shearwater abundance following a partial recovery during the 1990s, and (*v*) an interval of very high salmon abundance (Fig. 3 and *SI Appendix*, Fig. S2). Near or total nesting failures occurred in 1971 and 1999 due to heavy rainfall (107), so we did not use those years in intervals one to three. We used the intervals 1997–2015 and 2005–2015 at the Furneaux Islands and the single interval 2004–2015 at Wedge Island. The time series at Bruny Island was too short for these analyses.

Shearwater Abundance Versus Pink Salmon Abundance. We used annual catch plus escapement data reported by ref. 22 for the estimate of pink salmon abundance. These data do not have confidence intervals associated with them, as the methods used to derive the values do not lend themselves to variance statistics.

We compared the abundance of shearwaters at Montagu Island, the Furneaux Islands, and Wedge Island in the same intervals to summer rainfall and the abundance of four groups of pink salmon that were aggregated based on the winter ranges and return spawning migration corridors of stocks, as depicted by refs. 40 and 41. We included rainfall data because it has been shown to be important to chick survival at Montagu Island (107). Rainfall data for Montagu Island came from the Montagu Island Lighthouse, for the Furneaux Islands from the Flinders Island airport, and for Wedge Island from Tarana, Tasmania. All rainfall data are available at www.bom.gov.au/climate/data/index.shtml?bookmark=136. The pink salmon groups were: (*i*) Japan + Sea of Okhotsk, excluding Western Kamchatka Peninsula; (*ii*) Western Kamchatka Peninsula; (*iii*) Eastern Kamchatka Peninsula; and (*iv*) Alaska. British Columbia and Washington pink salmon were not included in the models because their at-sea range overlaps little with the winter distribution of the majority of short-tailed shearwaters. Although the winter distribution of pink salmon from Western Kamchatka Peninsula generally overlaps those of fish from Japan and elsewhere in the Sea of Okhotsk, they are predominantly even-year dominant stocks so were considered separately from the other stocks in the northwestern Pacific Ocean that are predominantly odd-year dominant. Also, their trend in abundance generally differs from trends of the other groups (*SI Appendix*, Fig. S2). Again, there were too few years for this analysis at Bruny Island.

Data Analysis. Mean values of shearwater abundances in even and odd years were compared using Student's *t* test. Shearwater annual abundance data were natural log-transformed to calculate trends in abundance using linear regression.

We compared the abundance of shearwaters to rainfall and the abundance of pink salmon using multiple linear regression. We first assessed the extent of collinearity among the salmon groups, but found little evidence for it, as variance inflation factors for all groups were $\leq$2.4. We used summer (December–February) rainfall as a fifth independent variable in the model for Montagu Island because chicks were counted there in March, and used only December rainfall in models for the Furneaux Islands and Wedge Island because census counts at those locations were made in December.

We compared shearwater chick counts at Montagu Island in March to pink salmon abundance values from the previous calendar year. Shearwater counts at the Furneaux Islands and Wedge Island were made in the same calendar year as salmon abundance estimates.

We did not select an a priori strict threshold for statistical significance. Instead, all correlation coefficients and significance values are presented and considered, along with temporal patterns in change and values of group means and medians, to make biological inferences.

Research Permits. BirdLife Tasmania holds all animal research and scientific permits required by law to undertake the surveys and research described in the study. All surveys were approved by the Animal Ethics Committee of the Department of Primary Industries, Parks, Water, and Environment. The University of Tasmania Animal Ethics Committee also approved research at Wedge Island and Fisher Island.

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North Pacific Anadromous Fish Commission

TECHNICAL REPORT 21

A Review of Pink Salmon in the Pacific, Arctic, and Atlantic Oceans

Technical Editor: William Stanbury

Vancouver, Canada, 2023

A Review of Pink Salmon in the Pacific, Arctic, and Atlantic Oceans

A report produced by the Northern Hemisphere Pink Salmon Experts Meeting, held: October 2–3, 2022, Vancouver, Canada.





Northern Hemisphere Pink Salmon Experts Meeting Organizers

ICES Working Group on Science to Support Conservation Restoration and Management of Diadromous Species (WGDIAD)
NPAFC Working Group on the International Year of the Salmon (IYS WG)

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A Review of Pink Salmon in the Pacific, Arctic, and Atlantic Oceans

Northern Hemisphere Pink Salmon Expert Group
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Abstract

The Northern Hemisphere Pink Salmon Expert Group Meeting was held on October 2–3, 2022 in Vancouver, Canada, immediately preceding the International Year of the Salmon (IYS) Synthesis Symposium. The rapid expansion of pink salmon was the theme for the meeting, and experts came together to discuss the current state of knowledge for pink salmon. Specific topics of focus included the range expansion into the Atlantic and Arctic oceans, trends in distribution and abundance, research and monitoring approaches, potential inter-specific interactions, mitigation efforts, and plans for future collaborations. The outcomes of the meeting were presented at the IYS Synthesis Symposium and are further disseminated through this NPAFC Technical Report. The Executive Summary section of this report provides a brief background, a condensed overview of each topic, and concludes with overarching takeaway messages that are intended to guide future collaborations.

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List of Abbreviations

ADF&G—The Alaska Department of Fish and Game

AHRP—Alaska Hatchery Research Program

BASIS—Bering-Aleutian Salmon International Survey

CU—Conservation Units

DFO—Fisheries and Oceans Canada

ICES—International Council for the Exploration of the Sea

IYS—International Year of the Salmon

LUKE—Natural Resources Institute Finland

NAC—North Atlantic Council or North American Commission, NASCO

NASCO—North Atlantic Salmon Conservation Organization

NEAC—North East Atlantic Commission, NASCO

NPAFC—North Pacific Anadromous Fish Commission

PICES—The North Pacific Marine Science Organization

WGC—West Greenland Commission, NASCO

WGBAST—ICES Assessment Working Group on Baltic Salmon and Trout

WGDIAD—ICES Working Group on Science to Support Conservation, Restoration and Management of Diadromous Species

WGNAS—ICES Working Group on North Atlantic Salmon

Executive Summary

Introduction

The International Year of the Salmon (IYS), which ran from 2018 until 2022, acknowledged the need to collectively generate and share new knowledge regarding the current state of salmon and engage communities to support the resilience of both salmon and the people who depend on them. An important aim of the IYS therefore was to bring scientists together and promote knowledge exchange on Pacific and Atlantic salmon. Through that initiative, the North Pacific Anadromous Fish Commission (NPAFC) and the International Council for the Exploration of the Sea (ICES) Working Group on Science to Support Conservation, Restoration and Management of Diadromous Species (WGDIAD) recognized there was potential for an inter-ocean-basin collaboration on salmon. On September 1, 2021, the NPAFC and WGDIAD launched their first joint (online) meeting in the form of a 'Pacific-Atlantic Salmon Round Table' where 70+ salmon experts from both ocean basins, as well as the Arctic, discussed a range of relevant issues. The topic that generated the most discussion was the recently observed range expansion of pink salmon. It became clear that there was a great desire for knowledge on this topic from scientists working in areas where this expansion was a relatively recent phenomenon, and to benefit from the knowledge present among scientists who had been working on this topic, and pink salmon ecology in general, for years. Therefore, a selection of experts (see Appendix A for list of participants and affiliations) in pink salmon ecology, stock assessment, and genetics, as well as a limited number of stakeholders, attended the first meeting of the Northern Hemisphere Pink Salmon Expert Group, which was held 2–3 October 2022, immediately preceding the IYS Synthesis Symposium. They discussed the current state of knowledge for pink salmon, focusing on the range expansion into the Atlantic and Arctic oceans, including trends in distribution and abundance, research and monitoring approaches, potential inter-specific interactions, mitigation efforts, and plans for future collaborations. The outcomes of the meeting were presented at the IYS Synthesis Symposium and further disseminated through this NPAFC Technical Report. This summary provides an overview of the topics discussed and more detailed information about each topic is provided in the relevant section of this report.

Topic 1: Trends in Distribution, Abundance, and Productivity of Pink Salmon

Pink salmon are small but mighty fish on a warming planet. Already the most widely distributed Pacific salmon species in the northern hemisphere, they have expanded in recent years. In the Atlantic, they have likely produced self-sustaining populations in northern Norway, Scotland, and Iceland and have been observed as far south as France. Vagrants have also been observed in eastern Canada from Nunavut to Newfoundland while non-anadromous populations occur in the Great Lakes. Pink salmon are also observed in the Arctic, with rapidly increasing catches from introduced and now self-sustaining populations in north-western Russia, and increasing trends in distribution and occurrence of presumed vagrants in the North American

Arctic. In the Pacific, pink salmon are the most numerous naturally-spawned Pacific salmon species in recent decades that typically display biennial patterns of abundance (more numerous in odd-numbered years). Warming temperatures may be fuelling increased pink salmon production at their northern distributional extent whereas those in the south are struggling with the cumulative impacts of environmental change.

Topic 2: Current Approaches to Assessment and Monitoring of Pink Salmon

Changes in pink salmon abundance and distribution in oceans and rivers have been documented using multiple monitoring approaches. In Alaska, surface trawls are used to assess pink salmon distribution and abundance in the northern Bering Sea as part of an ecosystem assessment. In north-eastern Russia, trawls similarly assess pink salmon distribution and abundance, with results from immature salmon predicting returns the following year. In rivers, adult pink salmon returns may be assessed and monitored by multiple means, and juvenile out-migration can be similarly monitored through the use of traps. Where pink salmon are rare, changes in distribution and occurrence may be monitored through community-led programs that monitor pink salmon harvested as bycatch in subsistence fisheries. Similarly, pink salmon range expansions in the Atlantic are monitored primarily in Norway through bycatch in scientific surveys and commercial or recreational fishing targeting other species and by river monitoring programs for Atlantic salmon. In other countries across the Atlantic, including Sweden, Ireland, Scotland, England, Wales, Faroe Islands, Greenland, Iceland and eastern Canada, pink salmon catches are lower than in Norway and they are mainly reported from recreational angling in rivers.

Topic 3: Competition and Interactions Between Pink Salmon and Other Species

Pink salmon spend approximately 18 months growing and rearing in the ocean but only weeks to a few months in freshwater before migrating to the ocean (they spend, on average, less time in fresh water after emerging from the gravel than other Pacific salmon species). The ecosystem consequences of interactions between expanding numbers of pink salmon, especially in certain years (as odd- and even-numbered years have different pink salmon abundances, depending on the geographic area), and other aquatic species remains a topic of scientific debate. Further research is needed, especially as pink salmon access new areas where effects may differ from those in areas of traditional occupancy. In the ocean, pink salmon overlap in diet with many other species and high abundances of pink salmon can deplete food resources. When numerous, pink salmon may affect the growth or mortality of non-salmon species, including fish, seabirds, and marine mammals, due to potential competition for zooplankton and other prey species. However, the ocean remains highly productive and pink salmon only consume a small fraction of the resources compared to more abundant species (e.g., walleye pollock). Pink salmon are also flexible foragers, eating a variety of prey and finding preferred feeding areas best suited to their traits. Indeed, the foraging areas and feeding habits among Pacific salmon species often indicate

complimentary, rather than competitive, interactions. In fresh water, adult and juvenile pink salmon rarely feed but, as fry, they can be important prey for other species after they emerge from the gravel in spring and quickly swim to the ocean. As adults returning to spawn in the fall, they can be aggressive on the spawning grounds, and may compete for spawning locations if suitable areas are sparse. They die after spawning and thus provide nutrients that can boost freshwater productivity.

Topic 4: Genetic Stock Delineation of Pink Salmon

The increase and range expansion of pink salmon is more pronounced in odd-numbered years, rather than in even-years, a trend that is especially prominent in the Atlantic Ocean. These odd- and even-year pink salmon populations are genetically distinct even within the same rivers, due to their strict two-year life cycle that prevents mixing among lineages. In fact, there is greater differentiation between these odd- and even-year lineages than among geographic regions, and odd-year pink salmon show more genetic diversity than the even-year salmon. There is genetic differentiation among pink salmon at a broad regional scale, however, as pink salmon group into Asia/Beringia or Gulf of Alaska/Pacific Northwest origins in the Pacific, and those sourced from the introduced, self-sustaining populations in north-western Russia. The geographic origins of expanding pink salmon can be explored using this differentiation; an effort that will require ongoing collaborations at an international level that will expand our understanding of biodiversity change amidst climate change.

Topic 5: Approaches to Monitoring and Predicting Future Changes in Marine Distribution

Pink salmon are on the move, but assessing the extent of these distributional shifts and predicting future change are difficult. Distribution models for both odd- and even-year pink salmon are being developed for the Pacific Ocean from historic catch records dating back to the 1950s. It appears that these lineages occupy similar habitats on the high seas and prefer similar temperatures. These thermal preferences may be used to understand current, and predict future shifts in distributions, especially as they move into Arctic waters.

Topic 6: Selective Methods and Removals, Opportunities for New Fisheries

The recent rapid expansion of pink salmon across the Atlantic has resulted in efforts to remove or eradicate them in rivers to mitigate potential effects on native species and ecosystems. Norway is the first country to implement an official strategy to eradicate pink salmon. Using various methods, over 100,000 pink salmon were estimated to have been removed from rivers across Norway in 2021. Experiences learned from those efforts guided the development of national mitigation measures now in place for 2023. In other areas with increasing pink salmon,

like Quebec, Scotland, and Ireland, anglers are encouraged to remove and report any pink salmon which are legally caught. Other removal systems, such as the placement of a trap, may be deployed on a trial basis in the lower reaches of the River Thurso in Scotland. It is also unclear how successful these efforts will be at eradicating pink salmon from Atlantic countries, especially if the general trends of increasing occurrences remain unchanged. The level of investment in eradication per country might be proportional to the perceived potential negative impacts of pink salmon. This underscores the need to better understand the potential impacts of expanding pink salmon on native species and freshwater ecosystems to inform appropriate management responses. Although there is limited interest in developing a commercial fishery for pink salmon in the Atlantic Ocean, this has not been pursued due to the risk of bycatch and increased mortality on native anadromous fish. In Norway, pink salmon are managed as an invasive species, with the focus on eradication.

Topic 7: Environmental DNA as a New Tool to Monitor Changes in Fresh Water Distribution

Environmental DNA (eDNA) is a new and cost-efficient tool that is being applied to monitor the occurrence of pink salmon and the related expansion in distribution. For instance, eDNA analyses from the Tana/Teno River demonstrated that pink salmon were distributed across all parts of the watershed in 2021, and that their distribution had increased since 2019. The different life-stages and age classes of Atlantic salmon and pink salmon present in rivers makes it difficult to assess differences in the relative abundance or biomass between the two species using eDNA. Pink salmon expansions into eastern Canada were also assessed using eDNA. While 39 rivers were sampled across nearly 1500 kilometres (km) of coastline from the Hudson Bay to the Ungava Bay, a single detection in Ungava Bay added growing evidence that, while pink salmon were present, they were likely not widely distributed and abundant in northern Quebec in 2021. Continued advances in eDNA approaches will increase opportunities for assessments of pink salmon expansions.

Topic 8: Information Exchange and Future Collaborations

The Northern Hemisphere Pink Salmon Expert meeting provided a venue for information exchange and highlighted the value of continued collaboration. Knowledge of pink salmon is unevenly distributed, yet there is an immediate need for information about pink salmon in areas experiencing abrupt population increases to guide and support management or conservation actions. Ongoing collaborations would facilitate the continued exchange of information and address topics of interest. The Northern Hemisphere Pink Salmon Expert group recommended the establishment of a Salmon Expert Group to provide the flexibility to address timely issues related to all salmon species. The NPAFC and ICES expressed interest in setting up this Salmon Expert Group, which would be science-based and thus complementary to the North Atlantic

Salmon Conservation Organization (NASCO) pink salmon working group, which is management-based.

Conclusions

The need to assess shifts in species distribution and the resulting potential impacts and opportunities, is an acute and increasingly international challenge across a rapidly changing planet. Pink salmon, a quintessential Pacific species, are increasing in abundance in the northern Pacific Ocean, are accessing the Arctic Ocean, and have been rapidly expanding across the eastern Atlantic Ocean in recent years. United in addressing this challenge, experts came together to share knowledge and developed takeaways that will guide further collaborations:

Takeaway 1. *The commonality of change highlights connections among our oceans and differences in perspectives*. The natural, slow northward progression of pink salmon in the Pacific basin leads to a management approach that focuses on production, whereas the invasive, rapidly expanding presence of pink salmon in the Atlantic basin shifts the management strategy to eradication. The Canadian Arctic will need to straddle the strategies as subsistence harvesters targeting Arctic species increasingly catch pink salmon originating from both basins.

Takeaway 2. *The pace of change catalyses the pace of response*. The immediate need for management and conservation action in the Atlantic basin can be guided by knowledge inherent to the Pacific basin, where the species is well-studied. Across the northern hemisphere, however, there is a fundamental gap in understanding the effects of interactions between pink salmon and other species in freshwater and marine ecosystems where the pink salmon are new or expanding in range and/or abundance and with species that have not encountered pink salmon before. There is an opportunity to apply what is known to better understand what is not known.

Takeaway 3. *The scale of change requires a similar scale of collaboration*. Monitoring and assessing the shifting distributions of pink salmon across the broad expanse of the northern hemisphere requires a continued coordinated approach to the exchange of information, methods, samples, and technology that is on pace with the changes taking place. Sharing what is known about pink salmon will assist in prioritizing knowledge gaps and will guide future strategies. A structured process facilitates this exchange.

Pink salmon are clearly on the move in the northern hemisphere. Although they represent one species among a global redistribution of life, they also represent an opportunity to better understand broad-scale biodiversity change across our connected ocean.

1. Pink Salmon Ecology, Distribution, and Abundance

Pink Salmon Ecology

As a biological species, pink salmon *Oncorhynchus gorbuscha* have existed for about 5 million years and are likely the most recently evolved of the salmon species (Glubokovsky 1995). In their native range, pink salmon have an almost exclusive two-year lifecycle, the

shortest of the Pacific salmon species, with populations that spawn in odd- or even-years having evolved into distinct genetic entities. Paired seasonal runs (early and late, or "summer" and "autumn") with distinct morphological characteristics and spawning areas within river basins separate most pink salmon stocks. Emerging pink salmon fry migrate downstream from late February to August. In the northern regions, timing of downstream migration is usually latest, and juvenile salmon are smaller than in the south. Rates of offshore migration are likely related to feeding conditions of a specific year (Radchenko et al. 2018, and references therein).

Both odd- and even-year types spawn during late summer and autumn in the clean, coarse gravel in areas of shallow (10–100 cm) pools and riffles of small to large rivers. Pink salmon prefer moderately fast (30–150 cm/s) currents and generally avoid spawning in deep, slow-moving water or on muddy, sandy, or silted substrate (Heard 1991). Water temperatures during the peak of spawning range from about 5°C to 15°C and are generally higher for southern populations. Pink salmon, especially from late-run stocks, tend to spawn closer to the head-of-tide than other species of Pacific salmon, generally within 50 km of a river mouth (Heard 1991). However, pink salmon populations from large river systems such as the Fraser River and Skeena River in Canada are known to migrate up to 500 km upstream to spawn, and a substantial portion of other populations may spawn intertidally (Jones 1978).

Pink salmon mature at the smallest average size of any species of Pacific salmon (1.0–2.5 kg) and show marked sexual dimorphism (Beacham and Murray 1985). Spawning populations throughout much of their natural range may be extremely large, often exceeding hundreds of thousands of fish (Heard 1991). Freshwater mortality of juvenile pink salmon is high, ranging from about 75% to over 99%, and mostly occurs before emergence from the gravel (Hunter 1959). After emerging, pink salmon juveniles migrate rapidly downstream, generally in schools and usually during the hours of darkness (Heard 1991). Juveniles grow most rapidly during their residence in the nearshore marine environment. Preferred marine prey are small crustacea, such as copepods, euphausiids, amphipods, and cladocerans (McDonald 1960; Karpenko 1998). The proportion of insects and fish larvae in the diet of pink salmon also is substantial in many regions (Karpenko 1998). After residing in estuaries and nearshore habitat for a few weeks to a few months, pink salmon move offshore where they migrate at sea for 12–16 months (Heard 1991). Adult pink salmon prey preferences include zooplankton, squid, and fish (Davis et al. 2009).

Smolt to adult survival in pink salmon appears to vary widely among years and locations. Cross et al. (2008) reported rates varying between 3–8% in Prince William Sound, Alaska. Radchenko (2007) estimated survival rates for the Sea of Okhotsk basin between 2.0–8.7% for 1989–2004 year classes. Kaev (2021) reported rates between 1–18% in populations from Sakhalin Island, Russian Federation. Early marine growth has repeatedly been correlated with overall survival in Pacific salmon species. Although there is a lack of understanding of the exact mechanism, the timing, magnitude, and sources of stage-specific marine survival and early growth of pink salmon are probably governed by a combination of prey availability, smolt quality, inter/intra-specific competition, predation and ocean conditions (Cross et al. 2008).

The levels of straying in pink salmon, or attempt reproduction at non-natal sites (Quinn 1993), varies widely among populations and within populations under different conditions. Pink

salmon may stray at higher rates than other species of Pacific salmon (e.g., Horrall 1981), with rates > 50% observed in some studies, whereas other studies reported lower rates between 0.1 and 12% (Hard et al. 1996). However, there is substantial evidence of rapid range expansion in pink salmon when conditions are favourable (e.g., Heard 1991; Pess et al. 2014, and references therein). The frequent occurrence of pink salmon in areas without permanent spawning populations well outside the usual spawning range (Figure 1) also suggests that pink salmon homing behaviour is highly plastic (Hard et al. 1996).

Pink Salmon Distribution

Natural Distribution

Pink salmon are the most widely distributed species of Pacific salmon along the Pacific Rim (Augerot 2005) (Figure 1). On the North American side, significant spawning populations of pink salmon extend from Puget Sound, the Strait of Georgia, the Fraser River northward to north-west Alaska. Spawning populations of the odd-year broodline tend not be self-sustaining below 47°N latitude on the Pacific coast of North America, although pink salmon have recently been observed in fresh water below 37°N, as far south as the Salinas River in 2011 (Skiles et al. 2013), and successful spawning has been detected in streams near 38°N latitude (Moyle et al. 2008). Populations belonging to the even-year broodline are probably not self-sustaining south of 49°N, going through short cycles of founding and extirpation (e.g., Snohomish River, Washington, WDFW 2022). Pink salmon can also access the Arctic Ocean coasts in the north; however, the existence of robust spawning populations of pink salmon in the North American Arctic remains debated (Nielsen et al. 2013). Based on the locations of commercial catches in the North American region, pink salmon stocks are in greatest abundance in central and south-east Alaska, including Prince William Sound, but are also present in large numbers in British Columbia during some years (Heard 1991; Fisher et al. 2007).

Along the Asian coasts, pink salmon spawn in rivers from northern Honshu Island in Japan and the northern Korean Peninsula to the north-east of Siberia. The most productive pink salmon stocks and main fisheries in this region are located on the eastern coast of Sakhalin and Iturup Islands and the western and eastern coast of Kamchatka (Radchenko et al. 2007; Shuntov and Temnykh 2008). Feeding areas in the open ocean extend from about 39°N in the Pacific Ocean (38°N in the Sea of Japan) to the northern Bering Sea. Along the coasts, pink salmon migration routes extend an additional 1–2° to the south, and to the Lena River mouth in Siberia.

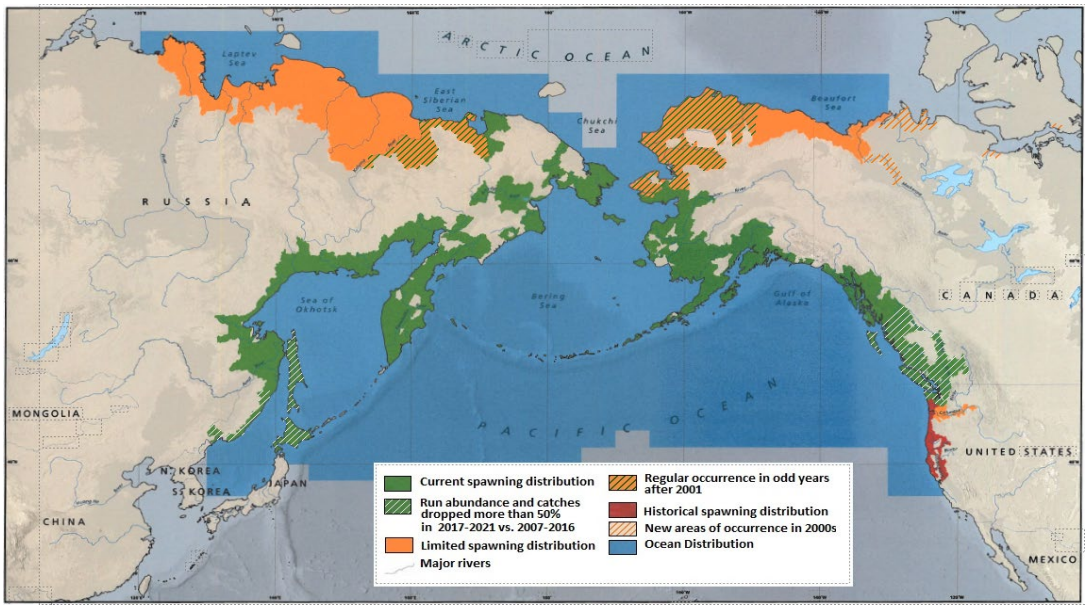


Figure 1. Pink salmon distribution (Augerot 2005) updated based on the recent reports on its penetration to the Arctic (Golub and Golub 2011; Dunmall et al. 2013; Farley et al. 2020; Stafford et al. 2022).

Introduced Distribution

Since the early 20th century, attempts have been made to introduce pink salmon outside its native range with the aim to create additional fishing opportunities (Heard 1991). One of the earliest attempts at pink salmon introduction into the North Atlantic Ocean was undertaken in the USA, when more than 40 million eggs were transplanted into the Gulf of Maine rivers between 1906 and 1926 (Ricker 1972; Lear 1975). This produced significant returns of subsequent year classes (several thousand fish) and their natural spawning. After 1927, however, few adult fish were observed (Gritsenko and Bakshtansky 1975; Heard 1991), although pink salmon were planted in Maine once again in 1982 (Randall 1984). Another introduction of pink salmon in the North Atlantic Ocean occurred in Newfoundland, Canada, between 1956 and 1966. Despite a maximum of 8,500 natural spawners in the peak year 1967, runs declined throughout the 1970s (Lear 1975). Pink salmon were captured on the east coast of Canada in northern Labrador and in Newfoundland up to the late 1970s (Dempson 1980). Pink salmon were also observed in New Brunswick in 1983 (Randal 1984) and in Nova Scotia (Crossman 1991). Small naturally occurring populations of pink salmon in Newfoundland remained a possibility in the 1980s (Dempson 1980). In the Hudson Bay area in northern Ontario, Canada, pink salmon ova, fry, and fingerlings were stocked into Goose Creek in 1956, but no adult pink salmon were subsequently reported from the Hudson Bay (Ricker and Loftus 1968).

In the Great Lakes in the USA and Canada, pink salmon were accidentally introduced into Lake Superior in 1956, and have since been firmly established in Lake Superior, Lake Huron,

Lake Erie, and Lake Ontario (Heard 1991; Kwain and Lawrie 1981). Some notable differences between these populations that complete their life cycle in freshwater and the anadromous donor population from the Lakelse River in British Columbia (Canada) are lower fecundity, smaller size, variable ages at maturity (three- and four-year-old adults are reported), and a different body shape (Heard 1991). These appear to be adaptations to the less favourable growth conditions in freshwater relative to the marine environment, possibly facilitated by rapid genetic drift due to small population size and genetic isolation from other pink salmon populations (Berg 1979). For Lake Superior and Lake Huron, catch-per-unit-effort was greater in even years (57 fish/night) than in odd years (30 fish/night) (Kennedy et al. 2005) indicating that the even-year broodline was likely more abundant.

In the north-western part of the Russian Federation, pink salmon were introduced into the river basins of the Barents and White Seas. In 1956–1972, about 199 and 46 million salmon eggs, respectively, were brought to the north-western region. Transportations of fertilised eggs initially were from the Sakhalin and Iturup Island hatcheries in late October to early November (Zubchenko et al. 2004). A relatively small amount of pink salmon eggs, about 2 million, from the western Kamchatka coast and 0.5 million eggs from the Magadan region, were transported to streams flowing into the Barents and White seas in 1959 and 1961. An additional 19.5 million eggs from the Magadan region were stocked out between 1984 and 1988 (Zubchenko et al. 2004). Since 1961, pink salmon fry hatched from ova collected from fish returning to local Kola Peninsula rivers of the Barents Sea were also released into these streams. Numbers of such releases reached a noticeable amount only twice, including about 2 million eggs in each of 1961 and 1973. In other years, releases varied from 50,000 to about 1.5 million eggs with one- to eight-year cessations until the program ended in 1999. Despite the relatively high pink salmon returns to rivers of the Kola Peninsula, Karelia, and Arkhangelsk regions in first years after introduction (e.g., 76,300 fish in 1960; 220,500 in 1973; 215,300 in 1975; and 162,700 in 1977), a decline in numbers of spawning fish was subsequently observed. Without the transport of new eggs, pink salmon returns rarely exceeded two to three thousand fish in odd years, whereas they were essentially zero in even years (Kudersky 2005; Dorofeyeva 2009). A restoration of pink salmon runs occurred after the resumption of ova transportation from rivers of the Magadan region to Kola Peninsula rivers in 1984. In 1987, the first pink salmon return was recorded from natural spawning in the local rivers. Catches ranged between 96–339 metric tonnes (mt) in odd years from 1989–2003 (Kudersky 2005).

Attempts of pink salmon introduction into the Caspian, Black, and Baltic seas have been unsuccessful. In 1962 and 1963, six million fertilised pink salmon eggs were transported to a trout hatchery in the Black Sea basin, but no information was available to assess survival after the two years of releases (Gritsenko and Bakshtansky 1975). Small pink salmon catches (about 1500 in total) were observed in the north-western Caspian Sea after the introduction of 2 million eggs in 1964 (Magomedov 1970; Karpevich et al. 1991). In the Baltic Sea, including along the Sweden coast, a few to several hundred pink salmon returned only in the year following release. Thus, pink salmon were able to feed and grow in the brackish Baltic Sea environment, but natural reproduction did not occur (Kudersky 2005).

Some attempts were made to commercially grow pink salmon in brackish-water lakes of the Krasnoyarsk region (Central Siberia). Pink salmon grew satisfactorily and reached sexual maturity. In 1979, 7.9 mt of marketable fish and food caviar were obtained. This project, although it was experimental in nature, showed the possibility of pink salmon commercial aquaculture in brackish waters (Kudersky 2001).

No other attempts of pink salmon introductions are known from the north-eastern Atlantic area, except for a small introduction attempt in southern Norway in 1976 (Sandlund et al. 2019).

In Japan, pink salmon eggs from the north-eastern Hokkaido rivers were introduced to Yurappu River, southern Hokkaido, in the 1950s–1960s (Ishida 1967) and to Akka River, Iwate Prefecture, Honshu Island, in the 1990s (K. Morita, personal communication). Sano and Kobayashi (1953) reported that the return rate of introduced marked pink salmon in the Yurappu River was 0.5%. In the case of Akka River, it is difficult to determine if these transplantations were successful or not, because small numbers of native pink salmon were present in these rivers. Although about 90% of released pink salmon fry were marked by a fin clip, marked fish were not recaptured. The recapture of only non-marked wild pink salmon in the returns suggest that the marked introductions were unsuccessful.

Range Expansion

Pacific to North-eastern Russia and Western Canadian Arctic Connection

Pink salmon have also extended their natural distribution range in the marine environment into the Russian and Canadian Arctic. In 2007, high abundances of juvenile pink salmon were reported from the Chukchi Sea, suggesting that the Arctic marine ecosystem may provide viable habitat in some years (Moss et al. 2009). Warming temperatures may facilitate increased pink salmon production at the northern extent of their natural range (Farley et al. 2020), and may also contribute to the occasional harvest of adult pink salmon in subsistence fisheries targeting other species across the Canadian Arctic (Dunmall et al. 2013). In the western Canadian Arctic, these occurrences have increased from the sporadic catch of individual fish prior to 2003 to more catches being reported in both even- and odd-numbered recent years, and across a wider geographic area (Dunmall et al. 2018, 2021). Pink salmon have also been reported, although rarely, from the eastern Canadian Arctic in recent years (McNicholl et al. 2021).

In the Russian Arctic, pink salmon westward penetration was also noted since 2011, when the abundance of pink salmon runs to the Chukotka Peninsula coasts sharply increased and reached 10 million fish (Golub & Golub 2011). The westernmost observations of pink salmon spawning in the (Asian) Russian Arctic are from the River Lena area around 127°E (Shuntov and Temnykh 2008). The Taymyr Peninsula appears to be a natural border that divides the pink salmon native and introduced ranges in the Russian Arctic (Prusov and Zubchenko 2022). Salmon straying to non-natal regions tend to reproduce poorly (due to maladaptive spawning dates and other factors, e.g., Zolotukhin 2006).

North-western Russia to Atlantic Connection

Currently, pink salmon are distributed over a wide range in north-western Russia. Prior to 2021, pink salmon were primarily recorded in the White Sea rivers and also east of the Kola Peninsula in the rivers flowing into the Barents and the Kara seas (Rivers Pechora, Ob, Taz, Yenisey, and others) (Figure 2, Figure 3), whereas in the Barents Sea rivers of the Murmansk region, adult abundance was modest. Between 2001 and 2021, the Pyasina river, in the southwest of the Taymyr Peninsula, is the easternmost location of pink salmon distribution in the Kara Sea basin (Figure 2, Figure 3) (Bogdanov and Kizhevatov 2007, 2015).

Observations of pink salmon in the North Atlantic have been reported from a much larger geographical area and occurrences have increased noticeably since 2017 (ICES 2022a, b). Outside the Russian Federation, pink salmon have been observed in a wide range of countries such as Norway and Finland (Sandlund et al. 2019), Faroe Islands (Eliasen and Johannesen 2021), Scotland (Armstrong et al. 2018; Skóra et al. 2023), Ireland (Millane et al. 2019a, b), Iceland, Germany, France, Netherlands, and Denmark (Bean, 2017; ICES 2022a) and Greenland (Nielsen et al. 2020). In France, odd-year fish have been observed as far south as the Élorn River in the north-eastern Atlantic area. Pink salmon have probably established successfully reproducing populations as far west as the Norwegian region of Finnmark in recent years (E. Thorstad/K. R. Utne/H. Berntsen, personal communication), with reports of smolts as far south and west as the Jølstra River in the Sunnfjord in western Norway (Sægrov et al. 2022) (Figure 3). In addition, smolts were reported from rivers in northern Scotland and western Iceland (Skóra et al. 2022) in recent years (Figure 3). In Norway, compared to 2001 (Figure 2) when frequent spawning was observed as far west as the Varanger Fjord in Norway and occasional spawning to the town of Gamvik (E. Thorstad/K. R. Utne/H. Berntsen, personal communication), the 2021 limits are much farther west and south. Reports of even-year fish outside northernmost Norway/Finland/Russia remained very low between 2017–2021 with only a single report from the UK (ICES 2022a).

In the north-western Atlantic area, pink salmon have been observed as far north as Clyde River, Nunavut (McNicholl et al. 2021) and as far south as the Gander River in Newfoundland (ICES 2022a).

The increase in abundance of pink salmon since 2017 is discussed in section 1.3 of this report.

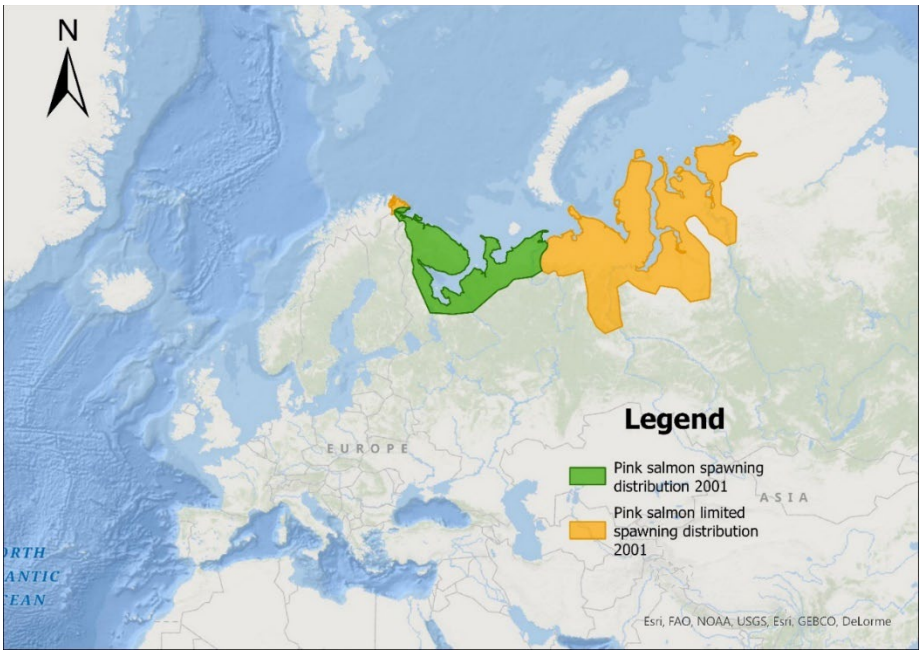


Figure 2. Pink salmon distribution in the Northeast Atlantic in 2001. Areas where pink salmon occurred and spawn regularly in odd years are highlighted by green, areas of adult pink salmon occurrence with limited or unknown spawning success are highlighted by orange.



Figure 3. Pink salmon distribution in the Northeast Atlantic in 2021. Areas where pink salmon occurred and spawn regularly in odd years are highlighted by green, areas of adult pink salmon occurrence with limited or unknown spawning success are highlighted by orange.

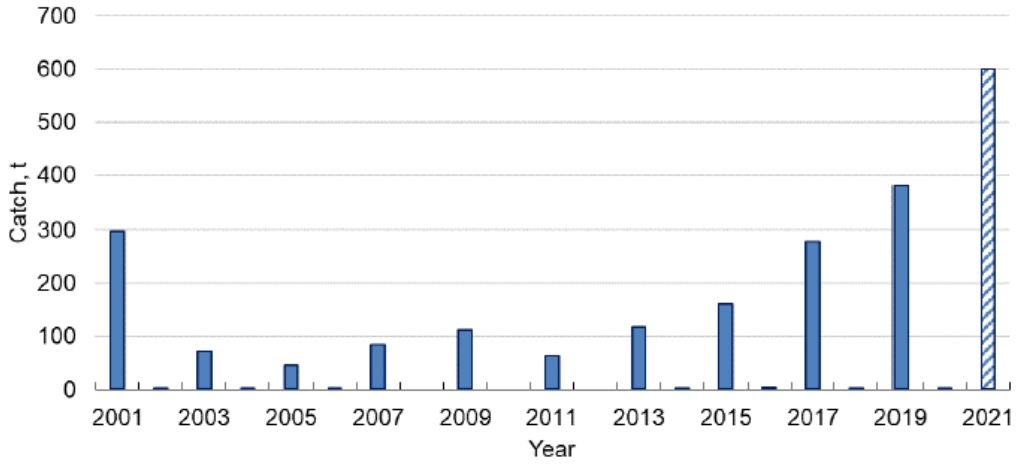


Figure 4. Pink salmon catches in Murmansk region in 2001–2021. Catch for 2021 is provisional (Prusov and Zubchenko 2022).

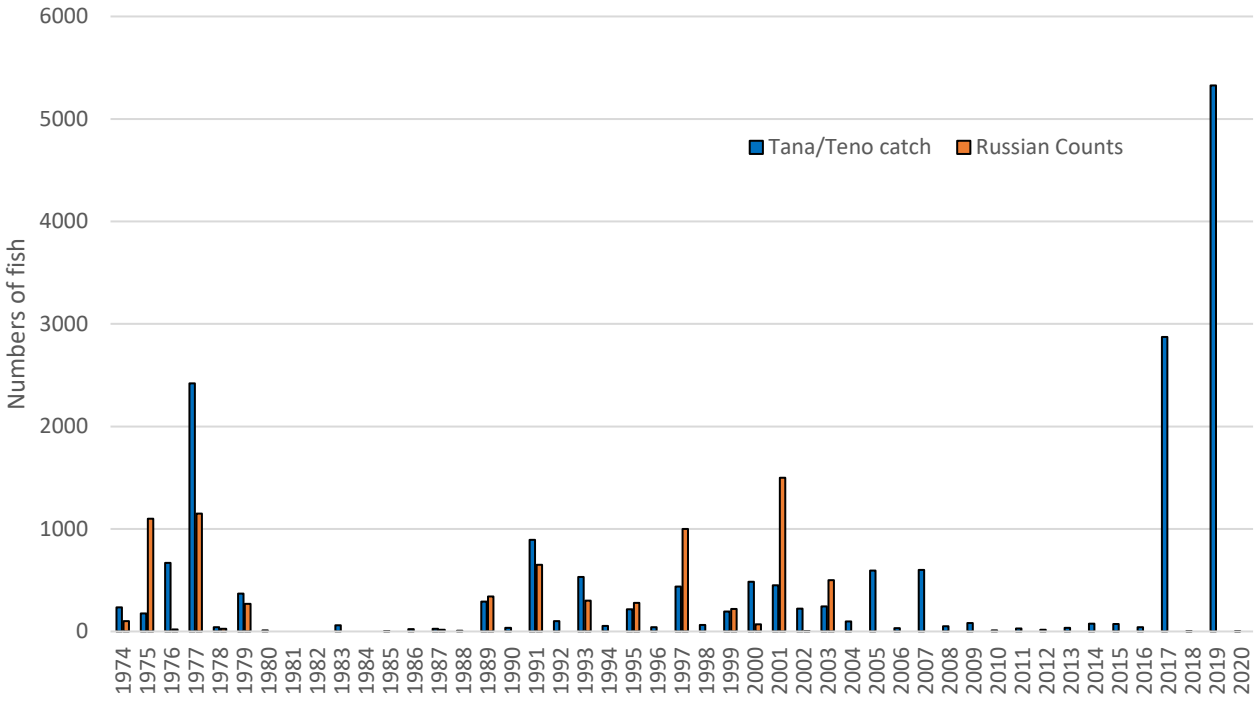


Figure 5. Sum of recorded catches of pink salmon in the river Tana/Teno in Norwegian and Finnish waters, 1974–2020 (data from LUKE and Tanavassdragets fiskeforvaltning, www.tanafisk.no), and counts of adult pink salmon in Russian catches 1974–2003 (Zubchenko et al. 2004).

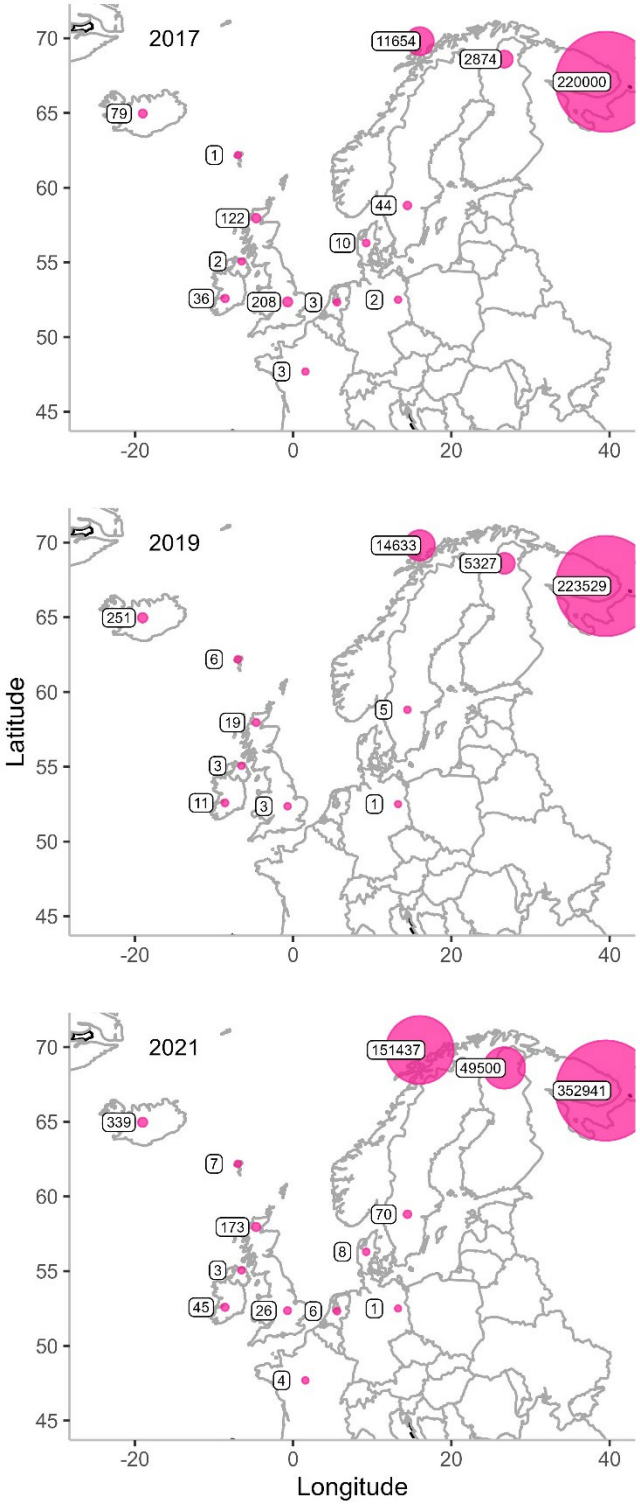


Figure 6. Numbers of pink salmon reported by jurisdiction in the NEAC area (2017, 2019, and 2021).

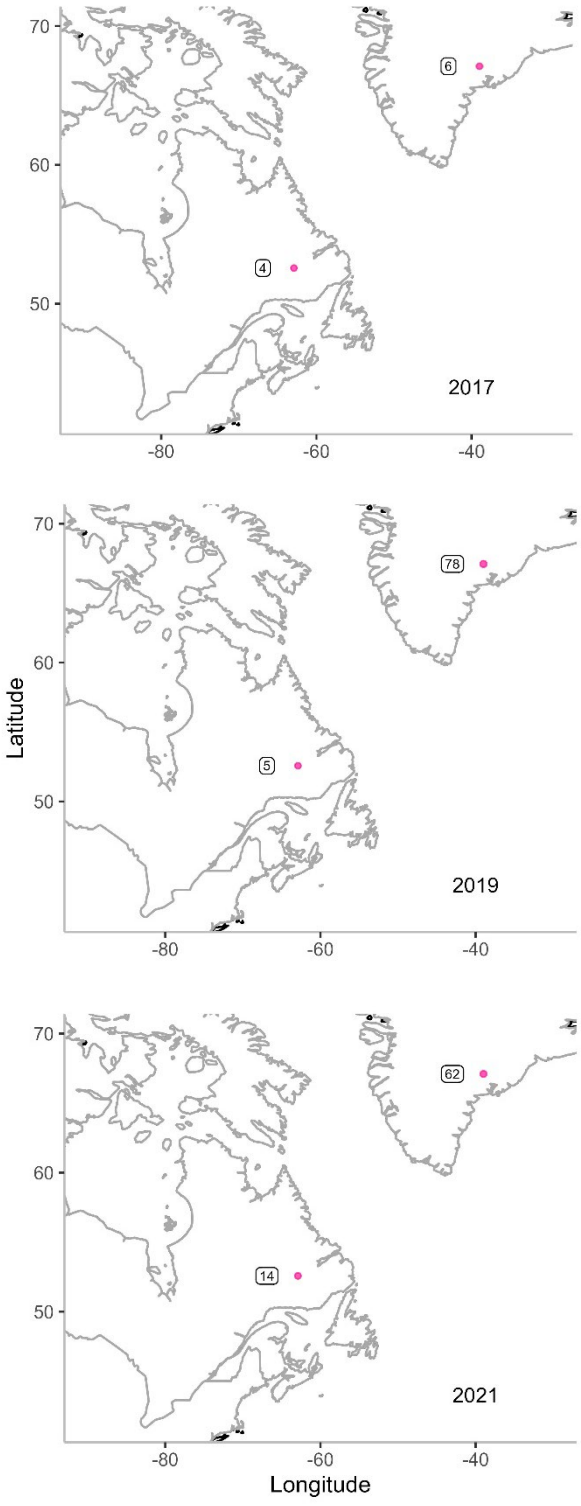


Figure 7. Numbers of pink salmon reported by jurisdiction in the NAC and WGC areas (2017, 2019 and 2021).

Pink Salmon Abundance

In the North Atlantic, pink salmon abundance pre-2000 was closely linked to the stocking activity in north-western Russia. Large numbers of adults were observed in rivers of the Kola Peninsula, Karelia, and Arkhangelsk regions in first years after introduction in the late 1950s (e.g., 76,300 fish in 1960; 220,500 in 1973; 215,300 in 1975; and 162,700 in 1977). During this time period large numbers of pink salmon were occasionally observed outside of north-western Russia, such as in 1960 when 20–25 mt were caught in northern Norwegian waters (Berg 1961). After stocking ceased in 1999, odd-year pink salmon catches in the Murmansk area increased to 300 mt in 2001 before settling close to 100 mt on average between 2003 and 2013 (Prusov and Zubchenko 2022). Catches then substantially increased above 100 mt again after 2015 reaching record numbers in 2019 (close to 400 mt) and 2021 (600 mt) (Figure 4). Even-year populations remained at low numbers during this time period. Abundant pink salmon runs in the White Sea coast rivers in 2021 led authorities to allow a commercial as well as a subsistence fishery on pink salmon. Predictions are that 1,200 mt of pink salmon will be harvested there in 2023.

Long-term time-series of pink salmon abundance outside north-western Russia are rare. The Sandlund et al. (2019) overview of catches in the Norwegian/Finnish Tana/Teno system in northernmost Norway and Finland between 1974 and 2017 (Figure 5) reported high catches in the 1970s, followed by a decline to zero after the first attempt to establish self-sustaining populations ended in 1979. In the 1990s, catches increased again to about 400–1000 individuals for odd-years, and below 100 for most even-years. Despite Russian stocking ceasing in 1999, odd-year catches between 2001 and 2007 reached their highest levels since 1977 and 1991, which means all these fish naturally spawned. Between 2007 and 2015 catches markedly decreased to some of the lowest levels seen for both odd- and even-years in the time-series. This was mirrored in a 2007–2017 time-series of pink salmon catches in the nearby Neiden River (Sandlund et al. 2019).

Since 2017, pink salmon catches and observations of odd-year fish have increased dramatically, both in the Russian Federation, northern Fennoscandia, and much further south such as central and southern Norway, the UK and Ireland, and as far south as France (Armstrong et al. 2018; Millane et al. 2019a; ICES 2022a, b) (Figure 6) and west and east Greenland (Nielsen et al. 2020; ICES 2022a, b). In 2017, pink salmon numbers reported to the International Council for the Exploration of the Sea (ICES) Working Group on North Atlantic Salmon (WGNAS) exceeded 230,000. In 2019, the number of pink salmon reported increased again to over 238,000 but with a much-reduced southern distribution. In 2021, the total number increased to well over 500,000 with record numbers reported from as far south as Scotland, Ireland, the Netherlands, and France. The north-west Atlantic area has also experienced an increase in pink salmon occurrences in 2017 and 2019 (Dunmall et al. 2018; McNicholl et al. 2021), and a record number of 14 individuals reported in 2021 (Figure 7). Even-year reports outside northernmost Norway/Finland/Russia remained very low between 2017–2021 with only a single report from the UK (England and Wales).

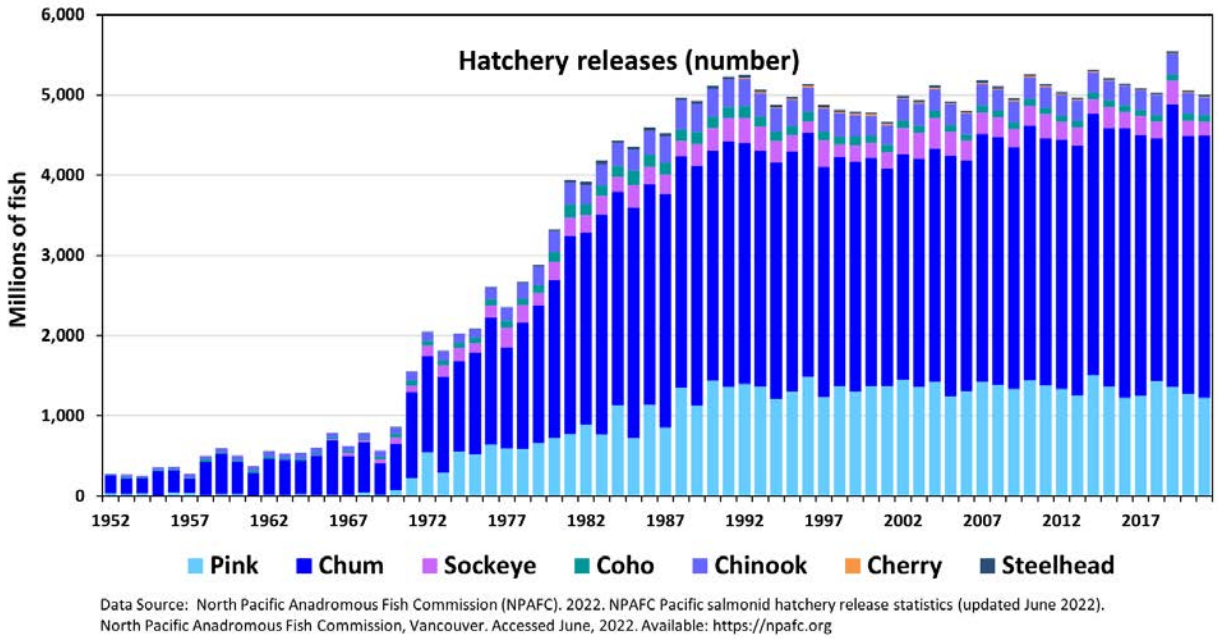


Figure 8. North Pacific Anadromous Fish Commission Pacific salmonid hatchery release statistics (NPAFC 2022b)**.**

In the Pacific, there have also been substantial increases in pink salmon abundance in recent years. However, a potentially complicating factor to establishing natural abundance in the Pacific is the hatchery releases of juvenile pink salmon undertaken by various countries to supplement natural production with a view to increase fishing opportunities. Hatchery supplementation of pink salmon in the Pacific has been relatively stable since 1990 with about 1,360 million juvenile pink salmon released annually (Figure 8).

Pink salmon have been the numerically dominant salmon species in the North Pacific Ocean since approximately 1990. In recent years, pink salmon comprised 67% of the total number and 48% of the biomass of all salmon in the North Pacific Ocean (Ruggerone and Irvine 2018). Naturally-spawned pink salmon were especially numerous during 1990–2015, averaging 379 million fish and up to 595 million fish (or 81% of the combined abundance of the three species) in peak years 2009 and 2011. Although even-year spawning pink salmon tended to be more abundant than odd-year fish during 1925–1935, odd-year spawning pink salmon were 27% more abundant than even-year pink salmon across the full period and 37% higher abundance during 1990–2015.

There is a clear north/south divide in the recent increased abundance of pink salmon in the Pacific. Conditions favour the pink salmon in the northern Pacific regions, where many large salmon populations occur in relatively intact habitats. Warming temperatures may facilitate increased production of pink salmon at their northern distributional extent (Farley et al. 2020) and pink salmon occurrences have also increased in the western Canadian Arctic in recent years (Dunmall et al. 2018, 2021). Contrastingly, many southern populations are adversely impacted

by habitat degradation, oceanic conditions, interactions with hatchery salmon, and overharvest in mixed-stock fisheries, resulting in abundance declines (Malick and Cox 2016; Ruggerone and Irvine 2018). Irvine et al. (2014) also observed declining abundances in some southern even-year pink salmon conservation units (biological units that are genetically and/or ecologically distinct from each other) in British Columbia, although not in odd-year populations (Figure 9). Significant negative interactions between even- and odd-year broodlines were found for several of the BC regions, but there was little evidence of competition between broodlines in the marine environment. Irvine et al. (2014) suggested that a more-southerly glacial refugium for odd-year than even-year pink salmon and temperature-related survival differences between these broodlines may be benefiting odd-year returning pink salmon more than even-year salmon during global warming.

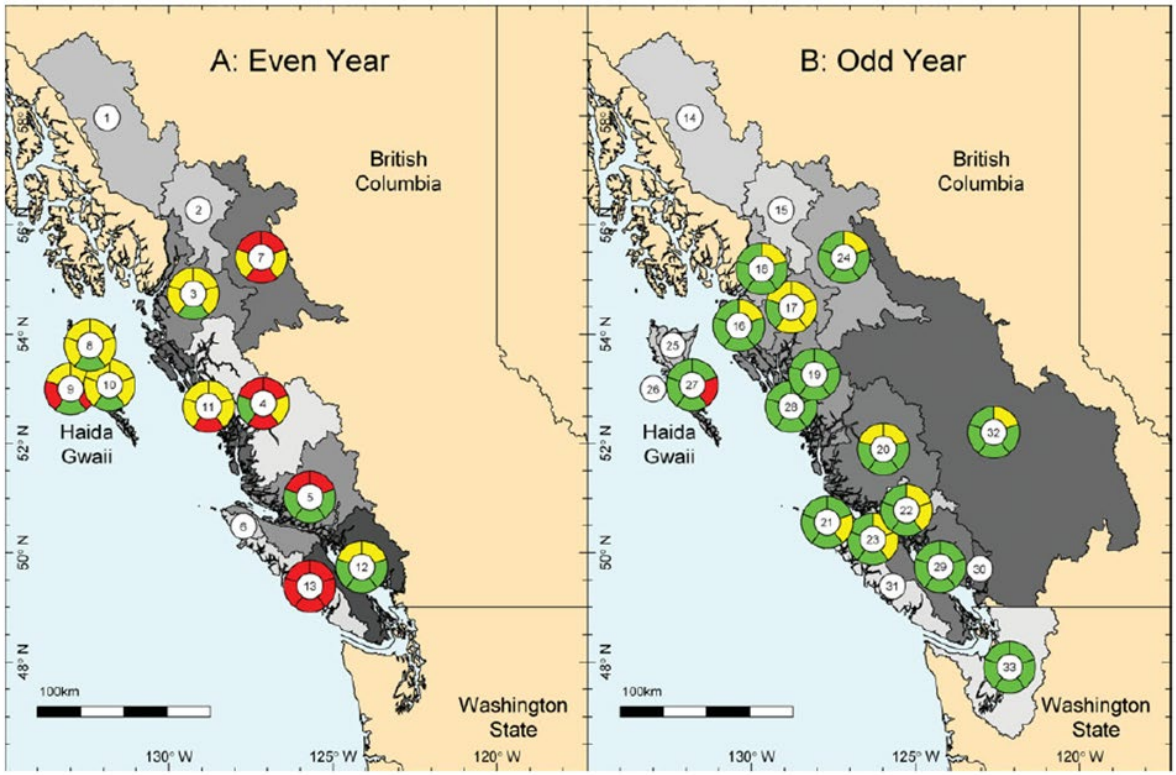


Figure 9. Status of (A) even-year and (B) odd-year pink salmon Conservation Units (CU) in British Columbia and Puget Sound (Washington State) depicted by five-piece circles in which the central number references the CU name and each piece shows the results from one time series approach. Green colours represent increasing numbers, yellow means no significant difference over time and red indicates decreasing numbers. See Irvine et al. (2014) for details.

2. Assessment and Monitoring: Current Schemes

Pacific Basin

The first Pacific salmon research programs in offshore waters were based on sampling conducted by the same gear as the commercial fisheries—gillnets, longlines, and purse seines. Offshore distribution, migration patterns, and feeding were studied, and a large amount of biological information was collected (Manzer et al. 1965; Neave et al. 1967; Takagi et al. 1981). In 1984–1990, the Russian research institute TINRO explored using a large-dimensioned rope trawl net to study migratory salmon and estimate their numbers in the Bering and Okhotsk Seas and adjacent Pacific Ocean as a part of pelagic ecosystem studies. A more practical two-season trawl survey was then developed with an abundance assessment of juvenile pink salmon migrating oceanward in October and an assessment of maturing returning fish in June–early July. With few exceptions, these surveys have been conducted in the north-western North Pacific annually since 1991 (Shuntov and Temnykh 2008, 2011; Radchenko et al. 2018). Extensive information was obtained on distribution, abundance, ecology, physiology, and trophic relationships of Pacific salmon that significantly supplemented and, in some cases, radically changed our existing knowledge base. Based on the trawl catches, annual calculations of pink salmon abundance, survival rate, and estimates of run magnitude, as well as abundance of all other fish and invertebrates' species in the survey areas, were made. In-season forecasting of pink salmon run magnitude and timing was mostly successful and notably contributed to the fishery season output.

Scientists from other NPAFC member countries have also tested the advantages of the new method of Pacific salmon studies on the high seas. In 1990–1991, Soviet and Canadian scientists conducted joint trawl surveys aboard the R/V *TINRO* in the central and eastern North Pacific Ocean (Morris et al. 1991, 1992). Since 1992, Canadian scientists have conducted trawl surveys on Pacific salmon aboard R/V *W.E. Ricker* and chartered Canadian fishing vessels (Beamish et al. 2003). In 1998, U.S. scientists developed salmon trawl surveys, off the north-western coast of the United States to study juvenile coho and Chinook salmon, and in the Gulf of Alaska to study all salmon species in the coastal area, and in Bristol Bay focussing on oceanward migrations of juvenile sockeye salmon (Farley et al. 1999). In 1997–2012, monthly trawl surveys across the Southeast Alaska straits were used to estimate pink and coho salmon production in the region (Orsi et al. 2013). In 1992, 1996, and 2006, Japanese scientists with colleagues from other NPAFC countries conducted salmon trawl surveys from the large-tonnage R/V *Kayo maru* (Ueno et al. 1996). In 1992, the first December offshore survey of salmonids in the North Pacific Ocean was conducted since the 1960s (National Research Institute of Far Seas Fisheries 1993).

An international research program called BASIS (the Bering-Aleutian Salmon International Survey) was developed by the NPAFC and implemented in 2002–2016. In 2002, the trawl survey aboard Japanese, Russian, and U.S. research vessels covered the whole Bering Sea and adjacent Pacific waters (about 3 million km^2). The goal was to clarify how Pacific salmon respond to climate change in the Bering Sea. The role of Pacific salmon as consumers of food resources in the pelagic fish communities of the Bering Sea was also assessed. The Pacific

salmon distribution in the western and northern Bering Sea was influenced, not only by the food supply, but also by increased advection of Pacific waters since the early 2000s. BASIS became a precursor to the expeditionary part of the IYS program (Radchenko 2022a).

Surface water trawl surveys in the Northern Bering Sea (NBS) were initiated by NOAA's Alaska Fisheries Science Center (AFSC) in 2002 as part of the BASIS program (Murphy et al. 2021). These surveys were continued through 2007 as part of the BASIS survey for the eastern Bering Sea shelf. The NBS was not sampled in 2008, but it has been sampled on an annual basis since 2009 to support research objectives on the ecology of salmon in the NBS and to improve our understanding of how the NBS ecosystem is changing in response to warming climate and loss of Arctic sea ice.

The NBS survey has supported a range of different survey operations and research objectives. Survey operations have included the following: surface and midwater trawl sampling for pelagic nekton, midwater acoustics, seabird and marine mammal observations, bongo net sampling for zooplankton and ichthyoplankton, electronic conductivity, temperature, depth (CTD) data, and water collections for chlorophyll-a, phytoplankton, and nutrients. The survey supports research objectives on salmon and other pelagic fish resources, including: juvenile salmon abundance and run-size forecasts (Murphy et al. 2017; Howard et al. 2019; Howard et al. 2020; Farley et al. 2020), size-selective mortality (Murphy et al. 2013; Howard et al. 2016), energy allocation (Andrews et al. 2009; Murphy et al. 2013; Moss et al. 2017), diet (Farley et al. 2009; Andrews et al. 2016; Cook and Sturdevant 2013; Honeyfield et al. 2016; Garcia and Sewall 2021), and species distribution (Murphy et al. 2009; Murphy et al. 2016; Andrews et al. 2016). The BASIS survey was the first to observe mass migrations of juvenile pink and chum salmon into the Chukchi Sea (Moss et al. 2009).

Data from the NBS survey were recently used to develop models for pink salmon life-history and provide insight into pink salmon production dynamics for this region (Farley et al. 2020). Arctic ecosystems, including freshwater and marine ecosystems in the northern Bering Sea, are warming at a rapid rate. Due to their two-year life-cycle, pink salmon respond rapidly to ecosystem change and can provide unique insight into ecosystem impacts of warming Arctic conditions. Life-cycle models suggest a lack of density-dependence for adult pink salmon spawners in the Yukon River but the potential for some density-dependence for adult pink salmon spawners in the Norton Sound region. Life-history models identify a significant positive relationship between the abundance index for juvenile pink salmon and average air temperature in Nome, Alaska during their freshwater residency (August to June). This relationship supports the notion that warming air temperatures in the Norton Sound region of Alaska (as a proxy for river and stream temperatures) are contributing to improved freshwater survival or increased capacity of freshwater habitats to support pink salmon production. Life-history models also demonstrate the number of adult pink salmon returning to Norton Sound and the Yukon River is significantly related to juvenile abundance in the northern Bering Sea. This indicates that much of the variability in survival for northern Bering Sea pink salmon occurs during early life-history stages and that juvenile abundance is an informative predictor of adult pink salmon runs to this region.

In Alaskan rivers, escapements are monitored annually using a variety of ground-based methods, such as weirs, sonar, counting towers and foot/boat surveys, or aerial surveys (see Tables 19–22 in Munro and Brenner (2022) for additional information). Because of the large number of streams where pink salmon spawn and the remoteness of many of them, most assessment in Alaska is by aerial survey. For example, in Southeast Alaska, wild pink salmon spawn in approximately 2,500 short, coastal streams and in-season escapement assessments are based on aerial surveys and peak aerial survey counts for about 700 streams (Heinl et al. 2021; Zadina et al. 2004). Aerial survey counts are used to estimate an annual escapement 'index' (i.e., not a total count) and to develop sub-area escapement goals. In Alaska, escapement assessments are used to assist with in-season management of the salmon fisheries and to determine annually if escapement goals are achieved (Munro and Brenner 2022).

In the Russian far east, the Sea of Okhotsk and the Bering Sea are monitored for Pacific salmon with medium-tonnage trawlers, with the primary goal to support forecasting purposes. These surveys study the abundance of salmon and environmental conditions that are relevant to salmon (including physical oceanography, plankton and nekton samples). Results for maturing salmon are predictive of the return of pink salmon in that year, whereas those for immature salmon predict the return in the following year (Shuntov 2010). This monitoring provides information on the spatial distribution of pink salmon (breadth and length of the migration flow), and on the sex ratio of the leading and trailing components of the migration. Samples are also collected for stock identification. Driftnet assessments in the Russian far east conducted from 1991–2008 began in May, whereas the current integrated trawl-based monitoring is focused mainly on pink salmon and begins in June. Both programs have shown that temperatures affect migration, altering route and timing relative to endogenous phenology as measured by gonado-somatic indices (e.g. Radchenko and Chigirinsky 1995). Scale patterns and body size have also been useful in detecting large fluxes of pink salmon to non-natal habitats (Kaev and Zhivotovsky 2017).

In nearshore and freshwater ecosystems of the Russian far east, programs to assess spawning ground and smolt abundances are also conducted within select coastal reference areas that represent multiple regions. Amongst other goals, this work informs escapement and hatchery production policies (Shuntov 2010).

Pink salmon are the most abundant Pacific salmon species in British Columbia (Radchenko et al. 2018), yet accurate and precise estimates of their abundance are often lacking, as are recent population assessments. This is probably due, in part, to a lack of recent conservation concerns for this species, as well as their relatively low commercial value. Pink salmon are not listed amongst the various stocks of concern in the most recent Integrated Fisheries Management Plans for Northern or Southern BC (Fisheries and Oceans Canada 2022a, b respectively), and most fisheries targeting pink salmon are primarily restricted due to concerns about catching non-target species.

Various indices of BC pink salmon abundance exist, each with strengths and weaknesses. These indices include expanded weights from canneries and other processing methods (e.g., Argue and Shepard 2005), commercial catch data (NPAFC 2022a), spawner abundance data

(available from or by request from Canada's open data portal https://open.canada.ca/data/en/dataset/c48669a3-045b-400d-b730-48aafe8c5ee6), and various combinations of catch plus spawner estimates (e.g. Ruggerone and Irvine 2018, Pacific Salmon Explorer 2022). Cannery data from the early 1900s are useful indices of abundance for Skeena/Nass and Fraser stocks but difficult to compare with other time series. Catch time series are often the best single abundance index but do not account for varying fishing effort and are best suited for large geographic areas. Spawner escapement estimates are often specific to a watershed or conservation unit (Fisheries and Oceans Canada 2005), but the effort and approaches used are highly variable. For instance, in BC, the most common spawner estimation methods are peak live-plus-dead counts and area-under-the-curve estimates, but there are also partial and total fence counts, mark-recapture, test fishery catch-per-unit-effort (CPUE), visual surveys from the ground and air, and expert opinion (Cousens et al. 1982; Jantz et al. 1990; Irvine and Nelson 1995).

In the Fraser River, BC, the return migration of pink salmon in odd-numbered years is monitored for abundance, run timing, and marine migration route. Much of the information for this monitoring is provided by test and commercial purse seine catch and biological sampling (including DNA for stock composition analysis). The Secretariat Staff of the Pacific Salmon Commission are responsible for collecting, compiling, and integrating this information for fisheries managers (Hague et al. 2022). Fisheries and Oceans Canada (DFO) no longer conducts comprehensive sampling and enumeration programs on spawning grounds (Grant et al. 2014), but escapement estimates to the Fraser River and partial monitoring of the migration to upstream spawning grounds are provided by hydroacoustic and test fishing programs (Hague et al. 2022).

Each even-numbered year, DFO monitors the juvenile out-migration of pink salmon from the Fraser River, mainly through the use of traps near the upstream limit of tidal influence in the lower river (Vernon 1966). These estimates provide a key input for the abundance forecast in the subsequent odd-numbered year. The forecast is also informed by Fraser River discharge, as well as sea surface temperature, and sea surface salinity measurements from coastal waters in the Salish Sea and off the west coast of Vancouver Island (Fisheries and Oceans Canada 2021).

The abundance and timing of adult out-migrating Fraser River pink salmon have fluctuated widely, obscuring simple trends. Trends that have been detected are a considerable decrease in body size from the 1960s to 1990s and increases in up-river habitat use within the Fraser River in recent years (Grant et al. 2014). In coastal areas near the Fraser River, concerns for conservation, and interest in harvest, tend to be low for pink salmon relative to co-migrating salmon species. As a result, detailed studies regarding the detection and especially mechanistic understanding of trends in pink salmon are limited in the published literature relative to encounters in monitoring programs. Importantly, research trawls have been conducted annually in marine areas near the Fraser River since the late 1990s, encountering both odd- and even-year pink salmon, yielding data on juvenile abundance indices, size, diet, parasites, and other information (Chrys Neville, DFO, personal communication). Analysis of the data collected in this program could fill information gaps in the monitoring of Fraser River pink salmon.

In Washington, pink salmon spawn in odd years in many Puget Sound streams and rivers. Spawning in even years is inconsistent and is constrained to a single watershed. Pink salmon escapements are monitored annually using ground-based or aerial surveys. Pink salmon are found in coastal Washington rivers, but spawning has been inconsistent in recent years (Hard et al. 1996) and they are not regularly monitored. Low numbers of pink salmon, thought to be strays, are recorded passing the lower-most Columbia River dam each year (Columbia River Data Access in Real Time; https://www.cbr.washington.edu/dart/query/adult_annual_sum). Finally, Washington Department of Fish and Wildlife and tribal co-managers use traps and visual marine estimates to evaluate juvenile abundance annually.

Canadian Arctic

In the Canadian Arctic, adult pink salmon are rare and those observed are considered to be vagrants or strays from sources outside the area (Dunmall et al. 2013, 2018). Juvenile pink salmon have yet to be reported in the North American Arctic (Nielsen et al. 2013), perhaps due to a potential colonization bottleneck linked to narrow thermal tolerances at early life stages (Dunmall et al. 2016). This lack of reported juvenile pink salmon, however, may also be related to a current lack of directed effort to sample for juvenile pink salmon (Dunmall et al. 2013) or low awareness that they may be present, hindering potentially critical opportunistic observations from other programs (Dunmall et al. 2022).

Occurrences of adult vagrant pink salmon in the Canadian Arctic are monitored through a community-based monitoring program called Arctic Salmon, which has documented the occurrences of unusual fish in subsistence harvests since 2000 (Dunmall and Reist 2018). Harvesters voluntarily contribute the fish (whole or head) to the monitoring program in order to address community-driven questions about fish biodiversity change (Dunmall et al. 2013). Reported occurrences of pink salmon are also provided to Arctic Salmon through other community observation networks and related collaborations, established DFO monitoring programs, and media (social and news) reports (McNicholl et al. 2021) including the Arctic Salmon Facebook page (www.facebook.com/arcticsalmon). All fish received are identified to species using taxonomic keys (e.g., Scott and Crossman 1973) and, when necessary, using genetic analyses (e.g., Dunmall et al. 2022), and multiple tissue types are sampled and archived for analyses following a defined protocol. On occasion, the fish are not provided and high-resolution photographs may be used for species identification when the obvious dorsal “hump” and large black spots on the tail are clearly visible (Dunmall et al. 2013; McNicholl et al. 2021). The use of both scientific and local observations to monitor rare species across a vast geographic area presents an exciting opportunity to connect people and knowledges to better understand the impacts of a rapidly changing Arctic.

Atlantic Canada

In Atlantic Canada, monitoring of aquatic habitats for pink salmon takes several forms. In the north-eastern Canadian provinces of Newfoundland and Labrador, and Quebec, environmental DNA (eDNA, see section 5.3) sampling targeting pink salmon has allowed detection of the species in several rivers. However, monitoring to date has been most commonly conducted through voluntary reporting of bycatch in Indigenous and recreational fisheries (ICES 2022b). Awareness campaigns and tracking networks have been put in place for this specific purpose (e.g., for instance MFFP 2021). Social media have been very effective in publicising these campaigns. The monitoring of adult Atlantic salmon using counting fences also contributes information on pink salmon abundance and distribution (ICES 2022b). Considering the low number of fishermen and monitoring projects relative to the number of rivers, and the fact that pink salmon in freshwater environments have mainly been caught in the fall (ICES 2022b), when many fishing and monitoring activities in this region are ending (Quebec Fishery Regulations 1990 (SOR/90-214), Newfoundland and Labrador Fishery Regulations (SOR/78-443)), the current monitoring scheme is far from comprehensive. Given local concerns regarding the effects of invasive pink salmon on native species, plans for more systematic monitoring programs are being developed. For instance, surveys targeting juveniles would be valuable to verify the presence of self-sustaining populations in this region.

North-eastern Atlantic

In the north-eastern Atlantic there are currently no large-scale national monitoring schemes that specifically target pink salmon. Rather, data on the distribution and abundance of pink salmon come from a range of fishing activities or surveys that target other species such as Atlantic salmon, sea trout, or char. Data on pink salmon can therefore vary substantially in quality. Outside of North-East Russia (White Sea/Kola peninsula), Norway has by far the highest abundance of pink salmon with > 200,000 fish caught in 2021 (Berntsen et al. 2022). Before the major range expansion of naturally reproducing Russian pink salmon in 2017, catches of pink salmon were only sporadically reported, and there are no reliable time series statistics for catches of this species (Sandlund et al. 2019). Since 2017, data on the distribution and abundance of pink salmon in Norway has been reported through multiple fishing activities in rivers and along the coast (see Diaz Pauli et al. 2023; Berntsen et al. 2022; Section 1 of this report). Norway therefore has the most experience in collecting data on pink salmon and this section will mainly summarise this activity.

In Norway, adult pink salmon returning to rivers are captured either in targeted removal fishing with nets or traps, or as bycatch during recreational angling for native salmonids (Diaz Pauli et al. 2023; Berntsen et al. 2022). Drift count surveys are conducted in specific rivers to assess the situation before removal fishing or for counting numbers of fish where removal fishing is not possible (County Governor of Troms and Finnmark 2022). Pink salmon are also caught or observed during surveys monitoring or targeting escaped farmed salmon, or they are observed in camera systems in fish ladders designed for monitoring river migrations of adult Atlantic salmon.

In addition, electrofishing for pink salmon fry or smolts is conducted in some rivers where spawning has been observed (Muladal 2018, 2020; Muladal and Fagard 2022; Kanstad-Hanssen and Monsen 2022; Jensen 2022). Targeted removal fishing, drift count surveys, and electrofishing surveys are primarily organized at a county or municipality level and may vary in spatial coverage and intensity between years.

In coastal waters, pink salmon are either caught during recreational fishing (angling, gillnetting or trolling) or in a licensed salmonid coastal fishery, using bag- or bend-nets inside fjords, targeting Atlantic salmon on their return migration to rivers. Recreational fishing is not strictly regulated except for various restrictions on the gillnet fishery, while the licensed coastal fishery is strictly regulated in terms of fishing locations and periods.

Information on the wider marine distribution of pink salmon comes from bycatch in commercial fisheries targeting other pelagic species reported by the Norwegian Reference Fleet (Clegg and Williams 2020) and in scientific trawl surveys such as the International Ecosystem Survey in Nordic Seas (IESNS) (Diaz Pauli et al. 2023).

Catches and observations of pink salmon from the activities described above are all reported through different channels or reporting systems, either online or in reports. Information on the distribution and abundance of pink salmon is therefore spread out over many data sources but the Norwegian Institute for Nature Research (NINA) collects all available data in a database and analyses are published in annual (odd-years) reports (Berntsen et al. 2018, 2020, 2022).

Catches of adult pink salmon reported from other countries such as Sweden, Ireland, Scotland, Faroe Islands, Iceland and Greenland are low compared to those in Norway (< 400 fish per country per year since 2017) and are mainly reported from recreational angling in rivers (Armstrong et al. 2018; Staveley and Bergendahl 2022; Nielsen et al. 2020; Millane et al. 2019b; Eliasen and Johannesen 2021). Although catches of adults are comparatively low, pink salmon juveniles were present in two rivers in Scotland in March 2022 and within the Botnsá river (Iceland) in May 2022. These fish were caught during targeted electrofishing efforts and net surveys to assess the potential establishment of pink salmon in those areas (Skóra et al., in prep).

3. Competition and Interactions Between Pink Salmon and Other Aquatic Species

Although the effects of pink salmon on freshwater ecosystems in their native range are reasonably well-understood, there is a lack of scientific consensus on the impacts of pink salmon in the marine ecosystem. Interestingly, most publications that support the hypothesis that pink salmon have top-down impacts on other marine species via the food web are from North America and are written in English, while most publications that argue that effects of pink salmon on the marine ecosystem are negligible or minor are from Asia in non-English, primarily Russian, sources. The purpose of this section is to provide a high-level summary that reflects both points of view and to recommend future work that can help resolve this controversy. We start by summarizing key facts about pink salmon that are not in dispute, then provide evidence

for and then against the hypothesis that pink salmon effects on other marine species are significant. Lastly, we provide some future direction to better understand and help resolve this debate.

Most scientists agree that:

1. Pink salmon have been the numerically dominant salmon species in the North Pacific Ocean since approximately 1990. In recent years, pink salmon comprised 67% of the total number and 48% of the biomass of all salmon in the North Pacific Ocean (Ruggerone and Irvine 2018).
2. Pink salmon that spawn in odd-numbered years are genetically isolated from those that spawn in even years (Irvine et al. 2014; Radchenko et al. 2018).
3. Data from prior to the mid-1930s indicate even-year spawning pink salmon were more abundant than odd-year in both the Western and Eastern North Pacific Ocean. Since then, odd-year spawning fish have generally been more abundant (Irvine et al. 2014; Radchenko et al. 2018). This is not the case everywhere, however, and there have been interesting switches between even and odd-year dominance in certain areas, primarily the western North Pacific (Nagata et al. 2007; Radchenko et al. 2018).
4. Pink salmon appear to be benefitting from ocean warming, especially in northern regions (Radchenko et al. 2007; Beamish 2012; Irvine et al. 2014). Warming contributes to recent range expansions in Arctic waters of North America (Farley et al. 2020) as well as Asia and Europe where hatchery releases in Russian waters allowed pink salmon to become initially established (Nielsen et al. 2013; Skóra et al. 2022, 2023; Diaz Pauli et al. 2023).
5. Pink salmon diet in the marine phase, of primarily large calanoid copepod zooplankton and euphausiids and increasing amounts of squid and forage fish as they grow (Brodeur 1990; Karpenko et al. 2007; Davis et al. 2009; Graham et al. 2021), overlaps with many other species (Johnson and Schindler 2008).

The following evidence based upon the highly unusual biennial alternation of high (odd years) and low (even years) pink salmon abundance years that serves as a natural "experiment" supports the hypothesis that in years of high pink salmon abundance, zooplankton and other prey populations can be cropped down, impacting many other species in the marine ecosystem:

1. Numerous studies support the hypothesis that pink salmon, when present in high numbers, can exhaust food supplies (e.g., zooplankton biomass), inducing trophic cascades down to the phytoplankton level (Shiomoto et al. 1997; Batten et al. 2018). Specifically, Batten et al. (2018) hypothesized that a trophic cascade, initiated by predation pressures due to abundant maturing eastern Kamchatka pink salmon in the Bering Sea in odd year summers, could explain biennial changes in the abundance levels of large phytoplankton and copepods. In another study, Sugimoto and Tadokoro (1997) found zooplankton biomass anomalies were negatively correlated with Asian pink salmon abundance, as was chlorophyll-a (a proxy for phytoplankton biomass).

2. Studies detail overlapping diet compositions of pink salmon and various non-salmon marine fish species that co-mingle in time and space. Reduced prey availability may directly or indirectly cause reductions in early marine growth and/or enhanced mortality of species competing for zooplankton resources at different stages of their marine life. One example is Atka mackerel—their growth was negatively correlated with the abundance of eastern Kamchatka pink salmon (Matta et al. 2020) except in 2013, a year of unexpectedly low pink salmon returns, highlighted by Batten et al. (2018). Other examples include sand lance in the Salish Sea that were 13 times more abundant in odd than even years (Baker et al. 2020) and Pacific herring (Deriso et al. 2008; Pearson et al. 2012).
3. Numerous studies document biennial fluctuations in various aspects of salmon productivity (Kaeriyama et al. 2000; Ishida et al. 2002; Ruggerone and Irvine 2018; Ruggerone and Nielsen 2004; Cline et al. 2019), including studies that focused on chum (Azumaya and Ishida 2000; Kaga et al. 2013; Litz et al. 2021), sockeye (Bugaev et al. 2001; Ruggerone et al. 2003, 2005, 2007, 2016, 2019; McKinnell & Reichardt 2012; Connors et al. 2020), Chinook salmon (Ruggerone and Goetz 2004; Kendall et al. 2020; Anderson et al. 2021; Claiborne et al. 2021; Buckner et al. 2023) and steelhead (Myers 2018).
4. Results demonstrate effects of zooplankton consumption by pink salmon in years of high abundance on a wide variety of other species ranging from resident and migratory seabirds (Springer and van Vliet 2014; Springer et al. 2018; Toge et al. 2011) to southern resident killer whales (Ruggerone et al. 2019).

Yet the link between the various biennial patterns and pink salmon remains a hypothesis. If pink salmon are not the cause, what might it be?

Opposing views on pink salmon competition with other species have been expressed as criticism of cited research as well as in studies on carrying capacity of the North Pacific marine ecosystems in relation to salmon ranching. These include the following points.

1. North Pacific Ocean zooplankton standing crops are very large and their productivity values are high. Estimates of Pacific salmon consumption represent only a small fraction of potential prey standing stocks and are negligible compared to intake by other fish species. For example, in far-eastern seas, zooplankton biomass in the upper pelagic layer is estimated at 0.8 billion mt with annual production of 28–32 billion mt, while annual zooplankton consumption by fish and squids was estimated to be 274.5 million mt in 1996–2005 (Shuntov et al. 2017).
2. Pacific salmon constitute a small fraction of pelagic nekton biomass, estimated to be a few hundred million mt for the whole Subarctic Pacific Ocean (Shuntov et al. 2017). Estimates of recent average annual adult pink salmon biomass range from 0.6–0.8 million mt (0.6 value from Ruggerone and Irvine 2018 for 1990–2005 and 0.8 value from Radchenko et al. 2018 for 1989–2008). The proportion of food consumed by

Pacific salmon accounts for only a few percent of the total food consumption by nekton and is considered unlikely to significantly impact the trophic web structure.

3. Pacific salmon are very flexible in diet ration composition and their prey include numerous fish and squid species. Copepods chosen as a trigger for trophic cascade effects contribute about 10% to the average pink salmon food ration with euphausiids and hyperiids as preferable items. If pelagic food webs were susceptible to impacts of such magnitude, we could expect much more prominent effects from other ecosystem events like annual variability of biomasses of walleye pollock, Japanese sardine, Pacific saury, mesopelagic fish, etc.
4. Significant overlaps of different salmon species' diet composition may lend credence to the sufficient food resources rather than competition between them. For instance, during the 2022 IYS Expedition, winter foraging areas of Pacific salmon species differed substantially, especially between sockeye and pink salmon, and yet those species demonstrated the largest overlap in prey composition (Radchenko 2022b). In addition, major stocks of pink salmon and sockeye salmon demonstrate the most positive abundance dynamics of all species and have both posted record catches in the current century (NPAFC 2022a).
5. Feeding habits of Pacific salmon species differ even in regions of co-dwelling. Morphological traits of Pacific salmon suggest that mostly planktivorous species (pink, chum, and sockeye salmon) can find their own preferable feeding spots in a mutual food supply (Radchenko et al. 2018). Specifically, chum salmon have a bulkier stomach than pink and sockeye salmon and their esophagus ends with a powerful sphincter, allowing them to consume larger amounts of low-caloric food that can be mechanically accumulated by eddies. Sockeye salmon, with more myoglobin in their muscles and larger eyes, dive for food below the thermocline. Pink salmon, with the largest proportion of caudal fin area to body size, can cover large distances during feeding migrations.
6. Even the most abundant Pacific salmon species, pink and chum, do not follow the principle of competitive exclusion (Gause's Law) during their marine phase. Multi-year (1998–2012) autumn observations of juvenile pink and chum salmon distribution and abundance in the Sea of Okhotsk show that these species behave as a complimentary, rather than competitive, species complex (Radchenko et al. 2013).

In fresh water, pink salmon fry and adults feed less than most other Pacific salmon (Heard 1991) and as a consequence, interactions with other species are limited. At the same time, migrating pink salmon fry can serve as an important food source for many types of fish, birds, and invertebrates in rivers and associated estuaries (Hard et al. 1996; Beamish et al. 2003; Karpenko 2003). As for the adults, nutrients provided by decomposing and frequently abundant pink salmon carcasses often have positive bottom-up effects on the productivity of aquatic and riparian food webs (e.g., Gende and Quinn 2006; Walter et al. 2006). Such cross-ecosystem nutrient subsidies positively affect terrestrial plant growth and reproduction (Dennert et al.

2023). Compared to other, larger Pacific salmon species, spawning pink salmon concentrate primarily in small streams and lower river reaches, diversifying beneficial effects on terrestrial ecosystems. Where suitable conditions are limited, e.g., towards the northern extent of their distribution, pink salmon may compete with other species for limited fresh water spawning habitat (Dunmall et al. 2016).

There have been concerns about the aggressive behaviour of pink salmon to other salmon in fresh water. While pink salmon have been seen attacking other fish on the spawning grounds, the redd-guarding behaviour of females and mate-guarding behaviour of males is typical for all salmon species (Quinn 2018) including coho salmon (Fleming and Gross 1994, Kitano and Shimazaki 1995), Chinook salmon (Anderson et al. 2015), and kokanee (Morbey 2003). It is unlikely that salmon attack each other in the marine phase as extensive analyses of salmon body injuries from at-sea catches do not reveal any wounds inflicted by other salmon (Zolotukhin and Kaplanova 2005).

The topic of competition and interactions between pink salmon and other species in marine ecosystems needs further research. Is it possible that both points of view described above are correct, but for different regions of the northern North Pacific Ocean? For example, higher production of zooplankton in western regions than in central and eastern regions may reduce competition for prey (Batten et al. 2018; Naydenko and Somov 2019). Perhaps pink salmon effects on the marine ecosystem vary between the east and west sides of the Kamchatka Peninsula? Or, more generally, between the western and eastern North Pacific? Alternate hypotheses leading to better understanding of the potential drivers of biennial variability in marine and freshwater ecosystems are important to better understand potential impacts of pink salmon abundance and variability. This is especially true as pink salmon colonize new areas in the Arctic and Atlantic. Continuing collaborative investigations such as documented in this publication will be important going forward.

4. Genetic Stock Delineation

International collaboration efforts are key to advancing our understanding of pink salmon genetic structure and stock delineation across the species' native and expanding range throughout the Northern Hemisphere. To date, pink salmon genetic structure has mostly been studied on a limited, fine-scale level where pink salmon populations of a single region, country, or lineage were examined. However, these fragmented studies across the native Pacific range have consistently observed: (1) greater genetic diversity within the odd-year lineage than the even-year lineage, and (2) greater genetic differentiation between lineages than between geographic areas (Aspinwall 1974; Olsen and Seeb 1998; Beacham et al. 2012; Limborg et al. 2014; Seeb et al. 2014; Tarpey et al. 2018). Broadly, coastwide genetic structure studies improve our understanding of the species' past, present, and future distributions.

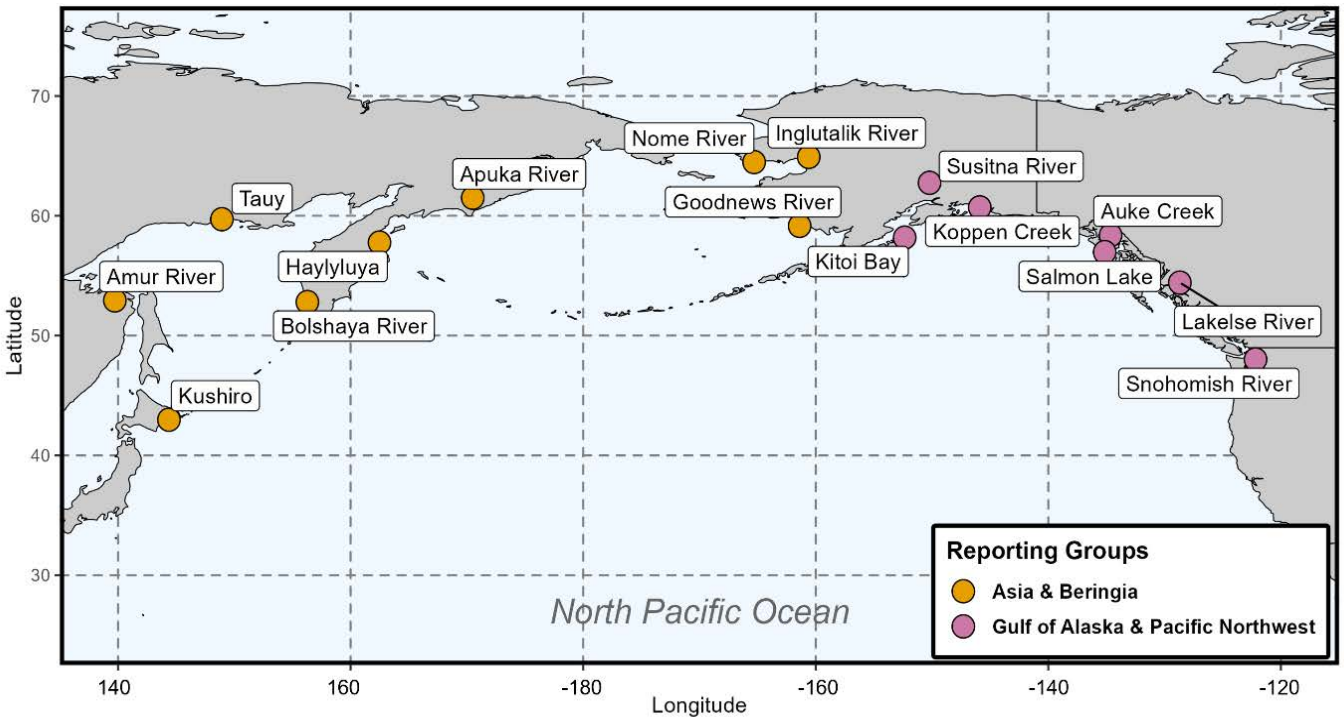


Figure 10. Spawning locations included in the North Pacific coastwide genetic baseline for pink salmon.

As an initial step towards developing a coastwide genetic baseline for the native Pacific range of pink salmon, the ADF&G Gene Conservation Lab built upon a North Pacific pink salmon study by Tarpey et al. (2018) and repurposed a pink salmon genetic marker panel developed for genetic parentage analysis in Prince William Sound, Alaska (Shedd et al. 2016). Alaskan pink salmon genotypic data were combined with genotypic data in Tarpey et al (2018) to establish a baseline of 262 genetic markers genotyped for 15 locations across the Pacific native range with paired odd- and even-year populations. Following guidelines defined by Barclay et al. (2019), the 15 locations were grouped into two reporting groups for each lineage: (1) Asia/Beringia even-year, (2) Asia/Beringia odd-year, (3) Gulf of Alaska/Pacific Northwest even-year, and (4) Gulf of Alaska/Pacific Northwest odd-year (Figure 10). This baseline represents an initial effort to understand genetic stock delineation of pink salmon, however inclusion of additional populations from throughout the species range will expand the potential applications of the baseline for pink salmon studies.

Stocking efforts in the White Sea eventually led to self-sustaining populations of pink salmon in the Atlantic. Genetic studies of White Sea pink salmon provide evidence of a bottleneck effect and genetic divergence of the odd-year population from the original source population, the Magadan region in Russia (Gordeeva and Salmenkova 2011; Gordeeva et al. 2015; Gilbey et al. 2021). However, early generations from the even-year population were still genetically similar to the Russian source population (Gordeeva and Salmenkova 2011; Gordeeva et al. 2015). Pink salmon have been documented in many Northern European rivers west of the

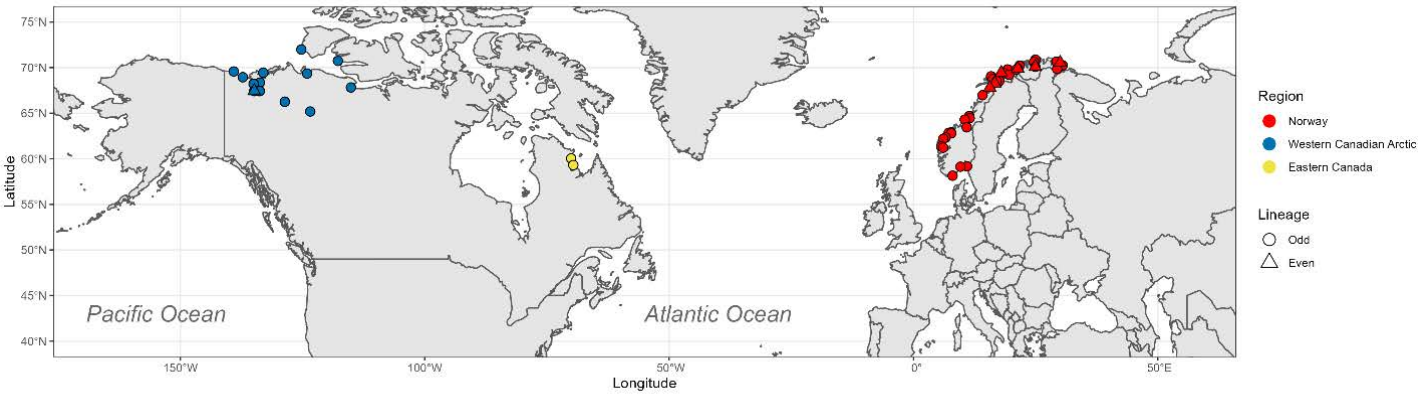


Figure 11. Location of pink salmon samples from Norway, Western Canadian Arctic, and Eastern Canada included in genetic analysis.

White Sea. A collection of pink salmon sampled across 34 Norwegian rivers from 2016 through 2020 (N = 384, Figure 11) were examined for genetic variation with the ADF&G pink salmon genetic marker panel and baseline. Similar to findings by Gordeeva et al. (2015) and Gilbey et al. (2021), the Norwegian odd-year samples genetically diverged from baseline populations representing the original Russian odd-year source population, the Asia/Beringia odd-year reporting group (Figure 12). Whereas, the Norwegian even-year samples were genetically similar to samples representing the Asia/Beringia even-year reporting group (Figure 12). Most of the invading pink salmon from the established populations in the White Sea are found in Northern Norway, with gradually fewer found further south in Europe. It remains to be seen if the invasion leads to the establishment of new self-recruiting populations and a further expansion. To pursue this question, genotypic data from the collection of Norwegian pink salmon samples were analysed in relation to where the fish were caught. These initial studies showed from simulations that full-sibling, half-sibling, and unrelated individuals were 100%, 97.7%, and 99.6% correctly assigned, respectively. A structured pink salmon genetic sampling program will be implemented by the Norwegian Institute for Nature Research (NINA) to study the distribution of full-siblings across Norway and provide information on dispersion, homing, and effective number of breeders. These are examples of genetic methods that could be used by Atlantic countries to monitor the pink salmon invasion and elucidate expansion mechanisms and patterns.

In recent years there have been increased reports of pink salmon observations across Canada, along both the Western Canadian Arctic coast and the Eastern Canadian coast (Dunmall et al. 2021; ICES 2022a). Similar to the analysis of the Norwegian samples, pink salmon samples collected by communities in the Western Canadian Arctic (N = 22) and Eastern Canada (N = 2) (Figure 11) were genotyped with the ADF&G pink salmon genetic marker panel and compared to: (1) the Pacific coastwide baseline samples representing the native range of pink salmon, and (2) the Norwegian pink salmon samples representing secondary colonizations from stocking operations in the White Sea. Both odd- and even-year Western Canadian Arctic samples were

genetically similar to baseline populations within the Pacific native range (Figure 12). Odd-year samples from Eastern Canada were genetically similar to the Norwegian samples representing the self-sustaining population of pink salmon in Northern Europe. There were no even-year samples analysed from Eastern Canada. These genetic findings suggest that the expansion of pink salmon in the Western Canadian Arctic originates from the Pacific native distribution of pink salmon, whereas the pink salmon in Eastern Canada are a part of the invasion from Northern Europe. This example illustrates how genetic methods can improve our understanding of the origin of expanding pink salmon populations and benefit research, monitoring, and management of the species.

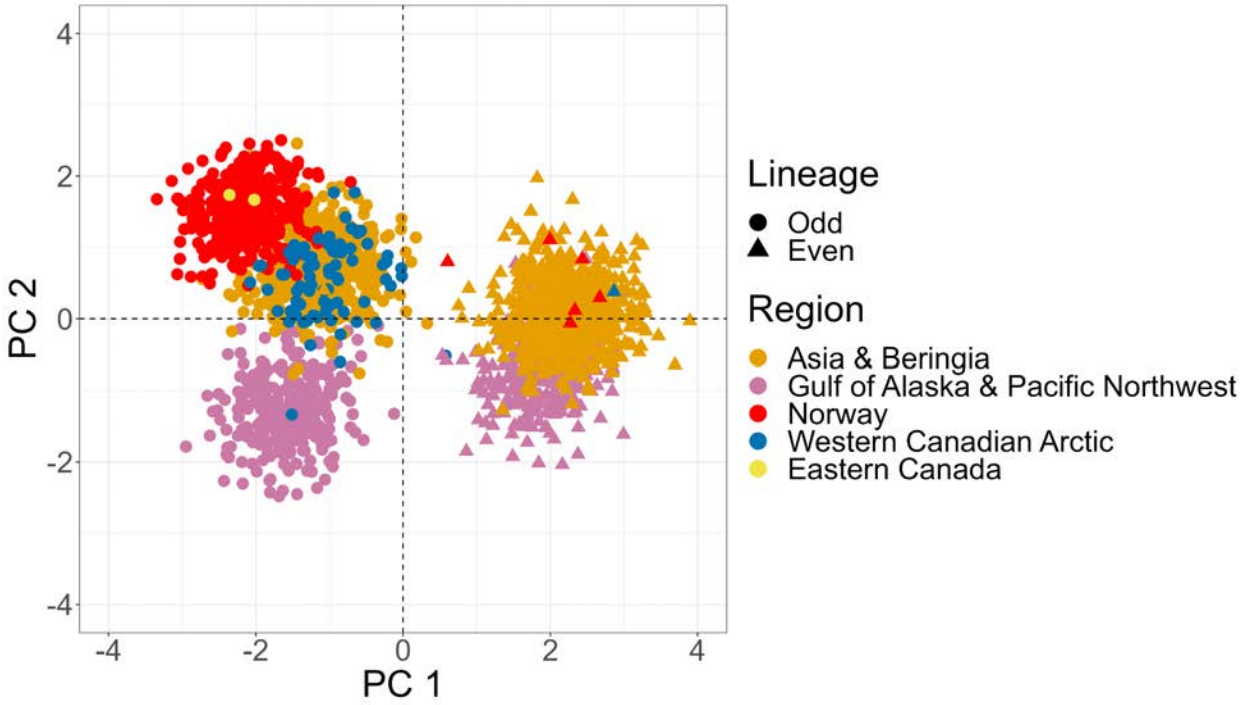


Figure 12. Principal component analysis (PCA) results of genotyped pink salmon samples from the North Pacific coastwide genetic baseline (Asia and Beringia reporting group and Gulf of Alaska and Pacific Northwest reporting group), Norway, Western Canadian Arctic, and Eastern Canada.

5. Approaches to Assessing Current and Predicting Future Distribution Changes

Pink salmon are encountered in a variety of surveys conducted on continental shelves around the Pacific Rim. However, regular sampling of areas of the North Pacific high seas large enough to support monitoring of salmon distribution changes is not logistically possible. Instead, inferences regarding current and future ocean distribution patterns of pink salmon must be made through analysis of historic data. The NPAFC, formerly the International North Pacific Fisheries

Commission, has supported research on salmon in the high seas since the 1950s. To date, these efforts, focused primarily on the spring and summer months, have resulted in the collection of more than 30,000 salmon catch records from across the basin.

Research is being conducted by Langan et al. (in prep.) to develop distribution models from these historic catch data. In order to investigate potential distribution differences between the brood lines of pink salmon, the data from even- and odd-years were modelled separately. Although this approach will not fully separate the brood lines of pink salmon in the catch records, limited available biological information suggests that even- and odd-year data will primarily represent the even- and odd-year brood-lines, respectively. Preliminary results suggest that the pink salmon brood-lines occupy similar habitats in the high seas and have similar temperature preferences. Positive catches of even-year pink salmon were observed between 1.0–19.4°C, while odd-year pink salmon were caught between 1.0–17.8°C. Preliminary estimates of the spring-summer mean preferred temperature range of even- and odd-year pink salmon derived from distribution model fits, meanwhile, suggest that most individuals of each brood-line will be observed between approximately 3–12°C , in general agreement with past research (Takagi et al. 1981; Abdul-Aziz et al. 2011).

Such estimates of pink salmon thermal preferences help to understand current and future potential shifts in ocean distribution patterns. Langan et al. (in prep.) compared past thermal conditions to recent warm periods in the North Pacific to suggest that optimal thermal habitats may move northward and toward the center of the basin under continued climate change. Similarly, these preferred temperature ranges are being used to investigate the growing presence of pink salmon in the western Canadian Arctic (Dunmall et al. 2018). Given that continued and rapid Arctic warming may increase the suitability of the region for pink salmon, anticipation of such changes will rely upon inferences gained studying historic data from the North Pacific.

6. Selective Methods and Removals, Opportunities for New Fisheries

Norway

Pink salmon is on the Norwegian Biodiversity Information Centre's Black List of alien species, in the "high risk" category. The strategy of the Norwegian Government is to eradicate pink salmon by targeted removal in rivers, and the Norwegian Environment Agency is responsible for the action plan. The rapid increase in numbers of pink salmon entering Norwegian rivers from 2017 somewhat surprised the managers and there was no national strategy on how to handle the river invasion even in 2021. In at least 46 rivers, local organisations voluntarily organized removal of pink salmon from the rivers in 2021. In at least 19 rivers, these organisations installed improvised traps to hinder pink salmon from entering the river (mainly relatively small rivers). The upstream migrating salmonids were trapped and most of the pink salmon were removed while letting native anadromous fish enter the river. Successful installation and maintenance of such traps depends on local knowledge and financial support, and are practically limited to rivers with shallower depths and installations during periods of low

flows. The experiences with *ad-hoc* traps in Norway in 2021 were mixed, some functioned well while others did not work as planned, but these will be valuable for further efforts in future years. In some of the largest rivers, including the Tana/Teno River, a proper eradication program with traps or gillnets was not possible in 2021.

Removal of pink salmon in rivers without functional traps was limited to gillnets, seine nets or spearfishing. Gillnets were avoided in river areas and periods when native anadromous fish were observed to mix with pink salmon. In general, the managers in northern Norwegian counties accepted the use of gillnets and trusted local organisations to operate these in a way that had minimal effect on native anadromous fish. However, in rivers where gillnets, seine nets and spearfishing were used as the main effort for removing pink salmon, it was estimated that hundreds or thousands of pink salmon remained to spawn in each river. In rivers with salmon ladders, these could be closed off and native anadromous fish could be sorted out and released above the ladder. A land seine was applied in some rivers although this gear could only be operated in slow-running rivers. In total, more than 100,000 pink salmon were removed from rivers (Diaz Pauli et al. 2023). However, the heavy involvement of volunteers in 2021 is not sustainable.

National mitigation measures are in place for 2023 with ~2.5 million Euro allocated to install traps in the rivers most impacted by pink salmon. The work to improve existing traps and install new traps was organized during the winter of 2022, before the expected invasion of pink salmon in 2023. The work benefitted from experiences in 2021. The main focus areas for the 2023 program were to: (1) maintain animal welfare for the native anadromous fish while removing pink salmon; (2) ensure the correct quality and dimension of the part of the trap closing the rivers, the appropriate dimensions of the catch chamber where fish are trapped, and the correct angle and placement of the parts used to guide fish to catch chambers; and (3) ensuing sufficient personnel to monitor and clean the traps. Resistance board weir traps were installed in some of the largest Norwegian rivers, as the ability of resistance board weirs to avoid collapse under high flow/debris levels allows them to resist ‘blow-out,’ which is normally when rigid weir structures get lost.

There is a growing interest among fishers to target pink salmon at sea. This potentially new fishery does not affect the present strategy of removing pink salmon in the rivers. To date, however, no targeted fishery using commercial gear for pink salmon at sea has been allowed due to the risk of bycatch (VRL 2022, 2023) and increased mortality of native anadromous fish. There will most likely be a minor research test-fishery in northern Norway targeting pink salmon at sea in 2023 to gain experience of catch efficiency and bycatch of both marine and anadromous species.

Other Countries

While Norway might be the first country to implement an official strategy to eradicate pink salmon, this approach is considered in other countries where this fish is non-native and

represents a threat to native species. To begin with, some governments removed any catch limit for pink salmon (for instance Quebec: MFFP 2021) and asked that all caught pink salmon must be killed immediately (for instance Sweden: Staveley and Bergendahl 2022). In Ireland, the state agency responsible for inland fisheries advises anglers to remove and report any pink salmon encountered and retain these for verification and scientific purposes (Millane et al. 2019b). There are also local initiatives developed by river organizations, and supported by relevant government agencies, to monitor and potentially remove pink salmon in some rivers in Scotland. However, apart from Norway, the approaches taken and the planned effort in 2023 are not well described at this time. Approaches based on the disruption of pink salmon nests have been judged too resource intensive and to be associated with too high human health and safety risks to be a viable option for widespread application (Armstrong et al. 2018). The attempts conducted in Norway will therefore benefit and guide others.

One key question for countries bordering the Atlantic Ocean is the likelihood of successful eradication of pink salmon. Indeed, there are cases of success and failure involving other species worldwide (Myers et al. 2000; Simberloff 2021). If the general tendencies of increased abundance and distribution observed between 2017 and 2021 remain unchanged, it is difficult to imagine how countries with thousands of remote rivers with potential spawning grounds can totally eradicate pink salmon when facing sustained propagule pressure from other source countries. Nevertheless, it might be possible to keep prioritized watersheds free of this exotic species, or at least prevent or limit the establishment of self-sustaining populations in 'new' rivers. The amount of investment in eradication by the different countries dealing with invasive pink salmon will likely be proportional to the perceived or demonstrated negative impacts, which remain to be investigated in more detail. The lack of knowledge of the scale of any impact is highlighted in the risk assessments for this species in the UK, Ireland, and Norway (Bean 2022). As such, ongoing surveillance through direct monitoring, as well as using indirect techniques such as eDNA, are key to quantifying the level of incursion and establishment in order to better inform appropriate management responses and appraise likelihood and effectiveness. Considering, for instance, that the economic benefit of some renowned Atlantic salmon rivers is estimated at more than one million Euros or American dollars annually (Atlantic Salmon Federation 2011; Myrvold et al. 2019), even without considering the additional intrinsic value of biodiversity, investing a fraction of this amount for their protection from non-native pink salmon can likely be justified.

7. New Tools: Using eDNA for Monitoring the Pink Salmon Invasion

eDNA: A Cost-effective Monitoring Tool

Monitoring the occurrence and distribution of pink salmon is crucial for understanding the dynamics of the invasion process. Analysis of eDNA is a new and cost-efficient method for detecting rare species, as it makes it possible to monitor more localities than using conventional methods. eDNA is the suspended DNA-remains in water, soil and air shed by most living organisms, consisting of saliva, scales, hair, slime and mucous, and that can be collected and

used with genetic analyses for identifying the species living in the sampled ecosystem (Taberlet et al. 2018). Comparisons with conventional methods also show that analyses of eDNA often are more sensitive in detecting rare species, and are very effective for detecting invasive species (Valentini et al. 2016; Fossøy et al. 2019; Sepulveda et al. 2020; Taugbøl et al. 2021). Collection of eDNA from water is usually done by filtering water through a fine-meshed filter, and the procedure is relatively simple and well suited for citizen-science projects (Biggs et al. 2015; Agersnap et al. 2022). The filters can be stored in ethanol or conservation buffers for some months, before being analysed.

For identification of single species, eDNA-samples are usually analysed using species-specific markers to screen many samples for the presence of a target species, e.g., pink salmon (Gargan et al. 2021; Fossøy et al. 2022). However, eDNA-samples can also be analysed using DNA-metabarcoding, where a more general DNA-assay is used to detect multiple species (Miya et al. 2015; Valentini et al. 2016). The former method is relatively simple and can be done in most genetic laboratories within a few days, whereas the latter method requires modern sequencing technology and advanced bioinformatic analyses (Taberlet et al. 2018).

While eDNA-analyses can detect and monitor occurrence, it cannot provide information on the absolute number of individuals, or biological characteristics such as the sex-ratio, age- or size class structures for the target species. However, relative differences in eDNA concentration can imply changes in relative abundance over time, and a recent review concludes that eDNA can be used for assessing fish population abundance and/or biomass (Rourke et al. 2021). For the monitoring of pink salmon, eDNA offers a cost-effective method for detecting possible increases in numbers of pink salmon and potential decreases in local fish species over time. This method makes it possible to monitor many rivers at a relatively low cost, although studies must carefully consider the temporal and spatial aspects of survey design if this approach is to be deployed effectively. The next two subsections describe two examples of applications in greater detail, before we conclude with considerations about future prospects.

Monitoring the Pink Salmon Invasion in the Tana/Teno River Using Species-specific eDNA Analyses

The large river Tana/Teno forms the border between northernmost Finland and Norway and supports the largest Atlantic salmon population among all Norwegian salmon rivers, so large in fact that salmon from several tributaries are considered separate stocks for management purposes (VRL 2022). Recently, the Atlantic salmon stocks have strongly declined (Anon. 2021) and salmon fishing has ceased. At the same time, numbers of non-native pink salmon have increased substantially. The estimated numbers of pink salmon entering the river system in 2000–2010 were only a few tens or hundreds (Sandlund et al. 2019). However, in 2017 and 2019 close to 5,000 pink salmon were estimated entering the river in each of those years. In 2021, the estimated pink salmon abundance had increased ten-fold and exceeded 50,000 individuals (Anon. 2021).

Until 2021, the monitoring programmes recorded the presence of pink salmon in the mainstem of the river, large headwater branches and some other large or mid-size tributaries of

the Tana/Teno system. To further increase the understanding of pink salmon distribution, eDNA samples were collected from 19 tributaries in 2019 and from 24 tributaries in 2021 (Fossøy et al. 2022). The eDNA water samples were analysed using a species-specific genetic primer for pink salmon (Gargan et al. 2021), and another primer for Atlantic salmon (Fossøy et al. 2019). The eDNA analyses detected Atlantic salmon in almost all tributaries in both years, with a pronounced higher DNA-concentration in the middle of the watercourse. Pink salmon were detected in five localities in 2019 and in 15 localities in 2021, reflecting the large observed increase in the number of pink salmon entering the river between the two odd-years. These detections were distributed across all parts of the Tana watercourse and showed the large-scale geographical span of pink salmon in this river. The upper part of Inarijoki represents the most upstream detection of pink salmon recorded in Tana/Teno River so far.

The DNA-quantities of Atlantic salmon appeared to be much higher than those of pink salmon (Fossøy et al. 2019), despite the fact that the numbers of pink salmon entering the river was approximately twice that of Atlantic salmon (Anon. 2021). There are likely to be species-specific differences in shedding and excretion of DNA that could affect these estimates. However, there was only one age class of pink salmon in the river at the time of sampling, compared to up to six different age classes of juvenile Atlantic salmon plus the adults returning from the sea. The continued presence of the juvenile Atlantic salmon makes it hard to assess the relative abundance of pink vs. Atlantic salmon using eDNA.

The first even-year study of eDNA in the Tana/Teno River was conducted in 2022. This should increase knowledge of the pink salmon juveniles from the 2021 spawning run, alongside adults from the spawning run of 2022. The results of this study have not been reported at the time of writing, but the goal for the project is to secure funding for sampling the same 24 tributaries every year in order to monitor eDNA-concentrations for both the native Atlantic salmon and the invasive pink salmon populations in the years to come.

Monitoring Pink Salmon Distribution and Fish Diversity in North-eastern Canada Using eDNA-metabarcoding

eDNA-metabarcoding analyses have been used in north-eastern Canada to study the early invasion of pink salmon (e.g., Côté et al., in prep.). Few people inhabit this region, and most rivers are difficult to access since they are not accessible by any roads, making it logistically challenging to assess the distribution of pink salmon and any other species. Monitoring pink salmon nevertheless remains extremely important since Inuit people rely heavily on aquatic resources. The main objective of this project was to improve knowledge on the occurrence of pink salmon in the northernmost part of the Atlantic salmon distribution and to compare the distribution based on the few pink salmon records (4) from Inuit fishermen that were suggested by eDNA detection (Coté et al., in prep.). A secondary objective was to compare the fish community assessed with traditional methods with the one assessed using eDNA-metabarcoding.

A helicopter was used in 2021 to obtain 43 samples from 39 rivers distributed across nearly 1,500 km of coastline in Quebec, from Hudson Bay to Ungava Bay. Those samples were mainly

collected near the river mouth, assuming that pink salmon abundance would be greatest in the lower reaches and considering that eDNA should be detectable a few km downstream from its source (Laporte et al. 2020; Jo and Yamanaka 2022). Five replicate samples were amplified using the primers from Miya et al. (2015). Bidirectional sequencing was conducted using the Illumina MiSeq sequencer (reactive V3, Illumina, San Diego, USA). Negative controls were included at each step of the procedure (filtration in the field, extraction and amplification in the lab).

Pink salmon were detected only at a single sampling site. This site is located in Ungava Bay within a 70 km radius of where three out of the four pink salmon have been caught in Northern Quebec. The fourth pink salmon was caught outside of the study area of this eDNA project, on the east side of the Ungava Bay. While results from eDNA must be interpreted with caution, this study suggests that pink salmon were not widely distributed nor abundant in Northern Quebec outside the Ungava Bay in 2021. It further confirms that Ungava Bay is a hot spot for pink salmon invasion in the northernmost distribution range of Atlantic salmon in North America.

Future Prospects for the Use of eDNA in Pink Salmon Management and Research

Methodological advances and improved knowledge of eDNA ecology should rapidly offer new opportunities to study pink salmon. For instance, increased understanding of the biotic and abiotic factors affecting the production and degradation of eDNA (Caza-Allard et al. 2022), as well as of the multidimensional dispersion of eDNA in fluvial environments (Laporte et al. 2020; Berger et al. 2020), will allow a stronger interpretation of eDNA results. However, the sensitivity of the tool is not without drawbacks, for instance regarding the risks of contamination and of eDNA movement issues. Combined with the analyses of eRNA, it appears possible to evaluate the age of eDNA material and therefore the time since its release into the water (Marshall et al. 2021). New methodological development, such as CRISPR-Cas (Williams et al. 2021), opens the door to real-time on-site detection. It is also possible to use eDNA for population structure studies (Adams et al. 2019). Thus, it is likely that eDNA will play an increasingly important role in fishery management in general, and specifically in the study of non-native species like pink salmon.

While eDNA samples in this context mainly are collected for analysing the presence of pink salmon and local fish species, these samples can also provide information on other taxa using different genetic assays. DNA-extracts from eDNA water samples represent most of the living organisms in the river, and hence they can also be used for assessing diversity of e.g. macroinvertebrates (Elbrecht et al. 2017), molluscs (Klymus et al. 2021) and amphibians (Valentini et al. 2016). DNA-extracts can be stored in ultra-freezers and reanalysed many years after collection, representing time-capsules of biodiversity for the sampled localities. This means that in addition to monitoring the invasion of pink salmon, the eDNA samples can also be used to assess the consequences of the invasion, where potential changes in diversity of local species across many taxa can be investigated in relation to changes in pink salmon abundance.

An effort of joining forces across nations for eDNA-monitoring of pink salmon was attempted already in 2019 and samples were collected across many countries

(www.1000rivers.net). There was, however, a more northerly distribution of pink salmon that year, and there were basically mostly negative results with the exception of northern Norway. In 2022, a new attempt was initiated with support from the North Atlantic Salmon Conservation Organization (NASCO) and potential start funding from the EU. Discussions are ongoing regarding choices and standardization of sampling equipment and analysis. Time will show if this initiative can provide a standardized monitoring of the pink salmon invasion across borders.

8. Information Exchange and Future Collaborations

Knowledge on pink salmon biology is not equally distributed throughout its natural and new range. Salmon scientists working in the North Pacific have a wealth of knowledge of pink salmon biology as the native species is the focus of extensive research and monitoring efforts. In north-western Russia, where the species was introduced in the 1950s, there is also a history of scientific research of pink salmon biology but it is not easily accessible for researchers without knowledge of the Russian language. In the Atlantic area, the northern parts of Norway and Finland had limited presence of pink salmon for many years prior to the large increase in abundance and distribution range from 2017 onwards, some scientific work has been conducted on this species over this extended time period. In the rest of the Atlantic area, however, research into pink salmon only started in earnest after 2017. Indeed, it was quickly recognised by many salmonid scientists from the Atlantic area that their knowledge on pink salmon biology was lacking when confronted with questions about pink salmon from policy makers and fisheries managers after the rapid expansion in 2017 (e.g., Bean 2022). This highlighted the importance of sharing knowledge of the potential impacts on ecosystems and implications for fisheries management.

At the October 2022 Northern Hemisphere Pink Salmon Expert Meeting in Vancouver, Canada, this important exchange of information on pink salmon led to discussions on future collaborations by scientists working across the Pacific, Atlantic, and Arctic Ocean basins. However, this knowledge sharing should not be limited to pink salmon, as pink salmon range expansion is far from being the only current issue in global salmon conservation and management. Therefore, the creation of a Northern Hemisphere Salmon Expert Group (NHSEG) is recommended to oversee and facilitate knowledge exchange throughout the three oceanic basins. This NHSEG should then form specialist sub-groups to address specific issues, such as the Northern Hemisphere Pink Salmon Expert Group (NHPSEG).

The NPAFC and ICES have expressed an interest in setting up the NHSEG. ICES Expert Groups like WGNAS, WGDIAD, and the Baltic Salmon and Trout Assessment Working Group (WGBAST) could link into this, and we would recommend other interested organisations be approached to join this group, for example The North Pacific Marine Science Organization (PICES).

At the same time, NASCO is creating a pink salmon working group. The Terms of Reference for this group are under development but we understand that the focus will be on management, and therefore this would be complementary to, rather than duplicating the science-

focussed Northern Hemisphere Pink Salmon Expert Group, though the two groups would undoubtedly share, cooperate, and collaborate whenever appropriate.

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Appendix

Appendix A: List of Meeting Participants

Name	**Affiliation**
Alan Walker	Centre for Environment, Fisheries and Aquaculture Science (Cefas)
Alan Wells	Fisheries Management Scotland (FMS)
Andrew Munro	Alaska Department of Fish and Game (ADFG)
Annie Cooper	International Council for the Exploration of the Seas (ICES)
Chris Habicht (virtual)	Alaska Department of Fish and Game (ADFG)
Dennis Ensing	Agri- Food Biosciences Institute (AFBI)
David Meerburg	Atlantic Salmon Federation
Dion Oxman (virtual)	Alaska Department of Fish and Game (ADFG)
Ed Farley	National Oceanic and Atmospheric Administration (NOAA)
Elizabeth Lee	Alaska Department of Fish and Game (ADFG)
Emma Hatfield	North Atlantic Salmon Conservation Organization (NASCO)
Henrik Berntsen (virtual)	Norwegian Institute for Nature Research (NINA)
Jaakko Erkinaro	Natural Resources Institute Finland
Jim Irvine	Fisheries and Oceans Canada (DFO)
Julien April	Ministère de l'Environnement, de la Lutte contre les Changements Climatiques, de la Faune et des Parcs du Québec (MELCCFP)
Karen Dunmall	Fisheries and Oceans Canada (DFO)
Katie Howard (virtual)	Alaska Department of Fish and Game (ADFG)
Kjell Utne (virtual)	Institute of Marine Research, Bergen, Norway
Michael Millane (virtual)	Inland Fisheries Ireland
Polina Orlov	North Pacific Anadromous Fish Commission (NPAFC)
Sten Karlsson	Norwegian Institute for Nature Research (NINA)
Steve Latham	Pacific Salmon Commission (PSC)
Tor Kitching	North Pacific Anadromous Fish Commission
Vladimir Radchenko	North Pacific Anadromous Fish Commission (NPAFC)
Wendy Kenyon	North Atlantic Salmon Conservation Organization (NASCO)
William Templin	Alaska Department of Fish and Game (ADFG)

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Original Article

Divergent foraging strategies between populations of sympatric matrilineal killer whales

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In cooperative species, human-induced rapid environmental change may threaten cost–benefit tradeoffs of group behavioral strategies that evolved in past environments. Capacity for behavioral flexibility can increase population viability in novel environments. Whether the partitioning of individual responsibilities within social groups is fixed or flexible across populations is poorly understood, despite its relevance for predicting responses to global change at the population and species levels and designing successful conservation programs. We leveraged bio-logging data from two populations of fish-eating killer whales (*Orcinus orca*) to quantify patterns of fine-scale foraging movements and their relationships with demography. We reveal striking interpopulation differences in patterns of individual foraging behavior. Females from the endangered Southern Resident (SRKW) population captured less prey and spent less time pursuing prey than SRKW males or Northern Resident (NRKW) females, whereas NRKW females captured more prey than NRKW males. The presence of a calf (≤3 years) reduced the number of prey captured by adult females from both populations, but disproportionately so for SRKW. SRKW adult males with a living mother captured more prey than those whose mother had died, whereas the opposite was true for NRKW adult males. Across populations, males foraged in deeper areas than females, and SRKW captured prey deeper than NRKW. These population-level differences in patterns of individual foraging behavior challenge the existing paradigm that females are the disproportionate foragers in gregarious resident killer whales, and demonstrate considerable variation in the foraging strategies across populations of an apex marine predator experiencing different environmental stressors.

Key words: **bio-logging DTAG, foraging behavior, Northern Resident killer whale, prey capture, Southern Resident killer whale.**

INTRODUCTION

Understanding the factors shaping group foraging is central to behavioral ecology. A group's foraging strategies are optimized to balance the benefits of increased resource acquisition and reduced predation risk with the costs of intragroup competition and interference (Clark and Mangel 1984; Cvikel et al. 2015; Senior et al. 2016; Lihoreau et al. 2017; Ding et al. 2020). In gregarious species, individual foragers can optimize group foraging by partitioning responsibilities such as sharing information about quality foraging habitats, hunting, prey provisioning, and alloparental care (e.g., Boesch et al. 2006; Gero et al. 2009; Friedlaender et al. 2011; Wright et al. 2016). Integral to the partitioning of foraging roles is the inherent diversity in nutritional requirements among individuals within groups (Maklakov et al. 2008; Furrer et al. 2012), for

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example mixed-sex groups in sexually size-dimorphic species, such as killer whales, *Orcinus orca* (Miller et al. 2010). Sex differences in energetic requirements can affect fitness via both survival and reproduction (Maklakov et al. 2008), and therefore sexual segregation of foraging tasks or areas is a common resource maximizing strategy across size-dimorphic vertebrate species (Ruckstuhl and Neuhaus 2000; Bonenfant et al. 2004; Baird et al. 2005; Bearhop et al. 2006; Breed et al. 2006; Catry et al. 2006; Maklakov et al. 2008; Beerman et al. 2016; Photopoulou et al. 2020). Demographic patterns can also play an important role in shaping foraging responsibilities. For example, lactation is associated with considerable energetic costs (Williams et al. 2011; Christiansen et al. 2016), especially if migration occurs concurrently (e.g., Lockyer 2007; Christiansen et al. 2016). It may therefore be advantageous for lactating mothers to remain with nursing offspring and provide protection rather than expend energy on foraging (Lacy et al. 2017). Moreover, lactation can be time-intensive and can restrict a mother's locomotory abilities (Videsen et al. 2017), thereby limiting the time and opportunities available for foraging. The presence of maternal kin can also shape foraging strategies. In species in which females have a prolonged post-reproductive phase, grandmothers have been shown to increase survival of offspring (Foster et al. 2012), in part due to prey-sharing, especially with their adult sons (Wright et al. 2016).

Environmental pressures, especially those from human-induced rapid environmental change, threaten cost–benefit tradeoffs of behavioral strategies that evolved in past environments (Sih et al. 2011). A defining characteristic of the Anthropocene is the unprecedented speed at which environments are changing (Steffen et al. 2011; Lewis and Maslin 2015). Under rapid change, previously optimal behaviors may be mismatched to present environmental conditions (Sih et al. 2011) and may become maladaptive (Merkle et al. 2022). Populations that have the capacity for behavioral flexibility in response to novel pressures, for example greater genetic variation or an evolved ability to be flexible in resource use, may have a greater chance of survival (Sih et al. 2011). In populations of gregarious species that engage in group behaviors with divisions of responsibilities, whether the partitioning of responsibilities is fixed across populations experiencing different stressors is poorly understood, despite the growing awareness that behavioral context shapes responses to environment (Ellison et al. 2012; DeRuiter et al. 2017; McHuron et al. 2017; Pirotta et al. 2018; Southall et al. 2019). Understanding behavior is critical for predicting wildlife responses to global change (Berger-Tal et al. 2011; Berger-Tal and Saltz 2016; Gil et al. 2020) and improves the success of species conservation programs (Blumstein and Fernández-Juricic 2010; Berger-Tal et al. 2011; Berger-Tal and Saltz 2016; Gil et al. 2020). Therefore, determining the factors driving the partitioning of individual responsibilities in group systems would advance an understanding of the capacity of gregarious species to cope with novel pressures, which could enhance conservation programs in the face of current and forecasted global declines in biodiversity.

We leverage a unique bio-logging data set that provides a rare opportunity to test whether the partitioning of foraging roles is consistent between sympatric populations of a social, apex marine predator that forage on the same prey species and display similar social structure, yet have experienced divergent population growth trajectories in recent years (Murray et al. 2021). Northern and Southern Resident killer whales (hereafter NRKW and SRKW, respectively) live in the coastal waters along the west coast of the United States and Canada, in the eastern North Pacific Ocean (Bigg 1982; Heimlich-Boran 1988; Ford et al. 1998). These populations are structured around matrilines, multiple groups of mature females and their philopatric offspring of both sexes, related to a common female ancestor (Bigg et al. 1990; Stredulinsky et al. 2021). Emigration between matrilines is extremely rare, emigration and immigration between NRKW and SRKW populations has never been documented, and both sexes remain with their natal matriline for life with rare exceptions (Bigg et al. 1990; Barrett-Lennard 2000; Ford et al. 2000, 2011, 2018; Parsons et al. 2009). The presence of a living mother increases the survival of her weaned offspring, particularly her adult sons (Foster et al. 2012) and the presence of living grandmothers, especially post-reproductive grandmothers, increases the survival of their grandoffspring (Nattrass et al. 2019).

The group foraging system of resident killer whales is characterized by group travel to foraging sites, individual pursuit and capture of prey followed by prey-sharing with group members (Wright et al. 2016). Specifically, groups are thought to employ collective ecological knowledge to travel to particular foraging areas as cohesive social units, and to search for and locate prey patches that group members then exploit individually. Individuals pursue prey, often simultaneously, and then share prey with one or more group members (Wright et al. 2016) as a critical and necessary mechanism for the group to meet its nutritional requirements. Therefore, the individual foraging behavior that begets prey consumption among group members is a fundamental component of the cooperative acquisition of nutrients that makes up the group foraging system in resident killer whales. Once-abundant and reliable stocks of salmon (*Oncorhynchus* spp.), primarily Chinook (*O. tshawytscha*) and to a lesser extent chum (*O. keta*) and coho (*O. kisutch*; Ford and Ellis 2006; Hanson et al. 2010, 2021; Ford et al. 2016), make up the majority of NRKW and SRKW diets. Typically, salmon are initially chased, depending on the species either at the surface or at depth, and then captured and brought up to the surface (Wright et al. 2017; Tennessen et al. 2019a) where they are broken apart and shared (Ford and Ellis 2006; Wright et al. 2016). Research has revealed that NRKW mothers and post-reproductive grandmothers disproportionately share prey with their offspring and grandoffspring, and maternal sharing with adult offspring is predominantly directed toward males, to maximize inclusive fitness (Wright et al. 2016) as male reproductive success increases with age (Ford et al. 2011, 2018). While it has generally been assumed that the partitioning of foraging and provisioning roles among age/sex classes is fixed across populations of resident-ecotype killer whales, this has never been investigated, yet has important implications for advancing behavioral ecology theory and for developing effective conservation programs. While both NRKW and SRKW experienced declines during the 1960s and 1970s driven by the live-capture fishery for aquaria (Bigg and Wolman 1975; Reeves and Leatherwood 1984), their population trajectories have since diverged (Murray et al. 2021), despite their overlapping spatial distributions and similar ecology and prey preferences. Since annual population censuses began in 1973, NRKW, listed as Threatened under Canada's Species at Risk Act (SARA; DFO 2017), have experienced nearly continuous growth, increasing by more than 50% of their 2001 population size between 2001 and 2017 (Towers et al. 2015; DFO 2020). In contrast, SRKW, listed as Endangered under both SARA and the US Endangered Species Act (NMFS 2016; DFO 2017), have exhibited virtually no net growth since population censuses began in 1976 (NMFS 2016). While the differences in causal mechanisms underlying the two population trajectories are not fully understood, models of cumulative impacts of primary

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threats including limited prey availability, vessel disturbance (both acoustic and physical) and exposure to persistent organic pollutants explain the observed population trends reasonably well (Murray et al. 2021).

The divergent population growth trajectories between these sympatric populations and their differing levels of environmental stressors including human-generated ambient noise, vessel traffic and legacy contaminants (NMFS 2016; DFO 2020), provide a rare opportunity to test whether individual foraging responsibilities in a gregarious species are fixed across populations. Here, we leverage fine-scale behavioral data from high-resolution, multisensor bio-logging tags attached to NRKW and SRKW killer whales, paired with demographic data from long-term population censuses, to understand the factors that promote diversity in foraging behavior. Specifically, we test 1) whether sex-based patterns of foraging behavior are consistent between NRKW and SRKW populations, despite divergent population growth trajectories (Murray et al. 2021), differences in population stressors (NMFS 2016; DFO 2020) and the potential for shifting cost–benefit tradeoffs of optimal foraging behavior strategies (Merkle et al. 2022). We furthermore test 2) whether foraging behavior is predicted by reproductive status and demography, given the costs of reproduction in long-lived mammalian species (Boness and Bowen 1996; Christiansen et al. 2016; Thometz et al. 2016; Miketa et al. 2018), the importance of post-reproductive females as leaders and prey provisioners in resident killer whale populations especially when prey are limited (Brent et al. 2015; Nattrass et al. 2019), and the benefit of a living mother on the survival likelihood of her adult sons (Foster et al. 2012).

METHODS

Broadly, we attached multisensor bio-logging archival tags (Dtag versions 2 and 3, Johnson and Tyack 2003) by suction cup to NRKW and SRKW to quantify individual subsurface foraging behavior in their core summer habitats in the inland coastal waters of British Columbia, Canada and Washington, United States. Following tag recovery, we downloaded and processed data, computed foraging metrics, and constructed statistical models to compare individual foraging behavior between populations.

Study design

NRKW were tagged in the Queen Charlotte Strait and Central Coast regions of British Columbia in August and September, between 2009 and 2012. SRKW were tagged in Haro Strait and the Straits of Georgia and Juan de Fuca around the San Juan Islands, Washington, in September in 2010, 2012, and 2014 (Figure 1). Tagging methodology is described elsewhere (NRKW: Wright et al. 2017; SRKW: Holt et al. 2017). Briefly, we identified individual killer whales using photo-ID catalogues based on unique natural markings on their dorsal fins and the gray areas immediately posterior to their dorsal fins (Bigg 1987). We applied Dtags at the base of the dorsal fin using a 7-m hand-held carbon fiber pole from the bow of a small research vessel. Thirty-four and twenty-three Dtags were attached to NRKW and SRKW, respectively. Individual reactions to tagging ranged from no response to flinching or diving, and all individuals returned to pretagging surfacing behavior within 5 min. Inspection of time series of subsurface diving behavior of tagged whales from NRKW and SRKW, generated from tag pressure sensor data during analysis (described below), indicated that individuals from both populations responded similarly to initial tagging and time to acclimation. Tags generally remained attached during daylight hours as programmed, although some fell off prematurely due to water flow, rubbing, or impactful behaviors at the surface (e.g., breaching). We tagged individuals opportunistically, ensuring whenever possible that we selected a balanced representation of age and sex classes. All tagged animals were at least 2 years old. One NRKW and two SRKW were tagged twice in different years. Dtags recorded depth, body orientation, and movement using triaxial accelerometers and magnetometers that sampled at 50–250 Hz, and sound using stereo hydrophones that sampled at 96–240 kHz (see

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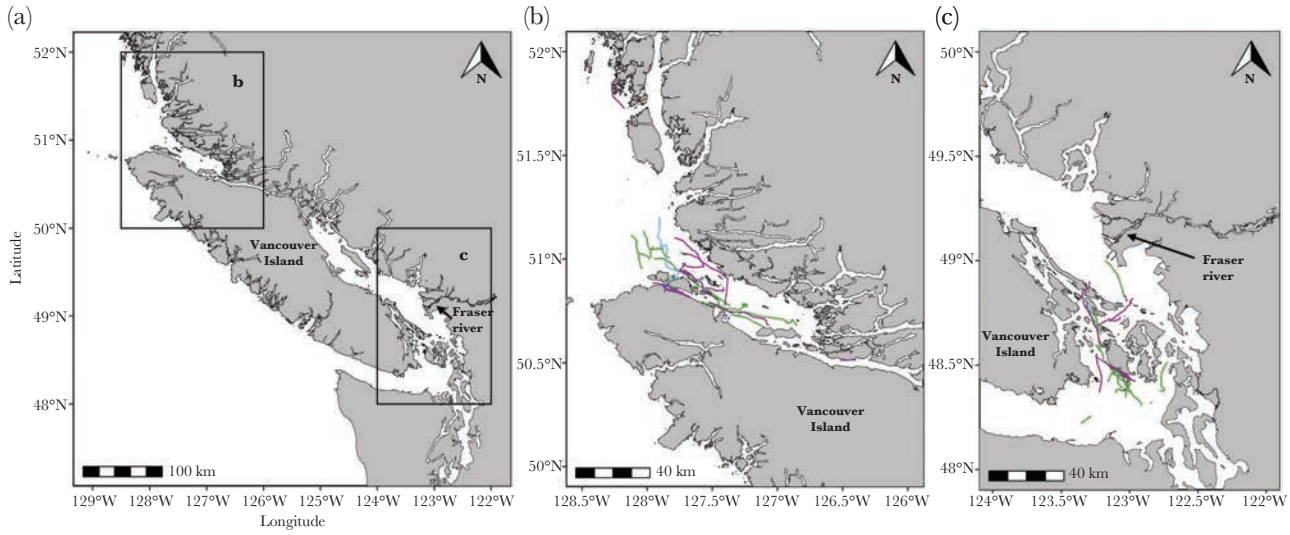


Figure 1
Map of study areas of Dtag deployments on resident killer whales in Washington State, United States and British Columbia, Canada (a). NRKW population (b) and SRKW population (c) were tagged on opposite ends of Vancouver Island (female = purple, male = green, unknown sex = blue).

details in Holt et al. 2017; Wright et al. 2017). We omitted five deployments: three NRKW tag deployments which fell off within minutes of deployment and were too short in duration to be calibrated, and two tag deployments (one from each population) for which the accelerometers malfunctioned.

We conducted focal follows of each tagged whale for the duration of the deployment as conditions allowed, during which we obtained periodic GPS fixes at surfacings (see details in Giles 2014; Wright et al. 2017) for subsequent track reconstruction (see *Data processing*). We also collected prey remains using fine-meshed dip nets (Ford and Ellis 2006; Hanson et al. 2010) to validate predation events and identify prey species by fish scale morphology or genetic analysis, and noted changes in tag orientation to aid data calibration. Prey species collected included Chinook and to a lesser extent chum and coho salmon, consistent with studies of diet composition of resident killer whales in the summer foraging habitat where our study was conducted (Ford et al. 1998, 2010, 2016; Ford and Ellis 2006; Hanson et al. 2010).

Data processing

We used a VHF receiver to locate and recover tags following detachment. We downloaded the data and used the 2014 Dtag toolbox (www.soundtags.org/dtags/dtag-toolbox) in MATLAB v R2016b (The MathWorks, Natick, MA) to calibrate sound and movement data based on sensor characteristics and tag orientation on the whale (see details in Holt et al. 2017; Wright et al. 2017). Several time series of data were produced over the duration of the deployment: temperature-corrected depth, triaxial orientation (pitch, roll, and heading), triaxial acceleration, and ambient sound (Johnson and Tyack 2003).

For each deployment, we parsed data into individual dives using the "find_dives" function from the 2014 Dtag toolbox, by searching for depth excursions >1 m bounded by surfacings <0.5 m (see details in Tennessen et al. 2019a). We omitted dives <4 s in duration, as these likely resulted from incomplete surfacings or from fluctuations in the pressure sensor data due to a high sampling rate. We checked dives manually to ensure accuracy. For every dive, we computed start and end times, and excluded dives that began within the first 5 min of the onset of the deployment, to account for short-term behavioral responses to tagging. We visually inspected all dive profiles to confirm that 5 min was a conservative threshold for the duration of these behavioral responses.

To obtain animal tracks and align foraging behavior with bathymetry, we computed geo-referenced pseudotracks (hereafter "tracks"; for details, see Wright et al. 2017). Because the Dtags did not contain GPS sensors, we used the 2014 Dtag toolbox in MATLAB to dead-reckon the accelerometer and magnetometer data to create best estimates of tracks, by identifying the next position in time based on the previous position (Wilson et al. 2007). To constrain accumulated spatial error associated with drift, we forced the tracks through known GPS coordinates taken periodically when whales surfaced (Wilson et al. 2007), using the TrackReconstruction package in R (Battaile 2019; R Core Team 2020). We used bathymetry data from the GEBCO database (www.gebco.net; 15 arc-second resolution) and the marmap R package (Pante and Simon-Bouhet 2013) to compute bathymetry values for every dive, taken as the water depth at the estimated GPS location of the start of each dive. Differences in the magnitude of track error between deployments are presumed to have negligible impact on bathymetry estimates because these errors are unlikely to exceed the spatial resolution of the bathymetry data.

Foraging metrics

Sounds of foraging activity detected in tag acoustic data can indicate prey pursuit and capture events (e.g., Holt et al. 2019; Wright et al. 2021). Excess noise in some audio recordings from water flowing over the tag or from nearby vessels prevented us from computing sound variables for some deployments. Therefore, we used kinematic detection of foraging behavior validated by available acoustic data to identify prey capture events, which is an established method that maximizes sample size in the absence of complete acoustic data (Allen et al. 2016; Tennessen et al. 2019a). We viewed spectrograms (512 point, Hann window, 50% overlap) alongside plots of depth and angle of arrival between the two hydrophone channels to identify all occurrences of foraging sounds: slow and fast echolocation clicks (interclick intervals of >100 and 11–100 ms, respectively, associated with searching for and pursuing prey), buzzes (interclick interval <11 ms, associated with final pursuit of prey) and prey handling sounds (those of crunching and tearing, produced during prey processing), and mapped these sounds to dives (see details in Holt et al. 2019). For movement data, we partitioned each dive into descent, bottom (≥70% of maximum dive depth) and ascent phases (Arranz et al. 2016; Tennessen et al. 2019a), and for each phase computed three variables previously demonstrated to predict prey capture (Tennessen et al. 2019a): jerk peak (maximum peak of the jerk signal, the rate of change of triaxial acceleration, adjusted by the median jerk signal, see Ydesen et al. 2014; Allen et al. 2016; Arranz et al. 2016; Tennessen et al. 2019a), roll at jerk peak (absolute value of the roll at the time of jerk peak, in degrees), and circular variance in heading using the "circ_var" function in the CircStat package (Berens 2009) in MATLAB.

We filtered prey capture dives from each deployment time series by setting minimum thresholds for jerk peak, roll, and heading variance determined from known prey capture dives identified using available acoustic data (see Supplementary Information, data presented in Supplementary Table S1). We determined these thresholds for each population separately by matching detection sensitivities between populations (true-positive rate of 100%, false-positive rate of 26%, for dives ≥50 m). Thus, the filter detected all acoustically confirmed prey capture dives, while minimizing the false-positive rate. When detecting prey capture events, there is a tradeoff between maximizing true positives (accuracy) and minimizing false positives (specificity). Since we were interested in quantifying prey capture in populations foraging under conditions of limited prey availability and accessibility (NMFS 2016; DFO 2017; Lacy et al. 2017), it was critical to maximize confidence in our ability to detect true prey captures (achieve a miss rate near zero) and accept the concomitant higher false-positive rate.

To quantify the total time a whale spent searching for prey during each deployment, we summed the duration of all dives during which only slow echolocation clicks were detected. While it is likely that some searching dives also included other foraging behaviors, such as pursuit and capture, this conservative approach allowed us to focus exclusively on those dives during which the individual was acoustically scanning the environment. Previous research suggests that this search phase is a distinct component of foraging behavior, which primarily occurs at the surface and is behaviorally differentiated from pursuit and prey capture phases (Tennessen et al. 2019b; Holt et al. 2021b). To quantify the proportion of time a whale engaged in prey capture, we summed the duration of dives that resulted in prey capture and divided this by the total deployment time. To quantify the proportion of time a whale engaged in travel or resting dives, we summed the duration of dives <30 m during

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which no echolocation clicks or sounds of prey capture or handling were produced (Holt et al. 2013; Noren and Hauser 2016) and divided this by the total deployment time.

We used photographic data gathered during population censuses conducted by the Center for Whale Research (SRKW) and Fisheries and Oceans Canada (NRKW) to assign demographic variables. These databases contain extensive maternal familial relationships established through field observations and genetic testing (described by Towers et al. 2015). For each adult male (≥12 years), we determined whether his mother was living and, for adult females (≥12 years), whether the individual had a living calf (≤3 years). We identified 3 years as the cutoff age for a calf because it approximated the mean calving interval for adult females during the period in which the tagging was conducted.

Statistical analyses

We constructed linear and generalized linear mixed effects models (LMM and GLMM) in R v.3.6.3 (R Core Team 2020) using the lme4 (Bates et al. 2015) and glmmTMB (Brooks 2017) packages. We constructed separate models with 1) all tag deployments (models a–f, Table 2) and 2) subsets of deployments to explore demographic effects of calf presence (adult females only, model g, Table 2) and living mother presence (adult males only, model h, Table 2). We constructed individual full models with fixed effects of 1) population, sex, and their interaction (models a–f, Table 2), 2) population, presence of calf, and their interaction (for adult females, model g, Table 2), and 3) population, presence of living mother, and their interaction (for adult males, model h, Table 2), and we included offset effects of the log-transformed deployment duration (models a, g, and h) and the square root-transformed cumulative searching time (model b, Table 2) for those models that contained counts as response variables. For beta regression models we transformed values of 0 and 1 following methods of Duoma and Weedon (2019), and we tested for fixed versus variable dispersion by comparing AIC scores for a model with fixed (null) dispersion to those with population, sex, or population:sex as variable dispersion terms (models c and d, Table 2), and retained the model with the lowest AIC score. For the beta regression model of the proportion of time spent in prey capture dives, the null dispersion model was optimal. For the beta regression model of the proportion of time spent traveling or resting, the model with sex as a dispersion term was optimal. Model response variables included total number of prey capture dives within a deployment (negative binomial and Poisson distributions, models a, b, g, and h, Table 2), proportion of deployment time engaged in prey capture dives (beta distribution, model c, Table 2), proportion of deployment time engaged in traveling or resting dives (beta distribution, model d, Table 2), maximum depth of a prey capture dive (Gaussian distribution, log-transformed to meet model assumptions, model e, Table 2), and bathymetry at the location of a prey capture dive (Gaussian distribution, log-transformed to meet model assumptions, model f, Table 2). For the models with count data as the response variable (models a, b, g, and h, Table 2), we explored several candidate models with Poisson and negative binomial distributions, with and without terms for overdispersion and zero inflation, and used AIC model selection to identify the optimal models. Additionally, we followed the protocol outlined by Zuur et al. (2009) to identify the optimal random structure, which involves including all reasonable random effects that are potentially important, constructing models with different permutations of these random effects, and using AIC model selection to identify the model with the lowest AIC score. There is debate over the appropriate threshold to use in AIC model selection (Grueber et al. 2011; Harrison et al. 2018). Earlier work suggested that small delta thresholds of 2 or less should be used to reduce the likelihood of including overly complex models with unnecessary predictors (Burnham and Anderson 2002), while later work suggested that larger delta thresholds may be necessary in certain cases, especially if models are overdispersed (e.g., Richards 2008; Bolker et al. 2009; Burnham et al. 2011). To identify the optimal random structure, we selected models with the lowest AIC score using a delta threshold of 2, and performed tests using the DHARMa package (Hartig 2020) to verify that our models were not overdispersed. This accepted approach provides a repeatable method by which to systematically eliminate nonsignificant random effects. We considered random effects of age (continuous), deployment year (factor), week-year (factor), and deployment ID (factor), alone and in combination. Deployment ID was defined as the unique tag deployment on an individual, and was used to control for the assumption that dives within deployments should be more similar than dives between deployments. This term allowed us to control for pseudoreplication for all models in which dive was the unit of analysis (models e and f, Table 2). Week-year was defined as the week of the year in which a given tag was deployed. There was no numerical relationship between week-year levels. Rather, this term accounted for the assumption that groups within the same week-year level were more similar than those from different levels, and allowed us to account for unmeasurable environmental variation between populations, especially variation in salmon abundance. It was not appropriate to use a continuous variable that could capture the potential covariance between weeks given that the study period spanned only a few weeks per study site each year. It is important to note that while week-year accounted for temporal nonindependence of observations across the study, deployment ID further accounted for potential spatiotemporal nonindependence within a given week-year since dives within the same deployment should be more similar than those between deployments.

For the model examining the relationship between the presence of a living mother and the number of prey capture dives by adult males (model h, Table 2), we additionally explored the importance of including a random effect of the categorical age of the tagged male's mother (dead, reproductive, or post-reproductive), but there was no support to include this random effect in the final model. The best models included week-year (all models, Table 2) and deployment ID (models e and f, Table 2) as random effects. We used recursive, single term deletion and model comparison of successively simpler models using Likelihood Ratio Tests to determine which fixed effects to omit from the final models. We used Tukey HSD tests to compare levels of model effects (see Supplementary Information, Table S2). For all tests, $\alpha = 0.05$. Where relevant in statistical analyses, we omitted one NRKW deployment (oo09_238a) for which sex was unknown because this juvenile died before its sex could be determined.

We were unable to use available salmon abundance indices due to 1) spatial incongruency between the salmon stocks/regions where these abundance data were sampled and the prey consumed by NRKW and SRKW during our study period and location, 2) issues with sporadic coverage and the degree to which effort had been accounted for in some of the existing salmon indices, and 3) reliability issues with applying widely used salmon data from the Albion Test Fishery situated on the Fraser River (e.g., Ayres et al. 2012; Ford et al. 2016; Wasser et al. 2017; Holt et al. 2021a), because of uncertainty in the proportions of salmon taking one of two possible

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Table 1

Summary of analyzed Dtag deployments in Northern and Southern resident killer whale populations between 2009 and 2014, ordered by population, sex, and age

Deployment	Date and time (yyyy-mm-dd hh:mm:ss)	Pop.	Sex	Age	Deployment duration (h)	No. dives analyzed	No. prey cap. dives	Calf[a] (years)	Mother alive[b] (years)	Time searching (h)[c]
oo10_260a	2010-09-17 11:25:12	NRKW	F	8	6.50	605	26	—	—	1.05
oo11_240a	2011-08-28 15:28:04	NRKW	F	9	3.77	363	4	—	—	1.24
oo09_235a	2009-08-23 14:17:32	NRKW	F	10	2.74	317	8	—	—	1.83
oo10_256a	2010-09-13 11:03:10	NRKW	F	10	7.13	821	35	—	—	3.40
oo11_224a	2011-08-12 08:51:17	NRKW	F	10	1.92	225	5	—	—	0.38
oo09_237c	2009-08-25 12:35:58	NRKW	F	12	0.97	95	2	1	—	0.09
oo09_247a	2009-09-04 10:27:05	NRKW	F	15	1.05	123	2	0	—	0
oo09_231a	2009-08-19 11:58:16	NRKW	F	16	7.01	539	16	N	—	—
oo10_265a	2010-09-22 15:31:15	NRKW	F	20	2.78	302	21	N	—	2.14
oo11_246a	2011-09-03 12:46:50	NRKW	F	30	3.50	441	18	0	—	2.16
oo11_267a	2011-09-24 11:01:53	NRKW	F	36	6.87	622	12	1	—	—
oo11_248a	2011-09-05 13:10:15	NRKW	M	6	0.35	29	0	—	—	0
oo11_248b	2011-09-05 13:53:25	NRKW	M	7	2.74	306	0	—	—	0.39
oo11_244b	2011-09-01 13:03:11	NRKW	M	11	0.77	69	2	—	—	0
oo09_239a	2009-08-27 11:41:28	NRKW	M	13	2.00	150	2	—	29	0.14
oo12_235b	2012-08-22 14:21:59	NRKW	M	16	4.31	471	11	—	32	2.70
oo09_245b	2009-09-02 17:51:45	NRKW	M	21	1.31	123	5	—	38	0.54
oo09_244a	2009-09-01 15:14:42	NRKW	M	22	3.92	297	19	—	41	1.45
oo09_237d	2009-08-25 16:09:04	NRKW	M	23	3.03	320	9	—	N	2.06
oo09_236a	2009-08-24 15:37:43	NRKW	M	24	2.18	158	1	—	38	0.54
oo09_245a	2009-09-02 13:34:01	NRKW	M	24	5.52	488	16	—	N	2.54
oo10_264a	2010-09-21 17:18:03	NRKW	M	24	1.48	125	2	—	N	0.11
oo11_244a	2011-09-01 09:24:22	NRKW	M	26	2.69	180	0	—	55	0.76
oo09_234a	2009-08-22 15:26:55	NRKW	M	27	3.72	348	7	—	N	2.65
oo11_245a	2011-09-02 07:58:13	NRKW	M	28	11.21	859	10	—	42	2.05
oo09_243a	2009-08-31 16:21:36	NRKW	M	29	2.80	234	7	—	43	0.63
oo11_224b	2011-08-12 16:19:13	NRKW	M	29	0.21	15	1	—	54	0.06
oo09_240a	2009-08-28 11:51:51	NRKW	M	32	3.31	341	13	—	N	2.24
oo10_261a	2010-09-18 15:14:55	NRKW	M	39	2.91	296	5	—	62	2.37
oo09_238a	2009-08-26 07:59:15	NRKW	Unk	3	11.19	1019	13	—	—	3.22
oo14_249m	2014-09-06 09:55:10	SRKW	F	5	5.58	567	10	—	—	1.30
oo12_266m	2012-09-22 10:39:21	SRKW	F	17	2.39	214	10	N	—	1.20
oo10_268m	2010-09-25 10:53:31	SRKW	F	19	7.13	629	3	N	—	—
oo12_267m	2012-09-23 14:56:07	SRKW	F	19	2.29	244	0	3	—	1.11
oo14_264m	2014-09-21 11:31:46	SRKW	F	19	0.65	60	2	N	—	0.45
oo10_264m	2010-09-21 12:37:09	SRKW	F	20	2.45	217	0	3	—	0
oo10_261m	2010-09-18 15:32:45	SRKW	F	24	0.61	36	0	N	—	0.16
oo10_267m	2010-09-24 14:34:45	SRKW	F	36	3.77	278	0	1	—	—
oo12_266n	2012-09-22 13:45:09	SRKW	F	38	0.42	51	0	2	—	0.35
oo12_250m	2012-09-06 10:51:13	SRKW	F	41	6.38	595	18	N	—	—
oo12_260m	2012-09-16 12:24:02	SRKW	M	2	2.67	153	3	—	—	—
oo10_259m	2010-09-16 15:50:54	SRKW	M	6	1.51	196	5	—	—	—
oo10_251m	2010-09-08 14:40:22	SRKW	M	7	0.99	117	3	—	—	0.46
oo10_265m	2010-09-22 12:15:42	SRKW	M	9	6.04	517	25	—	—	2.90
oo12_251m	2012-09-07 11:22:21	SRKW	M	11	1.53	145	8	—	—	0.87
oo14_266m	2014-09-23 10:53:41	SRKW	M	12	4.35	455	13	—	29	3.92
oo12_254m	2012-09-10 10:46:44	SRKW	M	16	6.46	574	9	—	N	3.73
oo10_257m	2010-09-14 14:00:35	SRKW	M	17	4.22	516	24	—	50	—
oo10_270m	2010-09-27 12:47:05	SRKW	M	21	1.01	111	5	—	50	—
oo14_250m	2014-09-07 09:52:25	SRKW	M	21	8.39	822	17	—	43	—
oo12_261m	2012-09-17 10:11:55	SRKW	M	22	2.02	174	3	—	N	0.78
oo14_263m	2014-09-20 11:57:15	SRKW	M	23	6.08	502	11	—	N	2.91

[a]Adult females (≥12 years) with or without (N) a living calf (≤3 years). Estimated age (years) is provided for all calves of tagged adult females.
[b]Adult males (≥12 years) with or without (N) a living mother at time of tagging. Estimated age (years) is provided for living mothers.
[c]Empty cells indicate deployments in which audio recordings could not be analyzed.

paths around Vancouver Island, BC to return to the Fraser River (Figure 1). Therefore, the week-year random effect allowed us to account as best as possible for temporal variability in salmon abundance and other environmental factors on a weekly basis that might be responsible for the differences in foraging patterns we measured within and between populations. However, we cannot rule out the possibility that longer-term differences in salmon abundance and availability between populations could have driven the observed differences in foraging strategies.

RESULTS

We analyzed 186.8 h of dive data from 52 Dtag deployments (109.9 h from 30 NRKW, 76.9 h from 22 SRKW; Figure 1). Mean

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Table 2

Summary statistics for best-fit models of foraging-related response variables for Northern and Southern Resident killer whales 2009–2014

Model ID	Response	Model type	Model family	Random effects	Offset effects	Dispersion parameter	Fixed effects	Obs. unit	*n*	df	Estimate	s.e.	*t* value or *z* value	*P* value
a	No. prey capture dives	GLMM	Negative binomial (nbinom1)	Week of year	log(deployment duration)	—	Population	Deployment	51	49	−1.1086−0.5990	0.3559	−3.115	0.0018
							Sex					0.2555	−2.344	0.0191
							Population:sex				1.5055	0.4358	3.454	0.0006
b	No. prey capture dives	GLMM	Negative binomial (nbinom1)	Week of year	sqrt(cumulative searching time)	—	Population	Deployment	41	39	−1.4160−0.7635	0.4996	−2.834	0.0046
							Sex					0.2664	−2.866	0.0042
							Population:sex				1.6041	0.5788	2.771	0.0056
c	Prop. time engaged in prey capture	GLMM	Beta	Week of year	—	—	Population	Deployment	51	49	−1.045	0.383	−2.73	0.0063
							Sex				−0.379	0.296	−1.28	0.2001
							Population:sex				1.471	0.470	3.13	0.0017
d	Prop. time engaged in travel or rest	GLMM	Beta	Week of year	—		Population	Deployment	51	48	−1.035	0.375	−2.76	0.0058
							Sex				−0.356	0.324	−1.10	0.2722
						sex					0.715	0.354	2.02	0.043
e	log(max. depth)	LME	Gaussian	Week of year Deployment	—	—	Population	Dive	428	40	0.4531	0.2066	2.1934	0.0342
							Sex			40	0.0390	0.2075	0.1879	0.8519
f	log(bathym)	LME	Gaussian	Week of year Deployment	—	—	Population	Dive	414	38	−0.2187	0.1499	−1.4591	0.1528
							Sex			38	0.3542	0.1482	2.3903	0.0219
g	No. prey capture dives by adult females	GLMM	Poisson	Week of year	log(deployment duration)	—	Population	Deployment	15	14	−2.1826	0.7091	−3.0780	0.0021
							Calf			14	−1.9471	0.7175	−2.7140	0.0067
h	No. prey capture dives by adult males	GLMM	Poisson	Week of year	log(deployment duration)	—	Population	Deployment	22	21	−0.2347	0.4060	−0.5780	0.5632
							Living mother			21	−0.1769	0.2175	−0.8140	0.4160
							Population:living mother			21	0.8554	0.3946	2.1680	0.0302

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deployment durations for NRKW and SRKW were 3.7 h (range = 0.2–11.2 h) and 3.5 h (range = 0.4–8.4 h), respectively. Of the total deployments, 30 were on males (54.4 h on 18 NRKW, 45.2 h on 12 SRKW), 21 were on females (44.3 h on 11 NRKW, 31.7 h on 10 SRKW), and one was on an individual of unidentified sex (11.2 h on NRKW; Table 1).

Foraging ecology

There was a significant interaction between population and sex on the number of prey capture dives, offsetting for deployment duration (GLMM, $z = 3.454$, $P = 0.0006$, Table 2, Supplementary Table S2, presented in Figure 2a as prey capture rate, prey capture dives per hour). NRKW females captured 167% more prey per hour than SRKW females. Additionally, SRKW males captured 152% more prey per hour than SRKW females, while there was an opposite trend that NRKW females captured 55% more prey per hour than NRKW males (observed mean values of prey capture dives per h, NRKW F: 3.29, NRKW M: 2.12, SRKW F: 1.23, SRKW M: 3.10). These trends were not due to differences in effort. Indeed, when controlling for cumulative time spent searching for prey there was a significant interaction between population and sex on the number of prey capture dives (GLMM, $z = 2.771$, $P = 0.0056$, Table 2, Supplementary Table S2, presented in Figure 2b as foraging efficiency, prey capture dives per h searching). NRKW females were 257% more efficient than SRKW females and 68% more efficient than NRKW males, while there was an opposite trend that SRKW males were 59% more efficient than SRKW females (observed mean values of prey capture dives per h searching, NRKW F: 12.13, NRKW M: 7.24, SRKW F: 3.40, SRKW M: 5.39).

Time spent engaged in prey capture versus traveling and resting dives differed between populations. There was an interaction between population and sex on the proportion of deployment time engaged in dives that resulted in prey capture (GLMM, $z = 3.13$, $P = 0.0017$, Table 2, Supplementary Table S2). NRKW females spent 91% and 23% more time engaged in prey capture dives than SRKW females or NRKW males, respectively. In contrast, SRKW males spent 114% more time engaged in prey capture dives than SRKW females (Figure 2c) (observed mean values of proportion of deployment spent in prey capture dives, NRKW F: 0.162, NRKW M: 0.132, SRKW F: 0.085, SRKW M: 0.182). Additionally, there was a population effect on the proportion of tag deployment time that a subject spent traveling or resting (GLMM, $z = -2.76$, $P = 0.0058$, Table 2, Supplementary Table S2). Across both sexes, NRKW engaged in traveling or resting behavior for 62% more time than SRKW (Figure 2d) (observed mean values of proportion of deployment spent in travel or resting dives, NRKW: 0.463, SRKW: 0.286).

Dive depth was an important factor contributing to population differences in foraging behavior. There was a significant effect of population on the log of the maximum depth of prey capture dives (LMM, $t = 2.1934$, $P = 0.0342$, Table 2, Supplementary Table S2). Average depth of SRKW prey capture was 20% greater than NRKW prey capture depth (Figure 2e) (observed mean values of maximum depth of prey capture dives, NRKW: 90.63, SRKW: 108.54). This difference was not explained by bathymetry, as the foraging habitats used by the two populations did not differ in depth. Additionally, there was an effect of sex on the log of the foraging habitat depth (LMM, $t = 2.3903$, $P = 0.0219$, Table 2, Supplementary Table S2). Across both populations, males tended to make prey capture dives in areas that were 13% deeper than areas in which females foraged (Figure 2f) (observed mean values of habitat depth at location of prey capture dive, F: 171.36, M: 193.12).

Demographic effects on foraging ecology

Population and the presence of a calf were significant predictors of the number of prey capture dives by adult females (GLMM, population: $z = -3.078$, $P = 0.0021$; calf: $z = -2.714$, $P = 0.0067$, Table 2, Supplementary Table S2). Across both populations, females without calves made more prey capture dives than females with calves. Accounting for deployment duration, NRKW adult females without calves made 133% more prey capture dives per hour than SRKW adult females without calves and 81% more than NRKW females with calves. NRKW females with calves captured more prey than SRKW females with calves, who captured no prey while tags were attached (Figure 3a,b) (observed mean values of prey capture dives per h, NRKW no calf: 4.91, NRKW with calf: 2.71, SRKW no calf: 2.11, SRKW with calf: 0). There was a significant interaction between population and the presence of a living mother on the number of prey capture dives by adult males (GLMM, $z = 2.168$, $P = 0.0302$, Table 2, Supplementary Table S2). Accounting for deployment duration, SRKW males with a living mother made 151% more prey capture dives per hour than SRKW males whose mother had died, whereas the opposite was true for NRKW, whereby NRKW whose mother had died made 17% more prey capture dives per hour than NRKW males with a living mother (Figure 3c,d) (observed mean values of prey capture dives per h, NRKW dead mother: 2.61, NRKW living mother: 2.24, SRKW dead mother: 1.56, SRKW living mother: 3.92).

DISCUSSION

Empirical studies investigating the partitioning of individual responsibilities within and between groups can advance an understanding of the factors promoting and maintaining diversity in behavior, and can inform predictions about how novel pressures may impact wildlife. Here, we demonstrate that patterns of individual foraging behavior by resident killer whales are not fixed across populations. We use kinematic and acoustic data from high-resolution bio-logging tags to reveal striking population differences in the sex-based and demographic patterns of individual foraging behavior. We demonstrate that the NRKW population, which has grown nearly continuously for the past two decades, employed a female foraging strategy characterized by females exhibiting a greater number of prey capture dives, greater foraging efficiency, and a larger proportion of time spent capturing prey compared with males, consistent with previous work (Wright et al. 2016). In contrast, in the SRKW population, which to date has exhibited virtually no net growth since annual censusing efforts began in 1976, female foraging behavior was greatly reduced, especially for females with dependent young. Moreover, there was a trend of greater prey capture by adult males, especially those with a living mother, and SRKW spent less time resting or traveling compared with NRKW.

The interpopulation differences in individual foraging behavior could be driven by fluctuations in population size and the concomitant changes in social dynamics. SRKW have experienced high mortality, including the loss of critical information-bearing post-reproductive matriarchs. In gregarious species, older group members often serve as "keystone individuals" that exert disproportionate influence on group behavior and stability of social hierarchies (McComb et al. 2001; Modlmeier et al. 2015;

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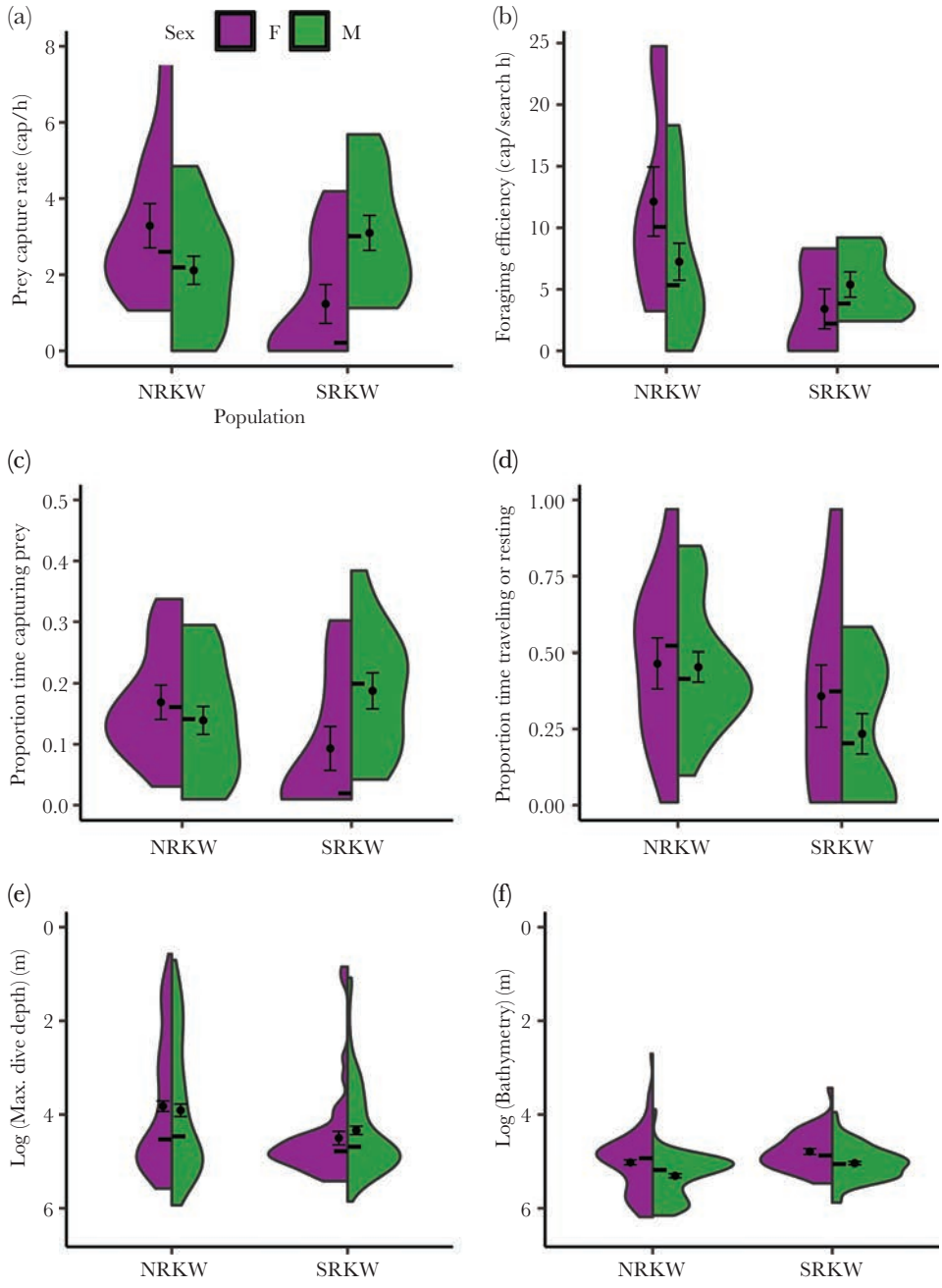


Figure 2
The relationship between sex and foraging behavior differed between killer whale populations. Violin plots depict trimmed kernel densities, points and bars depict means ± standard errors, and horizontal lines indicate median values for (a) total prey capture dives standardized by deployment duration in hours (NRKW female: $n = 11$; NRKW male: $n = 18$; SRKW female: $n = 10$; SRKW male: $n = 12$), (b) total prey capture dives standardized by searching effort in hours (NRKW female: $n = 8$; NRKW male: $n = 16$; SRKW female: $n = 6$; SRKW male: $n = 7$), (c) proportion of deployment time spent capturing prey (NRKW female: $n = 11$; NRKW male: $n = 18$; SRKW female: $n = 10$; SRKW male: $n = 12$), (d) proportion of deployment time spent traveling or resting (NRKW female: $n = 11$; NRKW male: $n = 18$; SRKW female: $n = 10$; SRKW male: $n = 12$), (e) log of the maximum depth of prey capture dives (m; NRKW female: $n = 149$; NRKW male: $n = 110$; SRKW female: $n = 43$; SRKW male: $n = 126$), and (f) log of the bathymetry at the location of prey capture dives (m; NRKW female: $n = 149$; NRKW male: $n = 110$; SRKW female: $n = 42$; SRKW male: $n = 113$).

Wooddell et al. 2016; Busson et al. 2019). Given that the role of post-reproductive matriarchs as leaders is likely critical in resident killer whale populations, the chance loss of key individuals and their personalities (i.e., repeated behavioral syndromes; Sih et al. 2004) could affect patterns and outcomes of behavior (Keiser and Pruitt 2014).

Alternatively, differences in individual foraging roles across populations may be the outcome of environmental pressures differentially impacting population growth rates, which may in turn affect behavioral strategies. SRKWs have experienced high levels of anthropogenic disturbance (NMFS 2016) including the disproportionate impact of vessel presence on female foraging compared

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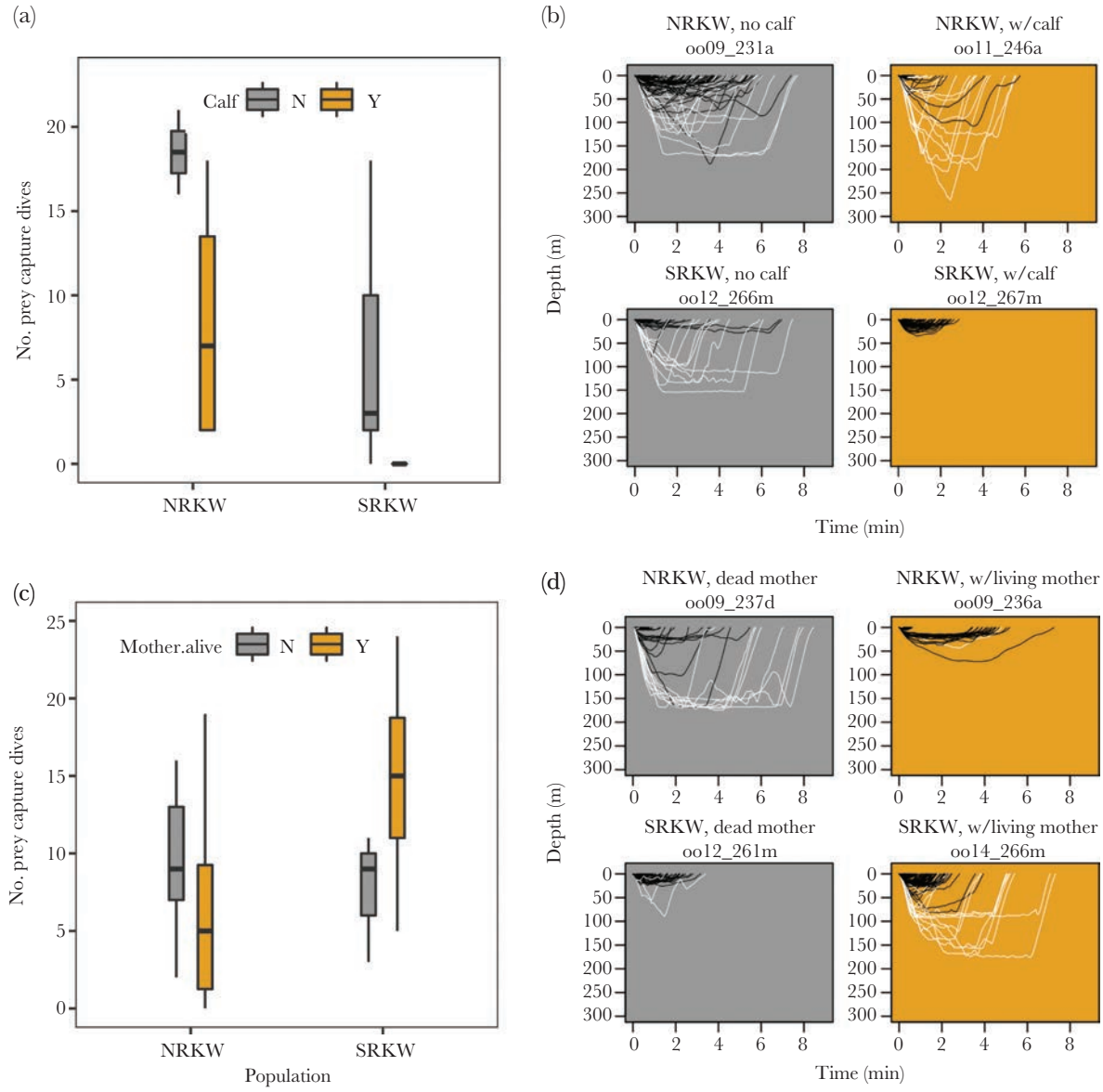


Figure 3

Demography affected the number of prey capture dives. (a, b) In both killer whale populations, the presence of a calf reduced the number of prey captured by adult females, and the effect was greatest for SRKW (NRKW no calf: $n = 2$; NRKW w/calf: $n = 4$; SRKW no calf: $n = 5$; SRKW w/calf: $n = 4$). (c, d) For NRKW, adult males with a living mother captured fewer prey, whereas for SRKW males, those with a living mother captured more prey (NRKW dead mother: $n = 5$; NRKW alive mother: $n = 10$; SRKW dead mother: $n = 3$; SRKW alive mother: $n = 4$). Boxplots (a, c) display median (horizontal line), interquartile range (boxes), and observations within 1.5 times the interquartile range (whiskers). Dive plots (b, d) depict all dives (white = prey capture, black = other) from representative deployments on tagged whales (gray shading = absence [of calf or living mother], gold shading = presence).

with male foraging (Holt et al. 2021b). These differences in disturbance have been implicated in the divergent population growth trajectories (Murray et al. 2021). Consequently, the decomposition of robust social structure within the SRKW (Williams and Lusseau 2006; Busson et al. 2019), potentially mediated by greater disturbance, could have shifted the cost–benefit tradeoffs underlying foraging strategies.

We demonstrate an effect of calf presence on prey capture across both populations. Adult females with a calf captured prey less than those without, and the effect of calf presence on foraging was more pronounced in SRKW. None of the SRKW mothers with calves engaged in any prey capture attempts at depth during the study period, whereas all NRKW mothers with calves continued to make prey capture dives, albeit fewer than the NRKW females without calves. Foragers must routinely balance the competing strategies of either conserving energy stores to minimize the likelihood of starvation (robust satisficing) or maximizing energy obtained from foraging (optimizing) (Carmel and Ben-Haim 2005). For SRKW experiencing scarce and patchy resources and uncertainty in prey capture due to the depletion of many Pacific salmon stocks (Brown et al. 2019; Hanson et al. 2021), robust satisficing by mothers with calves (conserving energy by conducting prey capture dives less frequently and potentially receiving prey from other individuals more often) may be favored (Carmel and Ben-Haim 2005). Additional

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data are needed to tease out the nuances of the effect of calf presence, given the relatively small sample sizes of deployments on females with calves. Furthermore, we cannot rule out the possibility that the presence of the tagging vessel influenced foraging behavior, especially of mothers with depending young. However, once the tag was applied, the tagging vessel typically remained at distances comparable to other commercial whale watching vessels in the area. Therefore, any impact from the tagging vessel may underscore the general sensitivity of lactating females to nearby vessels (e.g., Holt et al. 2021b). Given the number of vessels frequently in their proximity (Giles 2014; Holt et al. 2021a, 2021b), SRKW females with vulnerable calves may have been routinely foregoing foraging opportunities during the study period. Whether this loss of opportunity to consume prey is offset by food sharing from other individuals in the pod or translates to energy loss remains unknown.

The finding that adult SRKW males captured more prey if their mother was alive highlights the opposite patterns of foraging behavior we observed for adult males between the two populations. Males require more energy due to their larger size (Noren 2011), and the tendency for NRKW mothers to provision their adult male offspring should maximize maternal inclusive fitness (Wright et al. 2016), since older males sire a disproportionate number of offspring in resident killer whale populations (Ford et al. 2011). In the absence of living mothers, NRKW adult males may have to forage more to make up for the lack of maternal provisioning, which aligns with our findings for this population. In contrast, SRKW adult males with a living mother captured more prey than SRKW adult males whose mothers had died and NRKW adult males with a living mother, while there was no apparent difference in the number of prey captured by NRKW and SRKW males whose mothers had died. It is unlikely that the increased prey capture by SRKW males served the purpose of sharing prey to offset the lactation costs of their mothers, since none of the mothers of tagged SRKW adult males had calves (≤3 years), and the majority were post-reproductive (≥40 years). Instead, it is possible that greater prey capture by SRKW adult males with living mothers may be a strategy to help offset their post-reproductive mother's reduced foraging effort which we documented in SRKW females. Given the benefits of post-reproductive matriarch survival (McComb et al. 2001; Modlmeier et al. 2015; Wooddell et al. 2016; Busson et al. 2019; Nattrass et al. 2019), it is possible that adult sons in demographically unbalanced, endangered populations may attempt to promote survival of matrilineal members including their mothers, for example through prey-sharing. This hypothesis is supported by the fact that survival of male resident killer whales is impacted by maternal death (Foster et al. 2012). Moreover, prey-sharing between individuals is common in resident killer whales (Wright et al. 2016), and prey-sharing by adult males with their mothers and siblings has been observed in NRKW presumably as a form of pseudoreciprocity, albeit much less often than females provisioning related males (Wright et al. 2016). It is therefore possible that SRKW adult males engage in capturing prey and potentially sharing with maternally related group members including their mothers, while SRKW adult females engage in context-dependent robust satisficing to reduce overall energy use, particularly in areas of intensified anthropogenic pressure. This potential prey-sharing role of SRKW adult males challenges the existing paradigm that adult females are disproportionate provisioners in resident killer whale populations. However, if adult males are provisioning their mothers, one might expect increased survival probability of sons with the death of their mothers due to the released foraging burden. Rather, we see the opposite—that male survival probability decreases with maternal death (Foster et al. 2012). Additional evidence would be helpful for testing the hypothesis that sons share prey with their mothers, such as 1) demonstrated prey-sharing by SRKW adult males, either directly via observations (e.g., as in NRKW, Wright et al. 2016) or indirectly through increases in post-reproductive female longevity with the presence of adult sons, and 2) demonstrated increases in indirect benefits to adult males from prey-sharing with maternally related group members.

It is worth considering an alternative, nonmutually exclusive hypothesis related to the role of group leadership by post-reproductive females to explain the increased prey capture by SRKW males with living mothers. Given that post-reproductive females typically lead groups (Brent et al. 2015) and that pod members frequently share prey (Wright et al. 2016), leading the group to locations where adult sons and other related males can maximize prey capture and caloric intake could translate into increased survival of these males, which could maximize female inclusive fitness given that older males sire more calves (Ford et al. 2011). Moreover, we showed that males of both populations foraged in areas with deeper bathymetry than females, consistent with previous work (Beerman et al. 2016), and we revealed that SRKW captured prey at greater depths than NRKW, an effect not due to differences in the bathymetry of their foraging habitats. There may be a potential benefit to deeper diving, given that larger Chinook salmon are typically found at greater depths than smaller, less lipid-rich salmonids (Wright et al. 2017). SRKW adult males who routinely forage in deeper areas where searching for large Chinook is more likely to pay off may have greater access to larger prey of higher caloric value than SRKW females who tend to forage in shallower areas to remain with dependent calves and tend to be more sensitive to nearby vessels (Holt et al. 2021b). Consequently, females may lead the group to areas where their sons may have the greatest opportunity to feed on deeper, higher-quality prey, at the cost of reduced foraging by other pod members in vessel-disturbed areas.

Differences in prey abundance and availability between populations could have contributed to the differences in foraging strategies we document here. However, we could not use existing indices of salmon abundance in our analyses because these metrics do not address spatiotemporal uncertainty in the distributions of Chinook salmon returning along one of two paths to the Fraser River. The nuances of migration paths taken are directly related to accurately estimating salmon availability for each population, yet data at this fine-scale spatiotemporal resolution are not currently available. We suggest that future research should elucidate the complex relationships between 1) environmental factors including location, prey distributions, and availability, 2) the behavioral context of the animal at the time of tagging, and 3) differential population-level impacts of anthropogenic pressures, including impacts from tagging and vessel presence, on foraging behavior (e.g., Holt et al. 2021a, 2021b). Furthermore, it is important to determine whether population differences in individual foraging behavior persist throughout space and time, and whether individual roles are flexible within populations.

This study revealed considerable differences in sex-based and demographic patterns of individual foraging strategies, demonstrating that these strategies are not fixed across two ecologically similar populations of a gregarious marine predator. The total number of prey capture dives and proportion of time capturing prey was female biased in the growing NRKW population, and male biased in the endangered SRKW population. The presence of a calf

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reduced female foraging activity across populations, but disproportionately so for SRKW females. Adult SRKW males with a living mother exhibited increased foraging behavior, possibly as a compensation strategy to offset their pod's caloric deficits and/or as an outcome of matriarch-led navigation to areas that promote greater prey capture by their adult sons. Interpopulation differences in individual roles within social groups may have arisen with the loss of key individuals as populations shrink, or may provide small, unbalanced populations experiencing environmental stressors the necessary flexibility to respond to novel and unpredictable environments caused by human-induced rapid environmental change. Indeed, interpopulation variation in individual roles may be an important evolutionary strategy for promoting resilience in the face of change.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

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CONFLICT OF INTEREST

We have no conflicts of interest to declare.

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Tennessen et al. (2022).

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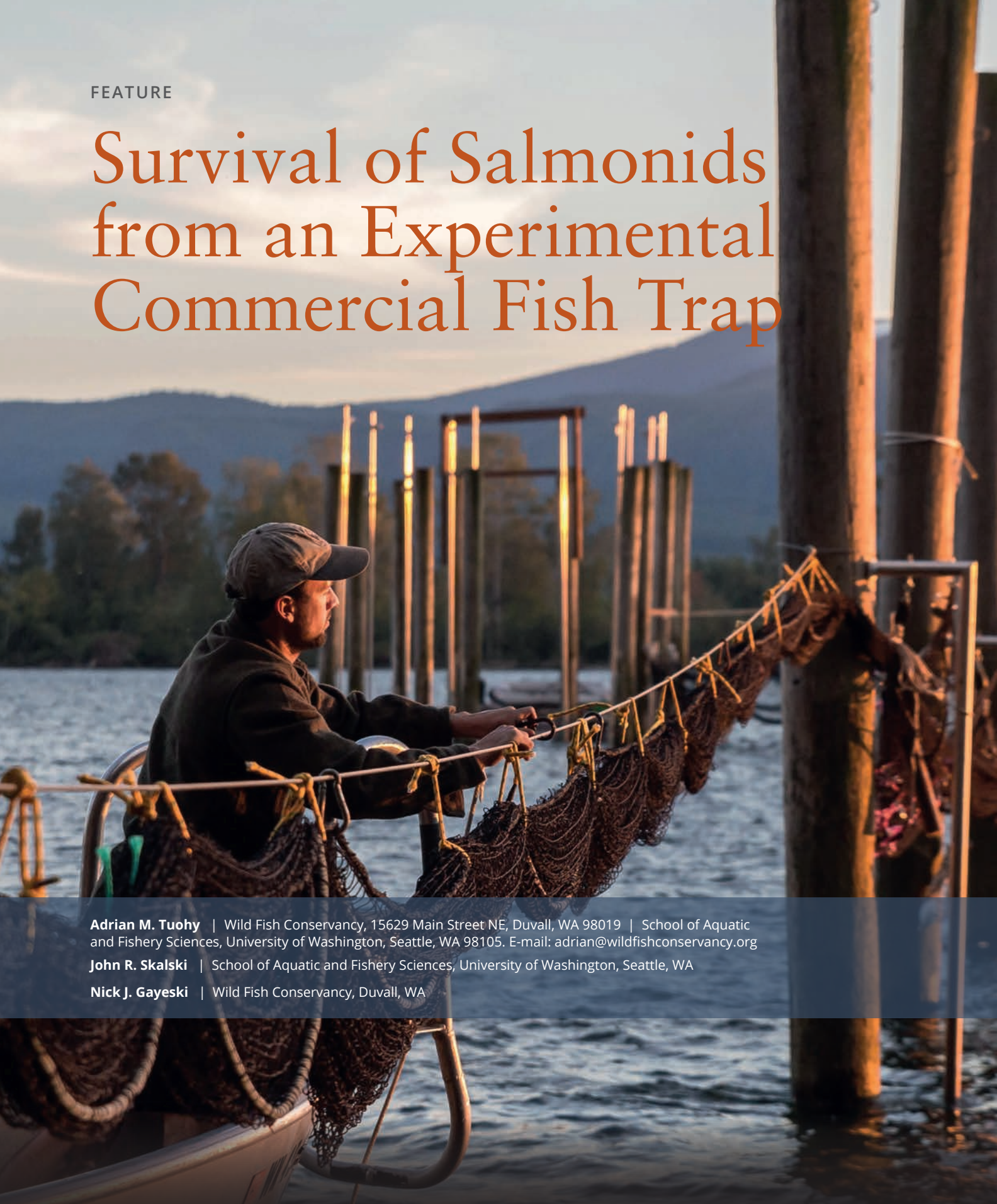
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FEATURE

Survival of Salmonids from an Experimental Commercial Fish Trap



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Conventional harvest techniques used in mixed-stock commercial salmon fisheries frequently result in bycatch mortality, thereby impeding salmonid recovery and constraining fishing opportunities in the U.S. Pacific Northwest. To address the problem, a postrelease survival study was conducted in the Columbia River to evaluate the potential of an experimental salmon trap for stock-selective commercial harvest. A modified fish trap was constructed and operated in 2017, from August through September, with the goal of minimizing entanglement, air exposure, crowding, and handling of all captured fishes. Postrelease survival from the trap was estimated through a paired release–recapture study. Results demonstrate that the trap effectively targeted commercially viable quantities of hatchery-origin Chinook Salmon *Oncorhynchus tshawytscha* and Coho Salmon *O. kisutch* while reducing bycatch mortality rates relative to conventional commercial fishing gears. During the study, 7,129 salmonids were captured. The postrelease survival effect over a 400-km migration ranged from 0.944 ($\overline{SE}$ = 0.046) for steelhead *O. mykiss* to 0.995 ($\overline{SE}$ = 0.078) for Chinook Salmon, supporting the potential application of traps for stock-selective commercial harvest.

INTRODUCTION

Since the late 1800s, wild salmonids of the U.S. Pacific Northwest have declined dramatically from the cumulative effects of harvest, habitat loss, dams, and hatchery production (Lichatowich 1999). Europeans extirpated various wild salmonid populations shortly after their arrival to the region, and many remaining salmonid population groups are now listed for protection under the U.S. Endangered Species Act (ESA; Nehlsen et al. 1991; Anderson 1993; Quinn 2005). Despite many efforts to recover wild salmonids, production hatchery programs continue throughout the region in order to enhance short-term harvest opportunities in commercial, recreational, and tribal fisheries (HSRG 2014; Gayeski et al. 2018a).

The effect of harvest on wild salmonids is frequently compounded by hatchery production (National Research Council 1996; Lichatowich et al. 2017). By enhancing fisheries through hatchery production, resource managers increase mixed-stock fishing effort and bycatch mortality to threatened wild stocks that co-mingle with hatchery stocks during ocean rearing and the spawning migration. State, tribal, and federal (both U.S. and Canadian) agencies manage harvest to maximize catch of hatchery-origin fish—attempting to address the genetic and ecological problems associated with escapement of hatchery fish (Naish et al. 2007; Chilcote et al. 2011; Lichatowich 2013), while minimizing mortality to wild stocks mixed within regional fisheries (Canada DFO 2005; WFWC 2009; ODFW 2013). However, bycatch mortality and mixed-stock harvest can impede recovery efforts of ESA-listed stocks in lacking fishing gears that can selectively harvest targeted stocks (such as hatchery-origin fish) while leaving non-targeted fish (such as wild fish) unharmed (Wright 1993; Flagg et al. 1995; Gayeski et al. 2018b). Although mortality rates differ between species and fisheries across the West Coast, Chinook Salmon *Oncorhynchus tshawytscha* bycatch mortality from conventional gill nets ranges from 51% to 57% in the lower Columbia River (Vander Haegen et al. 2004). Considering the severe impact of gill nets on captured stocks, resource managers often approve the harvest and sale of wild salmon that may be ESA listed (ODFW 2017b) Furthermore, conventional harvest practices can reduce the diversity, size, fecundity, and age structure of wild populations, thus diminishing their survival, reproductive success, and capacity for adaptation to global climate change (Ricker 1981; Hamon et al. 2000; Lewis et al. 2015).

Given the depressed status of wild Pacific Northwest salmonids and the inadequacy of conventional gears for selective harvest of hatchery-origin salmon, regional management agencies have drastically constrained commercial salmon fishing opportunities in order to foster salmonid recovery (Martin 2008; NWFSC 2015; ODFW 2017a, 2017b). Despite these efforts and many others, ESA-listed wild salmonid stocks have not recovered, and fishing opportunities have become increasingly limited (Lichatowich et al. 2017; Price et al. 2017; Gayeski et al. 2018a). Failure to achieve Pacific salmonid recovery and the continued mixed-stock harvest of salmon in marine settings have further altered ecosystem dynamics. The populations of southern resident killer whales *Orcinus orca* and other apex predators have declined to historic lows due to reductions in the quantity and size of marine prey (e.g., Chinook Salmon) and other factors (Ford et al. 2010; Ayres et al. 2012; Lewis et al. 2015; Lacy et al. 2017).

With hatchery production continuing throughout the region (Lichatowich et al. 2017), implementing stock-selective fishing gears has been recognized as necessary for recovering ESA-listed salmonids and sustaining the participation of fishing communities (ODFW 2013; WFWC 2013; HSRG 2014). Removal of the adipose fin from hatchery-origin fish enables visual differentiation between wild and hatchery stocks (HSRG 2014). To capitalize on advancements in stock identification, meet ESA recovery objectives, and maximize utilization of fisheries allocations, resource management agencies in Washington and Oregon were directed to develop and implement alternative fishing gear to maximize catch of hatchery-origin fish with minimal mortality to native salmonids (WFWC 2009, 2013; ODFW 2013). Although alternative gear and postrelease mortality research conducted through paired mark–release–recapture has demonstrated some limited success in the region (Vander Haegen et al. 2004; Ashbrook 2008; WDFW 2014), few viable alternative fishing practices to date have been identified and implemented to address the bycatch problem associated with the harvest of hatchery-origin salmonids (HSRG 2014; Gayeski et al. 2018a). Furthermore, removal of the adipose fin for hatchery-origin stocks in the USA remains imperfect, compromising the effectiveness of selective harvest efforts (HSRG 2014).

Recognizing the limitations of previously evaluated alternative commercial gears in reducing stock-specific bycatch mortality rates, fisheries scientists and managers alike have recommended fish traps as another potential alternative to gill nets (Ashbrook 2008; Tuohy 2018). Historically, the fish trap was one of the most popular and efficient gears used throughout the Pacific Northwest in salmon fisheries (Cobb 1930; Lichatowich 1999). However, response to wild salmon declines and political pressure from gillnetting communities caused bans in the gear across the North American West Coast from the 1920s through the 1950s (Higgs 1982; Lichatowich 1999).

Fish traps are a form of fixed gear, meaning that the tool remains deployed in one place to passively capture fishes (Cobb 1921). If sufficiently regulated and operated with a conservation-minded approach, fish traps have the potential to lessen sublethal physiological effects in fisheries by reducing air exposure, overcrowding, entanglement, and handling of

fish (Baker and Schindler 2009; Burnley et al. 2012; Raby et al. 2015). Furthermore, when used in fluvial settings, the fish trap allows for escapement of wild fish and does not deprive killer whales of the opportunity to secure the marine food resources required for their survival (Ford et al. 2010; Gayeski et al. 2018b).

The purpose of this study was to design, construct, and monitor the performance of a modified commercial fish trap in Washington State waters for the first time in over 80 years. Specifically, objectives were to estimate and compare immediate and postrelease bycatch mortality of wild fall Chinook Salmon and summer steelhead (anadromous Rainbow Trout *O. mykiss*) from an experimental fish trap relative to commercial gears that were previously evaluated in the lower Columbia River through paired mark–release–recapture (Vander Haegen et al. 2004; Ashbrook 2008; WDFW 2014). Given precise and unbiased estimates of catch composition and bycatch mortality for a fish trap, resource management agencies may evaluate the utility of using alternative commercial harvest gear for the recovery of wild salmonids and coastal fisheries in the U.S. Pacific Northwest.

METHODS

Trap Design and Study Location

Salmon traps or "pound nets" passively funnel returning adult salmonids along a lead positioned perpendicular to shore to a maze of walls and compartments (including the "heart" and "tunnel") for capture (Cobb 1921, 1930; Radke and Radke 2002). The final compartment, the "spiller," enables fish to swim freely within the trap until removal upon selective harvest or passive release (Cobb 1921; Tuohy 2018). In contrast to gillnetting, salmon that enter the spiller are captured without tangling of the teeth or opercula (Figure 1), thereby reducing physical injury and maximizing product quality (Baker and Schindler 2009; Tuohy 2018).

Based on historical trap designs, photographs, and anecdotes from the 1880s through the 1930s, untreated, 40.64-cm (16-in) diameter wood pilings were driven approximately 3–5 m apart in the Columbia River's Cathlamet Channel (Wahkiakum County, Washington) at river kilometer (rkm) 67, where salmon traps were once common prior Washington State's ban of fixed gear in 1934. This study site was a historically successful trapping location in the late-19th and early 20th centuries and was locally known for high abundances of salmon and steelhead. The experimental trap prototype consisted of a lead (~90 m), jigger (~10 m), heart (23-m length; 20-m maximum width), tunnel, and spiller (6 × 6 × 9 m), as well as a marine mammal deterrent gate at the entrance to the heart compartment (Figure 2). Black nylon mesh with a stretch of 7.94 cm was selected for application to the lead, jigger, and heart pilings (Christensen Net Works, Everson, Washington). The spiller and tunnel were constructed of 6.35-cm knotless-nylon mesh. Investigators selected these mesh sizes to minimize both the entanglement of fish and drag within the water column. All compartment nets were secured to the pilings from the bottom of the riverbed to about 1 m above the high-water mark, spanning approximately 8 m vertically. The marine mammal gate consisted of a series of vertical aluminum bars spaced at 25-cm increments to deter entry of mammals while enabling the passage of fish. The gate was hinged and could be opened or closed depending on the proximity of marine mammals to the study location.

The spiller/tunnel complex was engineered for deployment and retrieval to and from the river bottom with line and pulley. Steel weights at each corner of the compartment enabled gravity to draw the mesh flush to the river bottom during each soak period. A solar-powered electric winch was installed near the top of the pilings to pull the bottom mesh of the spiller upward through the water column to the shallows during each haul; this allowed captured fishes to be accessed swiftly from the depths of the river with minimal air exposure and stress. Adjacent to the spiller, a pontoon dock enabled sorting of the fish transferred from the spiller compartment within the confines of a perforated-aluminum framed live well (2.13 × 0.61 m). Within this compartment (holding capacity of ~40 adult salmonids), all fish remained free-swimming and submerged with continuously circulating river water. With the completion of a set, a small door to the live well was opened, allowing all captured fish to swim upstream with minimal handling.

Field Protocol

The study was conducted at the experimental trap site from August 26 through September 27, 2017. This late-summer to



Figure 1. Trap operators corralled fish in the shallows from the spiller to a live well with line, pulley, and a solar-powered winch. All captured fish could then be sorted for data collection and PIT tagging.



Figure 2. The experimental fish trap in the Columbia River (river kilometer 67) consisted of a lead, jigger, heart, tunnel, and spiller.

early fall period represented the peak of fall Chinook Salmon, Coho Salmon *O. kisutch*, and steelhead upriver migration in the lower Columbia River (Healey 1991). Hatchery-origin Chinook Salmon and Coho Salmon are commercially lucrative target stocks within the lower Columbia River fall fishery. Wild-origin summer steelhead, fall Chinook Salmon, and Coho Salmon populations are ESA listed and constitute common bycatch stocks that can constrain commercial fishing opportunities within the conventional fall fishery.

At the beginning of each fishing event, trap operators deployed the spiller to the river bottom and opened the tunnel door, initiating the soak period and enabling the capture of fishes. Investigators noted the beginning set time, tidal stage (m), tide height (m), water temperature (°C; Extech), and presence of marine mammals. The tunnel door remained open to fish passage until the capacity of the live well was visually determined to have been reached (minimizing potential physiological effects of overcrowding). During trap operation, the marine mammal deterrent gate was periodically closed to prevent entry of harbor seals *Phoca vitulina* and California sea lions *Zalophus californianus* to the heart and spiller compartments.

Once the soak period had ended (generally 3–60 min), the tunnel door was closed, preventing further fish entry or escape. Operators then lifted the spiller bottom using an electric winch to guide fish upward in the water column, concentrating captured fish in the shallows toward the spiller door (positioned adjacent to the live well of the sorting deck). Once the fish were guided into the live well, study investigators enumerated, measured (FL), and identified all specimens by species and origin (adipose fin clipped or unclipped, suggesting hatchery or wild origin, respectively). All adult Chinook Salmon and steelhead (except for those that escaped the handling and tagging process) were scanned for PIT tags with a Biomark 601 reader (Biomark, Boise, Idaho). If existing PIT tags were detected, codes were recorded directly into a computer database using P4 software (PTAGIS 2017); these fish were then passively released from the live-well chamber. In the absence of an existing PIT tag, adult Chinook Salmon (>57 cm) and steelhead were tagged in the peritoneal cavity with a 12.5-mm, 134.2-kHz, full-duplex PIT tag using an MK-25 Rapid Implant Gun (Biomark); each fish was scanned, and its tag number was recorded. In addition, 99.3% of PIT-tagged Chinook Salmon and steelhead also received a non-lethal 2-mm caudal fin clip for genetic analysis. Unique genetic sample numbers were recorded simultaneously with the PIT tag code of the tagged fish by utilizing P4 software. The PIT-tagged fish were placed into a recovery chamber of the live well with continuously recirculating river water (Farrell et al. 2001), after which they were passively released through the live-well door, and additional sets were performed. Due to the potential for upstream harvest and human consumption, fish were not anesthetized during the handling process.

Paired Release–Recapture Study

A paired mark–release–recapture methodology was used to estimate relative postrelease survival of fall Chinook Salmon and steelhead from the experimental trap to upstream detection points at main-stem dams (Cormack 1964). Although many Coho Salmon were encountered at the trap, mark–release–recapture was not performed due to the tendency of this species to spawn below upstream detection points. Mirroring prior alternative gear studies in the lower Columbia River, control and treatment groups of Chinook Salmon and steelhead were sourced at the study location, PIT-tagged, and released. The treatment group experienced commercial capture procedures that may impact survival after release. The control group did not undergo commercial capture procedures, and the fish were sourced one at a time with a rubberized dip net. As in all prior Columbia River alternative gear studies, hatchery- and wild-origin fish of each species were pooled to increase statistical power (assuming that rearing origin has no effect on adult in-river survival).

During each test-fishing day, control and treatment tagging sessions were generally assigned alternately. We employed these methods to reduce potential for violation of the following model assumptions: (1) the fate of each fish is independent; (2) control and treatment fish have equivalent handling and tagging survival; (3) control and treatment fish have equivalent stock composition, marine mammal predation, harvest pressures, environmental stressors, and tag loss; (4) all treatment fish have equal survival and recovery probabilities; (5) all control fish have equal survival and recovery probabilities; and (6) survival of handling/tagging effects is independent of in-river upstream survival. It must be noted, however, that there was some limitation to alternating control and treatment group tagging events due to water clarity, which affected the ability of field staff to randomly handle the catch. This increased the potential for unequal stock composition and recovery probability between control and treatment groups.

The treatment group consisted of individuals that were lifted en masse (mean = 19 adult salmonids) by the winch and spilled from the pound-net spiller to the live well. This process of capture mirrored how the gear would be operated in a commercial setting given the current status of fish trap engineering. After PIT-tagging and fin-clipping procedures were complete, fish were released from the live-well recovery chamber for upstream detection at PIT tag arrays (WDFW 2014).

A control group of Chinook Salmon and steelhead was passively captured at the project site, tagged, and released for detection upstream. Unlike the treatment fish (which experienced commercial capture procedures and made physical contact with the spiller mesh), the control fish were guided through the water on an individual basis with a rubberized dip net at the trap site to be handled in a live well for tagging, genetic sampling, and release.

Tag detection information from upstream arrays was accessed through the PIT Tag Information System (PTAGIS), which provides public access to the PIT tag data (PTAGIS 2017). Tag information was attained through upstream interrogations at dam and hatchery arrays. Main-stem dam array stations in the Columbia River basin are known to have detection rates over 99% (WDFW 2014).

Survival Analysis

A pair of Cormack (1964) single release–recapture models (a special case of the Cormack–Jolly–Seber model; Cormack 1964; Jolly 1965; Seber 1965) was used to estimate postrelease survival of treatment Chinook Salmon and summer steelhead relative to controls (τ) between the capture and release site (rkm 67) and upstream detection sites at Bonneville Dam (rkm 234), The Dalles Dam (rkm 309), and McNary Dam (rkm 470) on the Columbia River main stem

(Figure 3). The joint probability of survival and detection was also estimated for pooled detection sites above McNary Dam (Figure 3). The joint-tagging model helped to separate the effects of survival from detection and to adjust for the control effects of handling and tagging (Cormack 1964; Jolly 1965; Seber 1965). Analogous to prior Columbia River alternative gear survival studies that used the Ricker relative recovery method (Ricker 1958; Ashbrook 2008; WDFW 2014), immediate survival (τ_0) from capture to release from the gear, short-term survival (τ_1) from release to Bonneville Dam, long-term survival from Bonneville Dam to McNary Dam (τ_2 and τ_3), and cumulative survival ($\tau_0 \times \tau_1 \times \tau_2 \times \tau_3$) from initial capture at the trap site to McNary Dam were estimated (Figure 3). However, use of the Cormack (1964) release–recapture model for this study enabled estimation and correction for possible differences in treatment-specific detection probabilities (Cormack 1964; Jolly 1965; Seber 1965). Furthermore, it must be noted that the capture/release site used for this pound trap study differed from that used in previous postrelease survival studies. The tag-and-release locations for purse-seine, beach-seine, and tangle-net studies were between rkm 209 and 233 of the Columbia River (Ashbrook 2008; WDFW 2014). Our experimental trap was located at rkm 67. The consequence is that survival in this study is measured over a greater distance and duration and hence might be expected to be lower than that in past studies.

A Cormack (1964) single release–recapture model was used to describe the observed detection histories of the tagged fish at four upstream detection sites (i.e., Bonneville, The Dalles, and McNary dams and detection sites above McNary Dam). With four upstream detection sites, there were $2^4 = 16$ possible unique detection histories that could be observed for each of the control and treatment groups. The joint likelihood for the tagging study was expressed as a product of two multinomial distributions: the first describing the probability of seeing the control capture histories, and the second describing the probability of the treatment histories:

$$L(S_i,\tau_i,\vec{p}_{ci},\vec{p}_{ti},\lambda|R_c,\vec{m}_{ci},R_t,\vec{m}_{ti}) = \left(\frac{R_c}{\vec{m}_{ci}}\right)\prod_{i=1}^{16} P_{ci}^{m_{ci}} \cdot \left(\frac{R_t}{\vec{p}_{ti}}\right)\prod_{i=1}^{16} P_{ti}^{m_{ti}} \quad (1)$$

where, R_c = number of control group fish that were tagged and released, m_{ci} = number of control group fish with detection history i ($i = 1, \ldots, 16$), P_{ci} = probability of capture history i for the control group, R_t = number of treatment group fish that were tagged and released, m_{ti} = number of treatment group fish with detection history i ($i = 1, \ldots, 16$), and P_{ti} = probability of capture history i for the treatment group.

The probabilities for the various detection histories were in turn expressed as functions of reach survival, site-specific detection probabilities, and reach-specific treatment effects, where, S_i = survival probability in reach i for control group fish ($i = 1, \ldots, 3$), p_{ci} = probability of detection at location i for control group fish ($i = 1, \ldots, 3$), p_{ti} = probability of detection at location i for treatment group fish ($i = 1, \ldots, 3$), τ_i = treatment effect on survival in reach i ($i = 1, \ldots, 4$), and λ = joint probability of survival and detection in the last reach between McNary Dam and all upstream PIT tag sites for control group fish (e.g., $\lambda = S_4 \times p_4$).

For instance, the probability of a control fish being detected at all four upstream locations was modeled as

$$p_{c[1111]} = S_1 p_{c1} S_2 p_{c2} S_3 p_{c3} \lambda,$$

while a treatment fish with the same detection history had the probability of occurrence

$$p_{t[1111]} = (S_1\tau_1)p_{t1}(S_2\tau_2)p_{t2}(S_3\tau_3)p_{t3}(\lambda\tau_4).$$

Other detection histories were modeled analogously. As specified, the τ_i estimate is the survival of the treatment fish relative to the control fish (i.e., $\tau = S_{treat}/S_{control}$) on a reach-specific basis. Using this model formulation, the relative survival effects and their SEs were directly estimated by maximum likelihood estimation.

Unique detection histories at upstream dams were downloaded from PTAGIS. Previously PIT-tagged fish that were captured at the trap (tagged as juveniles or previously tagged at the trap site; $N = 13$) were excluded from the analysis due to the potential difference in handling survival relative to fish that had undergone the standard tagging procedure. Tag data were processed through the R platform and uploaded to Program USER (Skalski and Millspaugh 2006; http://www.cbr.washington.edu/analysis/apps/user) to estimate parameters of the joint likelihood model (Equation 1), including the treatment effects on postrelease survival, SEs, and the 95% profile likelihood confidence intervals (CIs). Program USER provides a convenient means of constructing multinomial and product multinomial likelihoods and numerically solving for maximum likelihood estimates and associated SEs. The most parsimonious model for parameter estimation was selected through a likelihood ratio test (LRT; Kendall and Stuart 1977). The LRT was used to test for homogeneous detection probabilities for control and treatment group fish (i.e., $p_{ci} = p_{ti}$, $\forall_i$) at $\alpha = 0.05$ (two-tailed).

Genetic Analysis

To ensure that there was equivalent stock composition between treatment and control groups (random assignment), the Conservation Genetics Lab (University of Montana) and the Eagle Fish Genetics Lab (Idaho Department of Fish and Game) analyzed 507 randomly selected Chinook Salmon genetic samples (241 control; 266 treatment) with Columbia River basin-specific single-nucleotide polymorphism markers. Chinook Salmon were selected for genetic analysis due to this species' propensity to return to tributaries below main-stem arrays in the study region (in contrast with steelhead, which were primarily destined for hatcheries and spawning grounds above McNary Dam). Since approximately 20% of Columbia River basin fall Chinook Salmon were forecasted to return to spawning grounds and hatcheries of major tributaries below Bonneville Dam (including the Willamette, Cowlitz, Lewis, and Kalama rivers; ODFW 2017a), genetic tests were used to assign individuals to natal populations either below or above Bonneville Dam with a 90% probability threshold (Piry et al. 2004; Miller et al. 2018). Given that Chinook Salmon and steelhead were randomly sampled and assigned to groups in identical fashion, Chinook Salmon genetic analyses were assumed to be sufficient for determining overall random assignment to treatment and control groups for both Chinook Salmon and steelhead.

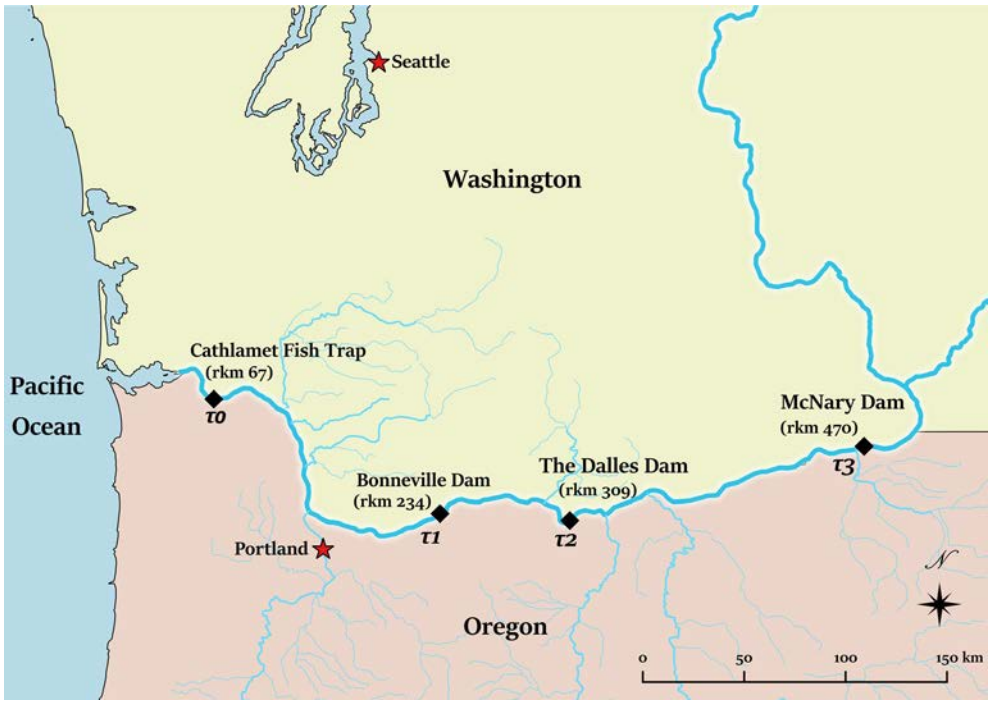


Figure 3. The effect on postrelease survival (τ_i) was estimated between the capture and release site at the experimental fish trap (river kilometer [rkm] 67) and the PIT tag arrays at upstream detection points: Bonneville Dam (rkm 234), The Dalles Dam (rkm 309), and McNary Dam (rkm 470). The last detection field consisted of all adult PIT tag detectors above McNary Dam.

Generalized linear modeling (GLM) based on a log-link and Poisson error structure was used in R (R Development Core Team 2008) to test the null hypothesis of homogeneity of Chinook Salmon population assignment to control and treatment groups at the $\alpha \leq 0.05$ significance level. This GLM test of homogeneity was used to evaluate the assumptions of random arrangement of fish to control and treatment groups. However, genetic population assignment in the Columbia River basin remains coarse due to the homogenizing effects from hatchery genetic introgression, limiting finer-scale genetic assignment and evaluation of stock composition equivalence (Myers et al. 2006; Hess et al. 2014).

RESULTS

Total Catch

Study investigators fished the experimental trap for 290.5 h over 33 d between August 26 and September 27, 2017. Water temperatures were consistently greater than 18°C within the Columbia River main stem and episodically reached 22°C (Columbia Basin Research 2018). During the study period, 381 sets were performed, with a median soak length of 36 min (mean = 46 min; SD = 36). A median of 13 combined jack and adult salmonids were spilled to the live well per set (mean = 19 salmonids; SD = 20).

In total, 7,129 salmonids were captured. Total catch comprised 49.1% Coho Salmon (3,501 total; 52.4% were adipose fin-clipped; 16.4% were jacks [<55 cm]), 37.4% Chinook Salmon (2,670 total; 47.9% were adipose fin-clipped; 16.3% were jacks [<57 cm]), 12.9% summer steelhead (921 total; 80.9% were adipose fin-clipped), 0.4% resident/residualized (<30 cm) Rainbow Trout (29 total; 77.8% were adipose fin-clipped), and 0.1% unidentified salmonids *Oncorhynchus* spp. (8 total fish). In addition to salmonid catch, we captured and released three American Shad *Alosa sapidissima*, one Largemouth Bass *Micropterus salmoides*, one Common Carp *Cyprinus carpio*, and one Peamouth *Mylocheilus caurinus*. The marine mammal deterrent gate was deployed 81 times over the course of 381 sets, with marine mammal entry to the heart occurring on 11 occasions (primarily due to operator error).

Survival of Chinook Salmon

Throughout the duration of the study, a total of 2,066 Chinook Salmon were PIT-tagged (976 control; 1,090 treatment), with only one adult suffering immediate mortality ($\hat{\tau}_0 = 0.9995$). The LRT found no significant difference in PIT tag array detection probabilities for control and treatment groups ($\chi^2_3 \geq 0.364$, $P = 0.948$), resulting in a reduced model with common detection probability (i.e., $p_{ci} = p_{ti}$; $i = 1, \ldots, 3$). Postrelease survival for the treatment group compared to the control group was high from release to Bonneville Dam (~150 km upstream; median travel duration = 6 d) at a $\hat{\tau}_1$ of 0.970 ($\widehat{SE} = 0.036$; Table 1). The treatment group survived at a higher rate than the control group between Bonneville Dam and The Dalles Dam, with the estimate of relative survival increasing in this reach to a $\hat{\tau}_2$ value of 1.060 ($\widehat{SE} = 0.051$). Relative release survival from The Dalles Dam to McNary Dam declined slightly but remained high at a $\hat{\tau}_3$ of 0.968 ($\widehat{SE} = 0.049$). Cumulative relative survival for the treatment group from capture at the trap site to McNary Dam (~400 km upstream; median travel duration = 13 d) was estimated to be 0.995 ($\widehat{SE} = 0.078$). The GLM/log-linear analysis of the genetic sample results indicated homogeneous population assignment to control and treatment groups ($\chi^2_1 \geq 0.000$, $P = 1.000$), suggesting equivalence in stock composition (Table 2).

Table 1. Relative treatment effects (i.e., relative survival $\tau = S_{treat}/S_{control}$) on postrelease survival by river reach for adult fall Chinook Salmon and steelhead, cumulative survival from the fish trap to McNary Dam (≈400 km), and associated 95% profile likelihood confidence intervals (CIs) are displayed.

	Chinook Salmon		Steelhead	
River reach	τ	95% CI	τ	95% CI
Immediate survival (τ_0)	0.9995	0.998–1.000	1.000	0.995–1.000
Trap to Bonneville Dam (τ_1)	0.9700	0.901–1.044	0.977	0.911–1.048
Bonneville Dam to The Dalles Dam (τ_2)	1.0600	0.965–1.166	0.983	0.935–1.032
The Dalles Dam to McNary Dam (τ_3)	0.9680	0.877–1.070	0.983	0.939–1.028
Cumulative ($\tau_0 \times \tau_1 \times \tau_2 \times \tau_3$)	0.9950	0.924–1.071	0.944	0.880–1.012

Table 2. A contingency table constructed based upon results of the generalized linear modeling/log-linear analysis for control and treatment group Chinook Salmon that were genetically assigned to a Columbia River basin population group (below or above Bonneville Dam). The observed frequency in each cell is shown, along with the frequency that would be expected (in parentheses) if there is no association between control and treatment group and the population group assignment.

Group	Control	Treatment	Frequency
Populations below Bonneville Dam	47 (46.91)	52 (52.09)	99
Populations above Bonneville Dam	188 (188.10)	209 (208.91)	397
Frequency	235	261	496

Survival of Steelhead

Overall, 782 steelhead were PIT-tagged over the course of the study (379 control; 403 treatment), with zero adult immediate mortalities ($\hat{\tau}_0 = 1.000$). For summer steelhead, the LRT found no significant difference in PIT tag array detection probabilities for control and treatment groups ($\chi^2_3 \geq 6.874$, $P = 0.076$), resulting in selection of the reduced model with common detection probability. Postrelease relative survival for the treatment group compared to the control group was high from release to Bonneville Dam (~150 km upstream; median travel duration = 6 d) at a $\hat{\tau}_1$ value of 0.977 ($\widehat{SE} = 0.035$; Table 1). Release survival remained high in subsequent reaches from Bonneville Dam to The Dalles Dam ($\hat{\tau}_2 = 0.983$; $\widehat{SE} = 0.024$) and from The Dalles Dam to McNary Dam ($\hat{\tau}_3 = 0.983$, $\widehat{SE} = 0.022$; Table 1). Cumulative relative survival of the treatment group for adult steelhead from capture at the trap site to McNary Dam (~400 km upstream; median travel duration = 18 d) was 0.944 ($\widehat{SE} = 0.046$).

DISCUSSION

This study represents the first successful attempt to design, construct, and operate a commercial pound-net trap for the capture of salmon in Washington State waters in over 80 years. Furthermore, it is the first-ever evaluation of salmonid postrelease survival from a commercial-scale salmon trap. Results demonstrate the feasibility of the gear for stock-selective harvest, offering a possible solution to hatchery and bycatch problems within salmon fisheries of the U.S. Pacific Northwest. Based on the capture of 7,129 salmonids with the prototype design, it is evident that the traps can effectively capture fish for commercial harvest purposes. Furthermore, when operated with a conservation-minded approach, operators of the gear can successfully release the great majority of non-target salmonids unharmed (Table 3). Depending on the conservation issues present within a fishery, the fish trap is yet another tool with which to address bycatch, hatchery management, and recovery of ESA-listed stocks while enabling continuation of commercial fishing.

Table 3. Relative survival estimates from the experimental trap presented in comparison with lower Columbia River cumulative survival estimates and associated 95% confidence intervals (if available; in parentheses) from prior studies.

Gear	Chinook Salmon survival	Steelhead survival
Fish trap	0.995 (0.924–1.071)	0.944 (0.880–1.012)
Gill net (20.320–22.225 cm [8.00–8.75 in])	0.520[a]	0.552[b]
Tangle net (9.525 cm [3.75 in])	0.764[c]	0.764[d]
Beach seine	0.750 (0.710–0.790)[e]	0.920 (0.820–1.000)[e]
Purse seine	0.780 (0.720–0.850)[e]	0.980 (0.930–1.000)[e]

[a]IFSP 2014.
[b]TAC 2008.
[c]TAC 2018.
[d]WDFW and ODFW 2018.
[e]WDFW 2014.

Bycatch Survival

Cumulative relative survival of Chinook Salmon released from the experimental trap represents a statistically significant ($P < 0.05$) and dramatic improvement over survival estimates produced from previous studies of alternative and conventional gears (Table 1). Analyzing the treatment effect on cumulative survival over a 400-km upriver migration and a median duration of 13 d for Chinook Salmon, the experimental trap outperformed all other gears used on the lower Columbia River, with cumulative relative survival estimated at 0.995 (95% CI = 0.924–1.071). This result was achieved with tagging operations occurring approximately 150 km farther downstream than prior bycatch mortality studies. Furthermore, capture procedures for the control group were likely less stressful than procedures used in previous Columbia River studies, during which fish were trapped at the Bonneville Dam adult fish passage facility, dipnetted, handled, PIT-tagged, and trucked downstream to the upstream end of the test fishing location at rkm 225 (Ashbrook 2008; WDFW 2014). Despite promising results from this study, further research should be conducted with the fish trap and other alternative gears to better understand the potential latent mortality effects of commercial fishing on salmonids destined for long-range upriver migration to spawning grounds (Baker and Schindler 2009; Bass et al. 2018). These investigations will require larger sample sizes to precisely estimate survival to spawning grounds or river reaches above McNary Dam in the Columbia River basin (Tuohy 2018).

For summer steelhead, cumulative relative survival from the experimental trap over a 400-km upriver migration and median travel duration of 18 d was 0.944 (95% CI = 0.880–1.012). This point estimate is a significant improvement over that of the gill net (Table 1) but is not significantly different than point estimates for the seine from prior Columbia River survival studies. These results suggest the need for further research to better determine which gear yields greater steelhead postrelease survival. It must be noted, however, that this analysis occurred over a far greater migration distance and longer postrelease duration than previous alternative gear analyses.

Catch Effectiveness

For commercial implementation of any alternative gear type, a fishing tool must not only demonstrate potential to achieve conservation objectives but also meet the economic needs of fishers and industry. Given the historical effectiveness and popularity of commercial fish traps throughout the U.S. Pacific Northwest (Cobb 1930; Lichatowich 1999), there is little reason to believe that modern trap designs (when well placed) would be less effective than conventional gears used within Pacific Northwest salmon fisheries. Although the design of this alternative gear study provided no means to precisely and accurately compare capture efficiency of trap operations to that of the conventional gill-net fishery, the performance of the experimental trap prototype suggests that the gear can once again be engineered to effectively capture salmon. Furthermore, coarse comparison with limited available evidence suggests that the trap captured at least a comparable quantity of combined hatchery-origin Chinook Salmon and Coho Salmon per hour relative to the average Columbia River gill-net vessel's combined harvest of both hatchery- and wild-origin fish of those species during overlapping periods of operation (ODFW 2017b; Tuohy 2018). Nevertheless, there is a need for further research under real-world commercial fishing conditions to evaluate and compare CPUE and assess the economic feasibility of the technology (e.g., total cost, revenue, and profit). The upfront costs of a trap are presently high and must prove surmountable and recoupable to fishers or cooperatives in order to produce anticipated long-term economic benefits (Tuohy 2018).

Potential Benefits

Retooling of commercial gillnetting fleets to lower-impact alternative gear types such as fish traps could provide substantial benefit to the Pacific Northwest salmon fishing industry (Gayeski et al. 2018b). Presently, commercial gillnetting opportunity is constrained from the onset of the fishing season; this is due in part to high bycatch mortality rates and ESA conservation and management concerns (Vander Haegen et al. 2004; Martin 2008). Considering gill-net impacts to ESA-listed stocks, harvest and allocation negotiations frequently result in limited fishing for the commercial fleet. For example, in fall 2017, the lower Columbia River commercial gillnetting fleet was authorized to fish on only seven occasions as a precautionary measure to protect low returns of ESA-listed steelhead (ODFW 2017b). In utilizing stock-selective harvest tools with low bycatch impacts to wild fish, commercial fishers would likely see greater allocations of the resource, lengthening the season and increasing profitability. Furthermore, commercial fishing fleets would be less prone to in-season closure from exceeding ESA take limits.

While enabling fishers to fish longer and more consistently, use of viable stock-selective harvest tools with substantially reduced bycatch impacts could enable more Pacific salmon fisheries to become certified sustainable in the marketplace, returning a greater price per unit weight (Gayeski et al. 2018b). Sustainable market certifiers brand seafood products in the marketplace that meet specific sustainability criteria. This branding can result in product differentiation to consumers and increased prices received by fishers and processors (Cooper 2004; Kaiser and Edwards-Jones 2006; Gayeski et al. 2018b). Concurrently, value-added practices (including bleeding and icing the fish on site, and direct marketing of a higher-quality live-captured product to restaurants and other buyers) could help retooled fisheries increase profitability (Johnson 2018). Transitioning to alternative gears and utilizing value-added practices in certified-sustainable fisheries could improve economic prospects within the industry, increasing fishing opportunity and the prices received for harvested products (Gayeski et al. 2018b).

For threatened and endangered wild salmonids in the Pacific Northwest, reduction of hatchery and bycatch impacts could prove essential to their survival and recovery (Lichatowich et al. 2017). The percentage of hatchery-origin spawners continues to exceed hatchery management targets, with many spawning populations in the region experiencing percentages of hatchery-origin spawners greater than 50% (reducing the fitness and survival of subsequent generations; Chilcote et al. 2011; HSRG 2014; WDFW 2018). Release mortality from gill nets remains significant, prompting management to allow harvest of both hatchery- and wild-origin salmon stocks indiscriminately in many Pacific Northwest fisheries (Buchanan et al. 2002; IFSP 2014; Teffer et al. 2017). Considering these impacts and the accelerating effects of global climate change, the need for selective harvest is urgent to improve targeting of hatchery-origin fish and escapement of wild salmonids (Lichatowich et al. 2017; Gayeski et al. 2018a).

Although transition from the ongoing fisheries management paradigm of production hatcheries and conventional harvest will prove challenging, change may be necessary to prevent further wild salmonid declines, degradation of genetic and life history diversity, and curtailment of fishing opportunities (Schindler et al. 2010; Lichatowich et al. 2017; Gayeski et al. 2018a). Partial solutions are at hand (e.g., stock-selective commercial harvest tools) to help remedy harvest and hatchery problems in the region. Despite the short-term discomfort that may be caused by changes in harvest strategy, long-term benefits from a well-orchestrated policy and management shift toward the use of stock-selective gears such as fish traps could improve the economic outcome for fishers and fisheries of the Pacific Northwest (Gayeski et al. 2018a). Use of traps could also reduce the challenges associated with commercial fisheries observation and enforcement and provide a means for low-impact ecological monitoring. Although further research is needed in other locations, seasons, and years, it is possible that the return to a historical fishery in the Pacific Northwest could prove to be a win–win situation for fishers, ESA-listed salmonid stocks, management, and the environment.

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DATA SHARING

All data for this study (including the results of genetic analyses) may be downloaded free of charge through the Wild Fish Conservancy webpage (www.wildfishconservancy.org) by clicking on the "Projects" and "Columbia River Pound Net Project" tabs. All PIT tag information can be accessed through the PTAGIS webpage (www.ptagis.com) utilizing the code "CPN" and name "Cathlamet Pound Net."

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ARTICLE

Modified Commercial Fish Trap to Help Eliminate Salmonid Bycatch Mortality

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Abstract

The utility of commercial salmonid *Oncorhynchus* spp. traps in the U.S. Pacific Northwest was recently revisited for the first time in decades to enable selective harvesting of hatchery-origin salmonids while reducing mortality of Endangered Species Act (ESA)-listed salmonids. Modifications to historical gear designs resulted in dramatic improvements in salmonid bycatch survival rates relative to conventional commercial gears in the lower Columbia River. Expanding upon this work, an experimental commercial fish trap was further modified to largely eliminate net contact, air exposure, handling, and crowding of fish. Studies were conducted from May to November 2019 in the lower Columbia River to estimate survival of bycatch and evaluate potential benefits from the modified passive capture design. Analyzed through two separate survival estimation techniques, the modified trap demonstrated no detectable effect on salmon release survival and a significant improvement over the previous prototype design. Estimated through a paired release–recapture methodology, the relative survival effect of catch and release compared to controls over a 400-km migration was 1.017 (SE = 0.032) for adult Sockeye Salmon *O. nerka*. For adult Coho Salmon *O. kisutch* that were held captive for a 48-h postrelease period, estimated survival (*S*) was 1.000 (lower 95% confidence limit: $S \geq 0.978$). These results suggest that trap modifications can be made to significantly reduce bycatch mortality of ESA-listed salmonids and provide increased opportunity for harvest of hatchery-origin salmonids.

Many wild salmonid *Oncorhynchus* spp. evolutionarily significant units in the Columbia River basin of the U.S. Pacific Northwest are currently listed as threatened or endangered under the Endangered Species Act (ESA) and remain in decline as a result of harvest impacts, habitat loss, hatcheries, and climate change (Nehlsen et al. 1991; Lichatowich 1999; NWFSC 2015; Crozier 2016). This includes 13 evolutionarily significant units of wild-origin steelhead *O. mykiss* (anadromous Rainbow Trout), Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Chum Salmon *O. keta*, and Sockeye Salmon *O. nerka* (NWFSC 2015). Hatchery production of salmonids is used

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for mitigation purposes in the region, theoretically increasing short-term commercial, recreational, and tribal harvest opportunities (Utter and Epifanio 2002; Naish et al. 2007). Nevertheless, the practice often threatens ESA-listed wild salmonid populations both genetically and ecologically (Chilcote et al. 2011; Naman and Sharpe 2012; Christie et al. 2014). Furthermore, hatchery production encourages increased fishing effort with gears that cannot effectively release wild salmonid bycatch unharmed (NRC 1996; WDFW 1997; Hilborn and Eggers 2000; Naish et al. 2007). In the lower Columbia River fishery, gill nets cause approximately 43–49% mortality of ESA-listed salmonids that are captured and released (Vander Haegen et al. 2004; TAC 2008). This conventional fisheries management paradigm of hatchery production, coupled with bycatch from fisheries, has impacted the recovery of wild salmonid populations (WDFW 1997; Lichatowich et al. 2017; Gayeski et al. 2018b). Consequently, many commercial, recreational, and tribal fisheries of the Columbia River (and elsewhere in the U.S. Pacific Northwest) are increasingly constrained by ESA management concerns (Martin 2008; ODFW and WDFW 2019).

Recognizing the need for harvest and hatchery reforms to promote salmonid recovery in the Columbia River basin, fisheries managers directed the Washington Department of Fish and Wildlife and the Oregon Department of Fish and Wildlife to develop and implement alternative commercial gear to enable in-river selective harvest of hatchery-origin salmon and reduce bycatch impacts to ESA-listed wild salmonids (WFWC 2009, 2013; ODFW 2013). Alternatives to the conventional gill net—including beach seines, modified purse seines, and tangle nets—were tested between 2001 and 2016 in the lower Columbia River (Vander Haegen et al. 2004; Ashbrook 2008; WDFW 2014, 2016; Takata and Johnson 2018). Limitations to the effectiveness of these gears subsequently inspired calls for evaluation of fish traps to further improve bycatch survival relative to in-river gill nets through reduction of entanglement, air exposure, handling, and crowding of captured fish (Tuohy et al. 2019).

The fish trap was a historically effective gear, popular in both indigenous and commercial salmon fisheries of the U.S. Pacific Northwest (Cobb 1930; Lichatowich 1999). The fishing method was banned in Washington State in 1934 and Oregon in 1948 due to the perceived contribution of the gear to salmon decline in these mostly unregulated fisheries (Washington State Session Laws 1935; Johnson et al. 1948; Higgs 1982). Contrary to the specified intent of the ban, resource managers failed to reduce total fishing effort or to meet biologically acceptable escapement goals after 1934 (Johnson et al. 1948; Boxberger 1989; Lichatowich 2013). Shortly after the elimination of fish traps and other fixed gears, Columbia River and Puget Sound salmon fisheries collapsed (Lichatowich 1999).

In 2016, the Wild Fish Conservancy (a nonprofit organization) and a local commercial fisher constructed the first operational pile trap in over 80 years in the Columbia River's Cathlamet Channel (Wahkiakum County, Washington; river kilometer [rkm] 67 [rkm 0 = mouth of the Columbia River]; Tuohy 2018; Tuohy et al. 2019). The experimental trap was modeled after designs historically used in the lower Columbia River but was modified to minimize physical and physiological damage to salmonid bycatch. Postrelease survival from the trap was estimated through a paired release–recapture study in 2017. Results demonstrated that the trap effectively captured hatchery-origin Chinook Salmon and Coho Salmon while improving salmonid bycatch survival rates relative to conventional gill nets. Relative survival of trapped fish compared to controls over a 400-km migration was estimated at 0.944 ($\widehat{SE}$ = 0.046) for steelhead and 0.995 ($\widehat{SE}$ = 0.078) for Chinook Salmon (Tuohy et al. 2019).

Although the prototype trap design dramatically improved upon bycatch survival rates of gill nets and other previously evaluated gears (Tuohy et al. 2019), some salmonid populations remain so heavily depleted within the U.S. Pacific Northwest that commercial gears encountering these fish must achieve nearly 100% survival of salmonid bycatch for fishers to operate effectively within ESA impact constraints. The purpose of this study was to fill existing data gaps for Sockeye Salmon and Coho Salmon and further modify the 2017 prototype fish trap design to nearly eliminate salmonid bycatch mortality. Specifically, our objectives were to estimate and compare immediate and postrelease bycatch mortality rates of wild Sockeye Salmon and Coho Salmon from the modified fish trap design relative to results from the prototype trap and other previously tested commercial gears through paired release–recapture and a net-pen holding methodology (Vander Haegen et al. 2004; WDFW 2014; Takata and Johnson 2018; Tuohy et al. 2019). This information may be used by resource management agencies and fishers coastwide to assess the utility of alternative commercial gear to increase sustainable fishing opportunities, enable selective harvest in terminal river locations, and minimize bycatch mortality for wild salmonid recovery (Knudsen 2000; Lawson and Comstock 2000).

METHODS

Study area.— The 2019 fish trap was located at rkm 67 on the Columbia River in the Cathlamet Channel (Wahkiakum County, Washington). The trap occupied the same location as used in the prototype study of Tuohy et al. (2019); salmon traps were once commonplace in this area before the Washington State ban on fixed gear in 1934 (Washington State Session Laws 1935). The Cathlamet Channel is 1.1 km wide at this point in the river, with a

maximum depth of 6.1 m at high tide and a minimum depth of 3.3 m at low tide. Daily tidal flux during the study ranged from 1.5 to 2.8 m.

Trap design and modifications.— By design, fish traps remain fixed in position by piling or anchor and passively funnel returning adult salmonids from the "lead" (a fine-meshed wall positioned perpendicular to shore) through a maze of mesh compartments from which fish rarely escape (Cobb 1930). Captured salmonids instinctively move against the current into progressively smaller compartments of the fish trap ("heart," "spiller," and "live well," respectively; Cobb 1930; Tuohy et al. 2019). The final compartment has dimensions appropriate for operators to sort the catch for harvest or passive release with little to no air exposure and handling. Salmonids remain free-swimming within the fish trap, and selected mesh dimensions minimize or prevent entanglement altogether (Tuohy et al. 2019).

Identical to the prototype described by Tuohy et al. (2019), the Cathlamet Channel fish trap consisted of a lead (~90 m), jigger (~10 m), heart (23-m length; 20-m maximum width), tunnel, and spiller ($6 \times 6 \times 9$ m; Figure 1). Black nylon mesh with a stretch of 7.94 cm was used for the lead and jigger (Christensen Net Works, Everson, Washington). The heart, spiller, and tunnel were constructed of 6.35-cm knotless-nylon mesh. Mesh sizes were

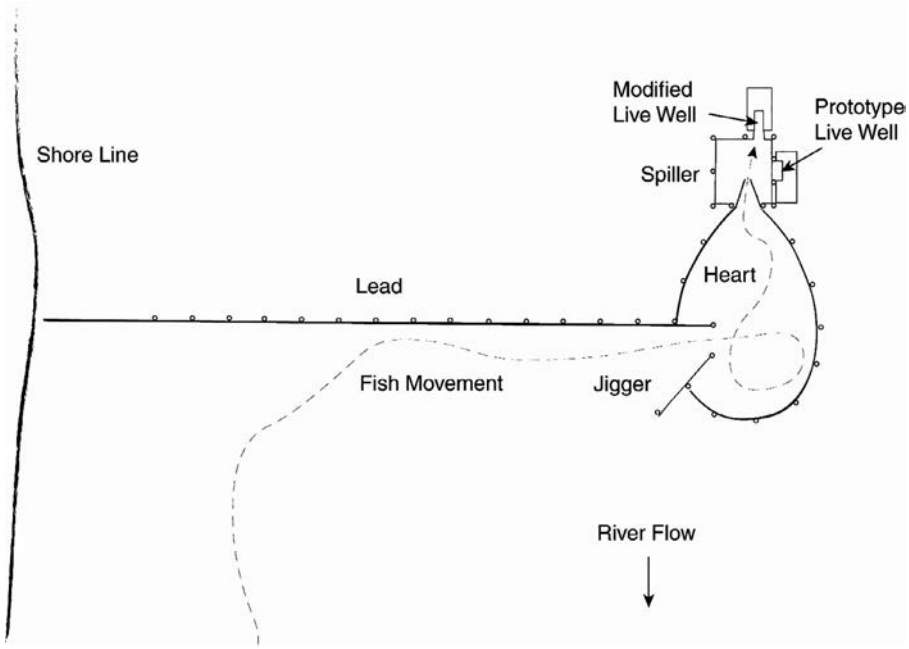


FIGURE 1. The fish trap constructed in Cathlamet Channel (lower Columbia River) consisted of a lead, jigger, heart, tunnel, and spiller.

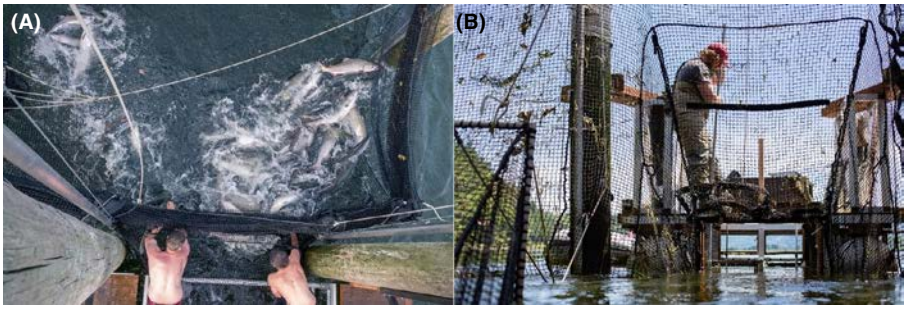


FIGURE 2. The prototype spilling technique **(A)** used a line-and-pulley system and an electric winch to corral groups of captured fish to a live well for sorting. The modified passive design **(B)** employed an upstream tunnel from the spiller compartment to allow individual fish to migrate volitionally from the spiller to an attached upstream live well for sorting, with zero air exposure and net contact. [Color figure can viewed at afsjournals.org.]

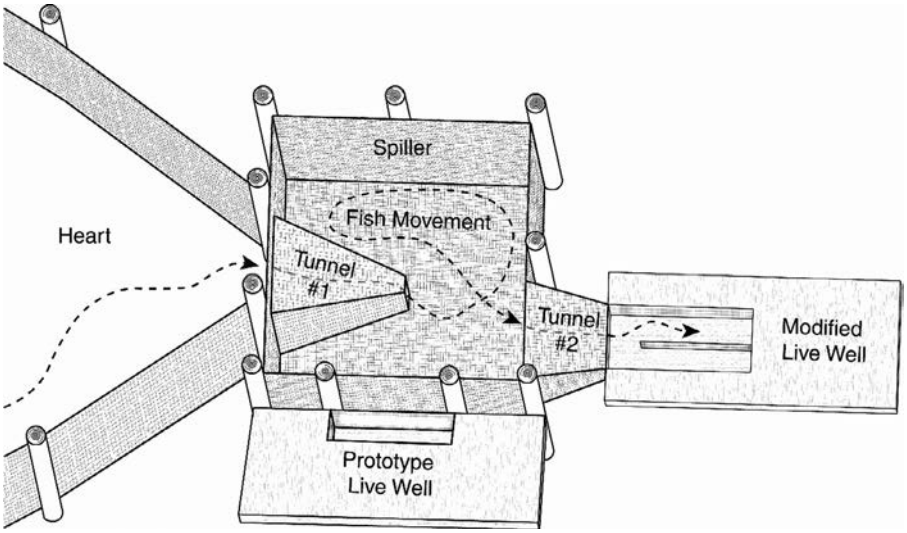


FIGURE 3. The modified trap design enabled free-swimming fish to be captured passively on an individual basis while eliminating air exposure and net contact from the commercial process.

carefully selected by study investigators to minimize entanglement of fish and minimize drag within the water column. All compartment nets were secured to untreated wood pilings (generally positioned 5 m apart) from the bottom of the riverbed to roughly 1 m above the high-water mark. As in the 2017 study, an aluminum marine mammal deterrent gate was installed at the entrance to the heart. This gate could be opened or closed to prevent entry of large mammals to the heart and spiller of the trap while maintaining some level of fish passage for harvest or data collection (Tuohy et al. 2019).

In efforts to improve the postrelease survival of captured fish from the gear, the spiller compartment and final capture processes were modified in 2019. In contrast with the 2017 prototype trap design (Tuohy et al. 2019: Figure 2A), a line-and-pulley electric winch system (henceforth, the "prototype treatment") was no longer necessary for hauling the mesh bottom of the spiller/tunnel complex to the shallows for sorting of the catch (a procedure that may cause physiological stress or minor physical damage to captured fishes). A modified passive capture design (henceforth, the "modified treatment") was implemented in 2019 by adding a new upstream tunnel to the existing spiller compartment (Figures 2B, 3). This upstream tunnel (6.35-cm knotless-nylon mesh) passively funneled migrating fishes from the spiller to the shallows of an attached upstream live-well trough. The live well was aluminum framed, with 3.81-cm knotless-nylon mesh walls to enable river water to constantly recirculate. It was equipped with two parallel rectangular chambers ($2.74 \times 0.61 \times 0.76$ m) and a mesh pivot capture door near the outlet of the upstream spiller tunnel. Operators could open or close the capture door to passively entrap migrating fishes in one chamber while enabling the vacant chamber to be occupied by fishes (Figures 2B, 3). Within the shallow live well, the free-swimming catch could be comfortably sorted by wading study investigators for harvest or data collection and passive release through an upstream mesh exit door. This 2019 modified trapping process largely eliminated fish air exposure, handling, overcrowding, and net contact associated with the 2017 prototype trapping process (with the intent of improving postrelease salmonid survival). Nevertheless, handling of fish within the live well remained necessary to restrain the catch for data collection purposes.

Research and test fishery operations.— Research and commercial fishing trials were conducted between May 5 and October 31, 2019, during peak migration periods for Sockeye Salmon and Coho Salmon in the lower Columbia River (Johnson et al. 1948; Burgner 1991; Sandercock 1991). Hatchery-origin Chinook Salmon and Coho Salmon are commercially targeted for harvest within Columbia River fisheries. Bycatch of ESA-listed steelhead, Chinook Salmon, Coho Salmon, Chum Salmon, and Sockeye Salmon evolutionarily significant units can considerably constrain commercial fisheries in the region (Martin 2008; NWFSC 2015).

To begin a fishing event, trap operators deployed the spiller from its suspended position above the water column to the river bottom. Tunnel doors were then opened, enabling the capture of free-swimming fish from the spiller compartment using one of three separate techniques: (1) the 2019 modified treatment, (2) the 2017 prototype treatment, or (3) a rubberized dip net (henceforth, the "control"). Investigators documented the beginning set time, tidal stage (ebb, flood, and slack), water temperature (°C;

Extech), presence of marine mammals, and the method of capture (modified treatment, prototype treatment, or control). Tunnel doors remained open to fish passage until a pause or cessation of fishing was desired. During trap operations, the marine mammal deterrent gate was occasionally closed due to the proximity of Steller sea lions *Eumetopias jubatus* and California sea lions *Zalophus californianus* to the project site.

Trap operators visually observed the spiller and upstream live well to determine fish entrance and occupancy through the modified treatment process. Once a live-well chamber was occupied by one or more fish, study investigators trapped the catch through closure of the capture door. Wading within the live well, biologists or fishers could then restrain fish by hand to enumerate, measure (FL), and identify all specimens by species and origin (adipose fin clipped [suggesting hatchery origin] or unclipped [suggesting natural origin]). All salmonids (except for those that escaped the live well) were scanned for PIT tags with a Biomark HPR Lite reader (Biomark, Boise, Idaho). If existing PIT tags were detected, codes were recorded using P4 software (PSMFC 2017); these salmonids were then allowed to passively migrate through the live-well exit door for detection upriver. To assess potential comparative benefits of the modified treatment process, adult salmonids were also captured individually through the control sourcing technique and en masse via the prototype treatment for data collection within a live well. Any fish that showed no signs of life at capture or release was analyzed for the cause of death and was noted as an immediate mortality.

Sockeye Salmon mark–release–recapture experimental design.— Similar to the 2017 fish trap study of Tuohy et al. (2019) and other alternative gear studies conducted on the lower Columbia River (Vander Haegen et al. 2004; WDFW 2014), a paired mark–release–recapture methodology was used to estimate relative postrelease survival of Sockeye Salmon exposed to commercial fish trapping processes (Burnham et al. 1987). Between May and August, Sockeye Salmon lacking an existing PIT tag (99.9% of those encountered) were randomly captured through treatment and control sourcing methods, assigned to corresponding treatment or control groups based upon the means of capture, restrained by hand within a live well, and tagged in the peritoneal cavity with a 12.5-mm, 134.2-kHz, full-duplex PIT tag using an MK-25 Rapid Implant Gun (Biomark). These fish were scanned to record PIT tag information, after which they were passively released through the live-well exit door for upriver detection. This paired mark–release–recapture approach was used to adjust for the physical and physiological effects of handling and PIT tagging, thereby isolating commercial treatment effects on adult salmon release survival in analysis.

During May–July operations, both treatment and control Sockeye Salmon were randomly captured and PIT-tagged so that each group was represented throughout the study period in nearly equal cumulative proportions. This effort to achieve proportional tagging over the course of the study helped to assure similar (1) handling and tagging effects, (2) stock compositions, (3) marine mammal and harvest pressures, and (4) handling, tag loss, and environmental stressors between groups.

The modified treatment group consisted of fish that migrated on an individual basis or in small schools through the upstream tunnel and were trapped by study investigators via closure of the pivot door. This method of capture mirrored how the gear would be operated in a commercial setting given the current status of fish trap engineering.

Any fish that remained in the spiller compartment at the conclusion of fishing trials were cleared from the fish trap to a live well via the line-and-pulley system, representing the prototype treatment group. With all fish transferred to a live well, the spiller was then hoisted out of the water column to a suspended position to enable fish passage from the heart. This procedure mirrored that of the commercial trapping process in 2017 (Tuohy et al. 2019). However, it must be noted that modifications to the spiller compartment (specifically, addition of the upstream tunnel) affected the ability of investigators to properly operate the line-and-pulley winch system relative to the 2017 study. Furthermore, there were other subtle differences in lifting mechanics and operations due to changing personnel.

To remain consistent and enable comparison with prior alternative gear analyses (Tuohy et al. 2019), the control group consisted of fish that were passively corralled at the project site. Free-swimming fish that were unexposed to potentially damaging commercial treatment processes were sourced on an individual basis with a rubberized dip net, enabling investigators to handle, PIT-tag, and release adult fish for detection upriver in a low-impact manner. This control sourcing technique was similar to but likely less stressful than procedures used in Columbia River purse-seine, beach-seine, and tangle-net studies, during which control group fish were trapped at the Bonneville Dam adult fish passage facility, dipnetted, PIT-tagged, trucked downriver to the test fishing location (~rkm 225), and transferred from a truck into the water to repeat the upriver migration for a second time (Ashbrook 2008; WDFW 2014). Consequently, survival in our study is likely biased low relative to past studies.

It must be noted that during the May–July study period, wild and hatchery-origin spring/summer-run Chinook Salmon were captured and PIT-tagged. However, a poor return of the species to the Columbia River basin compromised the sample, resulting in inadequate precision and accuracy of Chinook Salmon survival estimates (Tuohy et al. 2020). Although fall Chinook Salmon were captured

during commercial trials to potentially supplement the spring/summer Chinook Salmon sample, PIT tagging was not conducted due to concerns regarding interference with commercial harvest operations (Tuohy et al. 2020).

Sockeye Salmon mark–release–recapture analysis.— A pair of Cormack (1964) single release–recapture models was used to estimate the survival of treatment Sockeye Salmon relative to the control group ($\tau = S_{Treatment}/S_{Control}$) in upriver reaches between the fish trap site (rkm 67), Bonneville Dam (rkm 234), The Dalles Dam (rkm 309), and McNary Dam (rkm 470) on the Columbia River (Figure 4). The joint probability of survival and detection to upper basin detection sites above McNary Dam was also estimated.

The joint likelihood model for the tag analysis was described in detail by Tuohy et al. (2019) and was referred to as the complete capture history protocol by Burnham et al. (1987:112–125). With four upstream detection sites, each control or treatment release produced $2^4 = 16$ unique capture histories described in their respective likelihoods. Reach survival of the control group was parameterized by S_i ($i = 1, \ldots, 3$), whereas reach survival of treatment groups was parameterized by $S_i \times \tau_i$ ($i = 1, \ldots, 3$) in the joint likelihood model. In so doing, near- and far-field effects of the fish trap on survival of trapped and released Sockeye Salmon (τ_i) could be directly estimated from the model ($\tau_i = S_{i.Treatment}/S_{i.Control}$). Immediate survival ($\tau_0$) from capture to the time of release from the gear was observed directly. Cumulative relative survival from release to McNary Dam was estimated as $\tau_0 \times \tau_1 \times \tau_2 \times \tau_3$.

Detection histories for control and treatment groups were downloaded from the Columbia Basin PIT Tag Information System, which is operated by the Pacific States Marine Fisheries Commission and provides public access to all PIT tag detection data throughout the Columbia River basin. The tagging data were uploaded to Program USER (Lady and Skalski 2009) to calculate maximum likelihood estimates of survival as described by Skalski and Millspaugh (2006). Likelihood ratio tests were performed to identify the most parsimonious models for describing the capture process at $\alpha = 0.05$ (two-tailed).

Coho Salmon holding experimental design.— For Coho Salmon, we performed a net-pen holding study similar to those conducted by Buchanan et al. (2002) and Takata and Johnson (2018). Due to the migratory nature of Coho Salmon (which tend to spawn below main-stem Columbia River dams) and the limited PIT tag detection capabilities below Bonneville Dam, paired release–recapture has typically been ineffective in the absence of a very large sample size (WDFW 2014). As a result, Coho Salmon survival from prior alternative gear investigations has been directly estimated via net-pen holding in the lower Columbia River (Takata and Johnson 2018). This holding study was therefore performed to provide data that were comparable



FIGURE 4. Sockeye Salmon relative survival was estimated in river reaches between the Columbia River trap site (rkm 67) and Bonneville Dam (τ_1; rkm 234), The Dalles Dam (τ_2; rkm 309), and McNary Dam (τ_3; rkm 470). [Color figure can viewed at afsjournals.org.]
[Correction added on October 07, 2020, after first online publication: Figure 4 has been updated]

to those from past studies while supplementing the Sockeye Salmon release–recapture study.

During August–October, commercial fishing trials took place at the experimental trap to evaluate the performance of the gear in a commercial selective harvest setting. At the completion of a fishing week, adult Coho Salmon (>47 cm FL) that were randomly captured at the trap through the modified commercial treatment process were transferred one by one to a temporary holding chamber of the live well until a sample of approximately 20 fish was retained. In this sample collection process, it was necessary to use a rubberized dip net to clear the fish over a small-mesh barrier (extending ~15 cm above water surface level) to the temporary holding chamber of the live well; we assumed that the rubberized net and brief moment of air exposure had no impact on fish survival. With the desired sample size achieved after a 4–8-h collection period, investigators sealed the outlets to all spiller tunnels. Coho Salmon were once again enumerated, identified by origin (adipose fin clipped or unclipped), noted for capture condition ("lively," "lethargic," or "no signs of life"), and released from the live well by hand to the sealed spiller compartment (now functioning as a net-pen holding chamber, with dimensions roughly equivalent to those specified by Takata and Johnson 2018). Once the last fish was placed into the spiller compartment, investigators initiated a 48-h observation period and noted the date, time, water temperature (°C; Extech), and presence of marine mammals. For collection of all 48-h holding samples, trap operators randomly selected the first ~20 adult Coho Salmon that passively migrated into the live well from the spiller. As in prior studies conducted by Takata and Johnson (2018), Coho Salmon that exhibited prior injuries unrelated to the commercial gear were excluded from the holding study.

Coho Salmon holding analysis.— Postrelease survival of Coho Salmon captured with the modified commercial fish trap was estimated by holding and observing six treatment groups of fish for a 48-h period in a net-pen providing about 90.62 m^3 (3,200 ft^3) of holding space (depending on tide height). To determine fish mortalities during the holding period, treatment groups were checked twice daily at regular intervals from above and below the water surface (via snorkel survey). At the end of the 48-h holding period, all fish were cleared from the holding pen to a live well via the 2017 prototype line-and-pulley method (Tuohy et al. 2019). These fish were then enumerated, measured (FL), scanned for PIT tags, identified for species type and origin (hatchery or wild), noted for condition, and released. Postrelease survival was directly estimated by a binomial proportion (p = number that survived/total number) with associated binomial variance. In the case of no observed mortality, a lower one-tailed interval estimate of survival was calculated using the method of Skalski (1981). As in prior lower Columbia River holding studies, the effects of confinement on Coho Salmon were not controlled (Takata and Johnson 2018).

RESULTS

Total Catch

The experimental trap was fished over a 40-d period between May 5 and July 3, 2019, and over a 46-d period between August 19 and October 30, 2019. In total, 6,278 adult and jack salmonids were captured. Nonjuvenile catch comprised 64.1% Coho Salmon (4,024 total; 62.9% adipose clipped; 12.4% jack salmon [<47 cm]), 12.1% Chinook Salmon (758 total; 56.3% adipose clipped; 23.4% jack salmon [<57 cm]), 14.3% Sockeye Salmon (896 total; 0.00% adipose clipped), 9.0% summer steelhead (568 total; 70.8% adipose clipped), 0.08% Chum Salmon (5 total; 0.0% adipose clipped), 0.03% Pink Salmon *O. gorbuscha* (2 total; 0.0% adipose clipped), 0.19% resident/residualized (<30-cm) Rainbow Trout (12 total; 54.5% adipose clipped), 0.19% resident (<30-cm) Cutthroat Trout *O. clarkii* (12 total; 0.0% adipose clipped), and 0.02% unidentified salmonid (1 total).

In addition to salmonid catch, we captured 357 American Shad *Alosa sapidissima*, 80 Largescale Sucker *Catostomus macrocheilus*, 36 Northern Pikeminnow *Ptychocheilus oregonensis*, 16 Starry Flounder *Platichthys stellatus*, 11 Peamouth *Mylocheilus caurinus*, 2 White Sturgeon *Acipenser transmontanus*, 2 Pacific Lamprey *Entosphenus tridentatus*, 1 Largemouth Bass *Micropterus salmoides*, and 1 Common Carp *Cyprinus carpio*.

During the study, immediate mortalities occurred for a total of 5 Sockeye Salmon (<400 mm FL), 5 Coho Salmon jacks (<400 mm FL), and 253 juvenile Chinook Salmon smolts (150–250 mm FL; 91% adipose clipped). All immediate mortalities of salmonids occurred from wedging or gilling in relatively confined spaces of the trap. Juvenile Chinook Salmon were impacted by 3.81–6.35-cm stretch mesh in the spiller and live well; small-bodied Sockeye Salmon and Coho Salmon jacks (<400 mm FL) were predominantly impacted by a small panel of 7.94-cm stretch mesh deployed at the intersection of the heart and the jigger.

Survival of Sockeye Salmon

Sockeye Salmon were first encountered at the trap on May 28 and remained abundant when fishing ceased on July 3, 2019. Water temperatures during this study period ranged from 14.4°C to 19.2°C (mean = 17.0°C). Of the 896 Sockeye Salmon that were captured, a total of 402 control, 309 modified treatment, and 138 prototype treatment Sockeye Salmon were PIT-tagged in nearly equal cumulative proportions throughout the study (Figure 5).

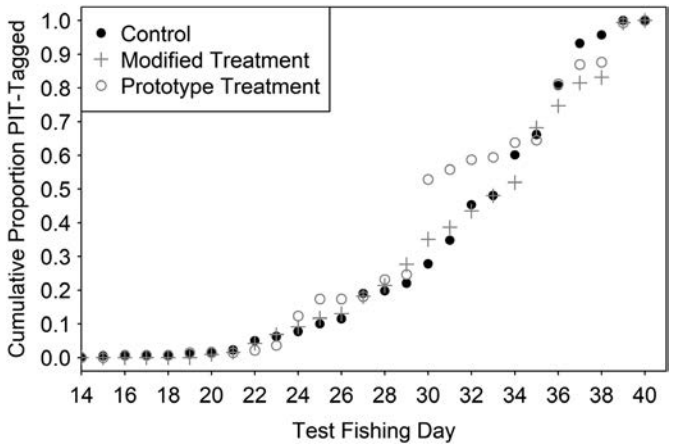


FIGURE 5. Sockeye Salmon were randomly captured, PIT-tagged, and assigned so that each treatment and control group was represented throughout the study period in nearly equal cumulative proportions. This sampling and assignment effort reduced the likelihood that model assumptions of homogeneous tagging conditions would be violated.

Over the course of research and commercial trials, five immediate mortalities occurred (all < 400 mm FL), resulting in an immediate survival rate ($\hat{\tau}_0$) of 0.994 (SE = 0.002) for Sockeye Salmon (Table 1).

Likelihood ratio tests found no significant difference in PIT tag array detection probabilities for control and modified treatment groups ($\chi^2_3 \geq 5.543$, $P = 0.136$), resulting in the selection of a reduced model with a common detection probability for control and treatment fish by location. Postrelease survival for the modified treatment group compared to the control group from their release at the trap to Bonneville Dam ($\hat{\tau}_1$) was 0.983 (SE = 0.021; Table 1). The survival rate of the treatment group was higher than that of the control group between Bonneville and The Dalles dams, with relative survival ($\hat{\tau}_2$) estimated at 1.008 (SE = 0.016); and between The Dalles and McNary dams, with relative survival ($\hat{\tau}_3$) estimated at 1.033 (SE = 0.019). Cumulative relative survival ($\tau_0 \times \tau_1 \times \tau_2 \times \tau_3$) for the modified treatment group from capture at the trap site to McNary Dam (~400 km upstream; 8-d median travel duration) was estimated to be 1.017 (SE = 0.032; Table 1).

Between May 28 and July 3, a total of 32 spiller hauls were performed with the prototype treatment design, of which only 21 hauls resulted in the capture of Sockeye Salmon. Likelihood ratio tests found no significant difference in PIT tag array detection probabilities for control and prototype treatment groups ($\chi^2_3 \geq 2.864$, $P = 0.413$), resulting in the selection of a reduced model with a common detection probability for the fish at a location. Short-term relative postrelease survival from the gear to Bonneville Dam ($\hat{\tau}_1$) was estimated at 0.796 (SE = 0.041; Table 1). Between Bonneville and The Dalles dams, survival was nearly equivalent to that of the control group, with $\hat{\tau}_2 = 1.004$ (SE = 0.024). Relative survival remained high in the final reach between The Dalles and McNary dams, with $\hat{\tau}_3$ equal to 0.974 (SE = 0.035). Nevertheless, survival of Sockeye Salmon that were exposed to the prototype treatment was significantly different from the survival of those exposed to the modified fish trap treatment ($|Z| \geq 4.963$, $P < 0.001$; Table 1), with cumulative relative survival from release to McNary Dam estimated at 0.774 (SE = 0.051).

Survival of Coho Salmon

The Coho Salmon holding study was conducted between September 27 and October 30, 2019. During this study period, water temperatures ranged from 12.1°C to 19.2°C (mean = 15.79°C). Encountering 3,523 adult Coho Salmon at the trap site over the course of the study, there were zero immediate mortalities of adult Coho Salmon, resulting in an immediate survival rate $\hat{S}$ of 1.000 (lower 95% confidence limit: $S \geq 0.999$). In total, 121 Coho Salmon were held in captivity after release from the commercial gear in six separate subsample groups (Table 2). Zero mortalities occurred during the 48-h holding period, resulting in a postrelease survival estimate $\hat{S}$ of 1.000 (lower 95% confidence limit: $S \geq 0.978$). All Coho Salmon that were encountered during the fish collection process for the holding study were lively and vigorous upon capture and release after 48 h, and no fish appeared lethargic or asphyxiated.

DISCUSSION

Bycatch Survival

Through two distinct research approaches, this study has demonstrated the potential of a modified commercial trapping technique to achieve essentially 100% survival of adult salmonid bycatch. Estimated relative survival ($\tau_0 \times \tau_1 \times \tau_2 \times \tau_3$) of Sockeye Salmon from the modified trap design using a paired release–recapture study was 1.017 (95% CI: $0.974 \leq \hat{\tau}_{cumulative} \leq 1.059$) over a 400-km migration to McNary Dam. Utilizing an alternative 48-h net-pen holding approach, survival of Coho Salmon was directly estimated at 1.000 (lower 95% confidence limit: $S \geq 0.978$). Regardless of the estimation technique employed, the modified passive capture design, which mostly eliminated air exposure and net contact and also minimized handling and crowding, had no detectable impact on salmon release survival. Despite the limitations of a single-year data set, these results suggest that fish trapping could significantly reduce salmonid bycatch mortality if applied in terminal commercial salmon fisheries (Table 3).

Relative to the performance of the prototype fish trap used in 2017, results from the modified fish trap design

TABLE 1. Relative treatment effect (i.e., $\tau = S_{Treatment}/S_{Control}$) on postrelease survival for Sockeye Salmon encountered at the trap in Cathlamet Channel, Columbia River. The 95% profile likelihood confidence intervals (in parentheses) were estimated by river reach for the modified commercial treatment and the prototype commercial treatment; *P*-values for two-tailed tests of equal survival are reported. Immediate survival (τ_0) was set equal between treatment groups, as all immediate mortalities resulted from processes that were shared by the two capture treatments.

River reach	Modified treatment survival point estimate	Prototype treatment survival point estimate	*P*-value
Immediate survival (τ_0)	0.994 (0.988–0.998)	0.994 (0.988–0.998)	
Gear to Bonneville Dam (τ_1)	0.983 (0.942–1.024)	0.796 (0.712–0.872)	<0.001
Bonneville Dam to The Dalles Dam (τ_2)	1.008 (0.974–1.041)	1.004 (0.948–1.045)	0.861
The Dalles Dam to McNary Dam (τ_3)	1.033 (0.995–1.072)	0.974 (0.899–1.033)	0.034
Cumulative ($\tau_0 \times \tau_1 \times \tau_2 \times \tau_3$)	1.017 (0.974–1.059)	0.774 (0.673–0.872)	<0.001

TABLE 2. Subsamples of Coho Salmon that were captured with the modified fish trap in Cathlamet Channel, Columbia River, were held for a 48-h period to directly estimate release survival; water quality conditions were recorded. Mean water temperature is presented with 95% CI in parentheses.

Subsample number	Date	Mean water temperature (°C)	Coho Salmon sample size	Number that survived	Coho Salmon survival
1	Sep 27–29	18.77 (18.69–18.85)	13	13	1.000
2	Sep 30–Oct 2	17.74 (17.64–17.84)	27	27	1.000
3	Oct 3–5	16.31 (16.24–16.39)	34	34	1.000
4	Oct 10–12	15.63 (15.53–15.74)	13	13	1.000
5	Oct 23–25	13.57 (13.50–13.65)	24	24	1.000
6	Oct 28–30	12.75 (12.64–12.85)	10	10	1.000
Total			121	121	1.000

TABLE 3. Comparison of cumulative survival estimates (with associated 95% CIs [in parentheses] if available) for salmonids by gear type. If lower Columbia River data were not available for comparison, lower Fraser River data were used.

Gear	Chinook Salmon survival	Coho Salmon survival	Sockeye Salmon survival	Steelhead survival
Gill net	0.520[a]	0.400[e]	0.400[e]	0.552[h]
Tangle net	0.764[b]	0.764[f]	0.900[e]	0.764[f]
Beach seine	0.750 (0.710–0.790)[c]	0.620[g]	0.950[e]	0.920 (0.820–1.000)[c]
Purse seine	0.780 (0.720–0.850)[c]	0.710[g]	0.900[e]	0.980 (0.930–1.000)[c]
Fish trap	0.995 (0.924–1.071)[d]	1.000 (0.978–1.000)	1.017 (0.974–1.059)	0.944 (0.880–1.012)[d]

[a]Independent Fisheries Science Panel (2014).
[b]TAC (2018).
[c]WDFW (2014).
[d]Tuohy et al. (2019).
[e]CDFO (2017).
[f]ODFW and WDFW (2018).
[g]TAC (2015).
[h]TAC (2008).

represent an improvement that warrants incorporation into all future commercial salmon traps. Although results from this 2019 study for Sockeye Salmon and Coho Salmon cannot be directly compared with and extrapolated to other species or other periods of study, it is highly likely that the modified passive capture design would achieve improved survival results for Chinook Salmon and steelhead if tested. In 2017, cumulative survival over 400 km to McNary Dam from the prototype trap design was estimated at 0.944 (95% CI: $0.880 \leq \hat{\tau}_{cumulative} \leq 1.012$) for steelhead and 0.995 (95% CI: $0.924 \leq \hat{\tau}_{cumulative} \leq 1.071$) for Chinook Salmon through an

equivalent mark–recapture methodology (Tuohy et al. 2019). Further research is warranted to investigate potential improvements in survival for these species from recent engineering advancements in fish trap technology.

Analyzing differences between Sockeye Salmon survival estimates from the two trap designs (modified treatment and prototype treatment) in 2019, the older prototype trapping method demonstrated a surprisingly deleterious and significant effect on Sockeye Salmon survival relative to the new modified passive trapping method (Table 1). The cause of this poor performance relative to the 2017 results for Chinook Salmon and steelhead exposed to the prototype treatment remains unknown; however, the relatively poor performance may be attributable to several factors, including the scarcity of hauls performed, addition of the upstream tunnel for passive capture, annual differences in lifting mechanics, operator error, or water quality conditions. With significantly fewer hauls performed in 2019 by using the prototype method ($N_{2017} = 381$; $N_{2019} = 32$), operators had less opportunity to learn from their mistakes and adjust spiller mechanics. It was noted on multiple occasions that spills were poorly performed during the spring season study (often due to the presence of the upstream tunnel for passive capture), potentially causing physiological stress to captured fish. Investigating the prototype treatment data set, results were heavily skewed by four major spill events (>10 Sockeye Salmon spilled and tagged) and one significant outlier in which relative release survival was only 0.093 (likely due to operator error). This result (1) highlights the need for skilled and attentive operators if the line-and-pulley prototype technique of 2017 is employed and (2) lends support for the modified passive capture design, which dramatically reduces the likelihood of potential operator error and significantly improves the release survival of fish (Table 1). Differences in water quality conditions could also affect survival between years and seasons of study, with warmer water temperatures generally reducing the survival of captured and released salmonids (Crossin et al. 2008; Gale et al. 2013; Raby et al. 2015). Nevertheless, the Sockeye Salmon results for the prototype design in 2019 should perhaps be taken lightly given the small sample size available for analysis (i.e., 138 fish), the scarcity of hauls performed (i.e., 32), flaws in spiller operations, and the obsolescence of the prototype method of capture.

Management Recommendations

Bycatch impacts vary in relation to commercial gear types, users and designs of a specific gear type, localized environmental factors, and biological factors (Raby et al. 2015; Teffer et al. 2017; Bass et al. 2018). This variance is a challenge to management of all fisheries and gear types (CDFO 2017). As resource managers in the U.S. Pacific Northwest consider commercial or research application of fish traps in fluvial settings, regulations specific to trap design and operation should be carefully considered to optimize performance and maximize conservation benefits. Recent engineering advancements have demonstrated promise for dramatically reducing salmonid bycatch mortality and expanding sustainable fishing opportunities in fluvial settings similar to the lower Columbia River (Table 2). However, as is the case for all commercial gears, not all trap designs, operations, and their impacts to salmonid survival appear equal.

We recommend that trap designs approved for future operation be heavily regulated, with operators certified to achieve maximum conservation benefit. First, fish traps must be researched and tested if deployed in a new regional environment to ensure compatibility with the ecosystem. Investigators or fishers must consider the ecology of aquatic fish, invertebrate, and marine mammal species at all life history stages during site selection and engineering processes. Specifics such as mesh size and material, depth, location, marine mammal deterrence methods, lead length, heart configuration, and spiller design should be carefully considered and regulated by management within a watershed to maximize benefits and minimize potential harm to the ecosystem (e.g., bycatch mortality, enhanced marine mammal predation, or delayed fish migration timing; Tuohy et al. 2020). Spiller mechanics should be based on this 2019 design, operating as passively as possible to minimize bycatch impacts and the likelihood of operator error while being managed according to a design's unique performance record. Operators in any fishery must be privy to fish identification for selective harvest and passive release of bycatch, causing minimal harassment to nontarget stocks. To ensure compliance with fishery-specific regulations and achieve desired conservation outcomes, electronic monitoring systems are recommended for use at each fish trap site (Tuohy et al. 2020). Depending on the turbidity conditions encountered within a fishery, underwater video cameras could be employed within each live well for stock composition and regulatory compliance monitoring.

If regulated and managed appropriately in a watershed to meet the biological needs of unique salmonid populations (Gayeski et al. 2018b), modified fish traps have the potential to dramatically reduce bycatch mortality of ESA-listed salmonids, maintain the age and size structure of harvested fish populations (Ricker 1981; Lewis et al. 2015), alleviate commercial fishery constraints, increase selective fishing opportunity for robust or hatchery-origin fish stocks, and improve the quality of harvested seafood products. Trap fisheries operating in-river do not deprive southern resident killer whales *Orcinus orca* of marine food resources (Ford et al. 2010; Lacy et al. 2017). Benefiting wild salmon recovery and preserving a key trophic link for killer whales, the gear could be certified

sustainable in the marketplace and branded for both quality and sustainability to improve prospects for fishers and depressed coastal fishing communities of the region (Johnson 2018; Gayeski et al. 2018a). Commercial fishing operations could be paired with low-impact data collection by resource management agencies at trap sites to better understand fish behavior and ecology (Link and English 2000). Although further research of the gear is necessary (e.g., new river locations, modified designs, potential fish migration delay effects, marine mammal interactions, electronic monitoring applications, and economic viability), results of this study show that modified fish traps have the potential to significantly reduce salmonid bycatch mortality for the benefit of the commercial fishing industry, fisheries management, wild salmonid conservation, and the environment.

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Maximizing salmonid bycatch survival with passively operated commercial fish traps

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ABSTRACT

Commercial fish traps were recently implemented at a limited scale in the lower Columbia River in efforts to selectively harvest hatchery-origin fishes with minimal mortality of wild-origin salmonids listed under the U.S. Endangered Species Act. Prior studies of a modified passive trapping technique demonstrated nearly 100 % survival among adult salmonids released as bycatch. Building upon this research, additional survival studies for adult coho salmon, spring-run Chinook salmon, and summer-run Chinook salmon were conducted between 2019 and 2021 at two separate fish trap sites in the lower Columbia River. Over three years of study, we used mark-recapture and net pen holding methodologies to estimate post-release survival of Chinook salmon and coho salmon, respectively. Evaluating detections of Chinook salmon tagged and released from a passively operated fish trap in 2019, detection at Bonneville Dam over a mean 6.5 d upriver migration (167 km) was 1.000 (95 % CI: $S \geq 0.970$) for the sample genetically assigned to populations originating upriver of Bonneville Dam. Through two separate net pen holding studies, post-release survival of coho salmon was estimated at 1.000 (95 % CI: $S \geq 0.975$) over 4 d in 2020 and 0.965 (95 % CI: $0.948 \leq S \leq 0.969$) over 6 d in 2021. Given that these analyses lacked control groups to adjust survival estimates for confounding mortality effects, study results are inherently conservative. Ultimately, the findings of our research support the conclusions of prior studies and further suggest that passively operated fish traps may allow for selective harvesting of targeted fish stocks with little to no mortality of adult salmonid bycatch.

1. Introduction

Bycatch and mixed-stock harvesting of Endangered Species Act (ESA)-listed Pacific Salmonids (*Oncorhynchus Spp.)* constrains fishing opportunities for abundant hatchery-origin fishes and impacts wild-origin salmonid populations throughout the U.S. Pacific Northwest (NRC, 1996; WDFW, 1997; Anderson et al., 2020). Mostly to the detriment of wild salmonid population genetics and ecosystems (Naish et al., 2007), millions of hatchery fish are produced annually from federal, state, and tribal hatcheries to increase short-term fishing opportunities (Mahnken et al., 1998; Utter and Epifanio, 2002). However, absent fishing practices that can selectively harvest hatchery-origin fishes while releasing ESA-listed wild-origin salmonids unharmed, neither hatcheries nor salmon fisheries can be managed effectively to achieve conservation or harvest objectives (HSRG, 2009; Gayeski et al., 2018). In the Columbia River, this management paradigm of production hatcheries and mixed-stock harvesting contributed to the decline and extirpation of wild salmonid populations (Cramer et al., 1991; NRC, 1996; Lichatowich, 1999). Although efforts have been made to reform both harvest and hatchery management (WFWC, 2009, 2013; US v. OR MA, 2018), it is evident that these same management factors continue to limit the recovery of wild-origin salmonids (Lichatowich et al., 2017; Anderson et al., 2020). For example, the proportion of hatchery-origin spawners consistently exceeds biological targets designed to protect wild salmonid population fitness throughout the basin (HSRG, 2009; WDFW, 2022). Furthermore, mixed-stock harvesting with gill nets continues to impact ESA-listed fishes and severely constrain fishing opportunities to remove hatchery-origin fish that have been produced for the purpose of increasing short-term harvest opportunities (ODFW and WDFW, 2020). Clearly, management goals for wild salmonid conservation, hatchery reform, and harvest reform are not being achieved through the existing salmon management paradigm and not one of thirteen ESA-listed salmonid populations groups have recovered (NWFSC, 2015; Gayeski et al., 2018; WDFW, 2018).

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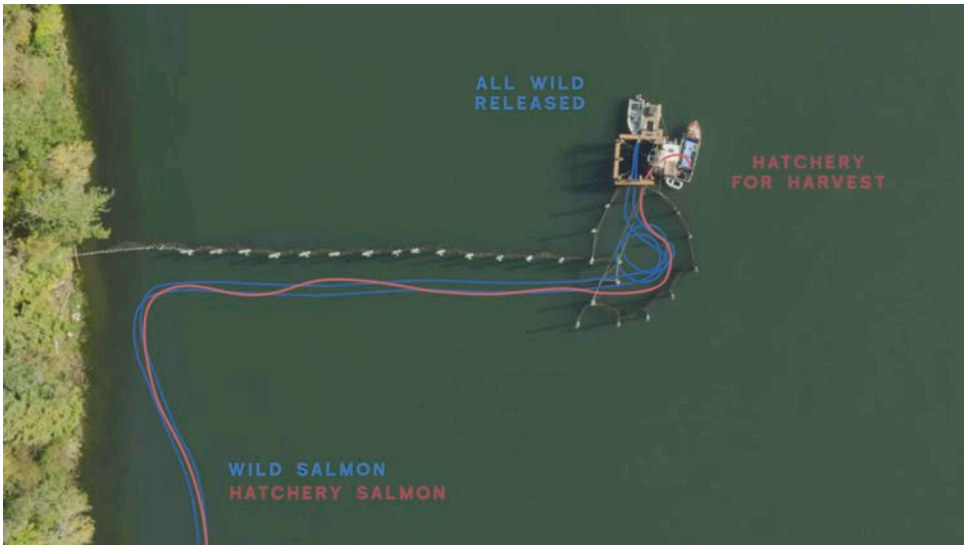
In efforts to increase harvest opportunities for hatchery-origin fishes and improve survival of wild-origin salmonids, fish and wildlife commissioners of Washington and Oregon directed resource managers to develop and implement low-impact selective alternatives to conventional gill netting in the Columbia River and elsewhere throughout the region (WFWC, 2009, 2013, 2015; ODFW, 2013). Alternative gears—including beach seines, modified purse seines, and tangle nets—were tested between 2001 and 2016 in the lower Columbia River to estimate bycatch mortality rates and bycatch encounters for comparison to that of the conventional gill net (Vander Haegen et al., 2004; WDFW, 2014; Takata and Johnson, 2018). Gill nets were studied for post-release bycatch mortality effects to spring Chinook salmon (*Oncorhynchus tshawytscha*) (Vander Haegen et al., 2004), however, no data were collected for estimation of gill net post-release mortality impacts to other critical bycatch stocks in primary commercial fisheries (NMFS, 2018). Due in part to apparent bycatch impact limitations of studied alternative gears in fall season fisheries, amongst other factors, state policy directives to develop and implement alternative gears while phasing out gill nets in the mainstem Columbia River did not materialize (WDFW, 2018).

In 2016, the nonprofit organization Wild Fish Conservancy (WFC) and a local commercial fisher constructed the first operational fish trap (or, "pound net") in over 80 years since the ban of fixed-gear fishing methods in the lower Columbia River's Cathlamet Channel (Wahkiakum County, Washington; river kilometer (rkm) 67). The gear was deployed to assess a low-impact methodology for fisheries monitoring, reduce bycatch impacts in commercial fisheries, and improve selective harvesting of hatchery-origin salmon (Tuohy, 2018; Tuohy et al., 2019).

By design, fish traps remain fixed in position by piling or anchor and passively funnel returning adult salmonids from the "lead" (a fine-meshed wall positioned perpendicular to shore) through a maze of mesh compartments in which fish rarely escape (Cobb, 1930). Salmonids encountering the lead instinctively move against the current into progressively smaller compartments of the trap ("heart," "tunnel," "pot/spiller," and "live well," respectively) (Cobb, 1930; Tuohy et al., 2019; Video 1). The final compartment has dimensions appropriate for operators to sort the catch for harvest or release with little to no air exposure and handling. Salmonids remain free-swimming within a fish trap and mesh dimensions are designed to prevent entanglement (Tuohy et al., 2019).

Similar to historical fish trap designs used in the Columbia River, the experimental fish trap installed in 2016 functioned to passively corral returning adult fishes from the lead and heart walls to an upstream-positioned pot compartment (~6 m wide x 6 m long x 6 m deep). When approximately 10–40 fishes could be observed free-swimming in the pot, the catch was quickly brailed (or, "spilled") to the shallows en masse (depth 0–1 m) using line-and-pulley and a solar-powered winch (Tuohy et al., 2019) (Video 1). After the brailing process was completed within ~20–45 s to transfer the catch to an adjacent submerged live well (depth 1 m), the fishes were hand sorted by species and adipose fin-clip status (suggesting hatchery or wild origins) with all fishes remaining underwater. Bycatch were then released by hand over the outer wall of the live well (approx. 5 cm above the water surface), exposing fish to air for ~1 s. In contrast with gill netting, these methods eliminated entanglement of adult salmonids and dramatically reduced air exposure and handling effects known to contribute to bycatch mortality (Donaldson et al., 2014; Raby et al., 2015a, 2015b). It must be further noted that free-swimming fishes passively captured in the pot prior to brailing could also be individually dip-netted into a live well for data collection and passive release through a submerged exit door to the live well. This technique was less efficient for operators but essentially eliminated potential mortality effects from air exposure and overcrowding and reduced stress during capture relative to brailing (Tuohy et al., 2019; Cox and Sippel, 2020).

To evaluate the effects of the alternative gear to bycatch, post-release survival from brailing operations with the prototype fish trap was estimated through a paired release-recapture study in 2017 using passive integrated transponder (PIT)-tags (Tuohy et al., 2019). Survival of trapped and brailed fish compared to passively released dip-netted controls over a 400-km migration to McNary Dam was estimated at 0.944 ($\widehat{SE} = 0.046$) and 0.995 ($\widehat{SE} = 0.078$) for summer-run steelhead (*Oncorhynchus mykiss*) and fall-run Chinook salmon (including both lower river tule and upriver bright populations), respectively (Tuohy et al., 2019). In a separate analysis conducted by the Washington Department of Fish and Wildlife, relative survival of fishes brailed from the fish trap compared to control groups of fishes previously tagged in the juvenile life-history stage and redetected in the lower river as adults was estimated at 0.947 (CI ($S \geq 0.724$) = 0.95) for steelhead and 0.935



Video 1. An experimental fish trap in Cathlamet Channel, WA funnels returning adult salmonids from the lead wall to a sorting compartment in 2019. In the final moment of capture, the catch can be brailed or funneled passively to the sorting compartment for data collection and release, or selective harvest.A video clip is available online. Supplementary material related to this article can be found online at doi:10.1016/j.fishres.2022.106495.

(CI ($S \geq 0.648$) = 0.95)) for Chinook salmon (upriver bright populations only) (Cox and Sippel, 2020).

Research by Tuohy et al. (2019) and Cox and Sippel (2020) demonstrated high post-release survival rates for steelhead and Chinook salmon bycatch brailed from fish traps. Yet another critical finding from these studies was that fishes unexposed to brailing (e.g., those dip-netted and passively released from fish trap operations) survived at greater rates than those that were brailed. As detailed in Cox and Sippel (2020), there appeared to be no detectable impact to the survival of dip-netted and passively released steelhead and Chinook salmon and from the fish trap in 2017.

Given promising results from these early studies, efforts were made to further improve post-release survival of all captured and released fishes from the gear through development of passive capture operations and the phasing-out of brailing techniques. The fish trap design and final capture processes at the Cathlamet, WA site were modified in 2019 in efforts to eliminate fish air exposure, handling, overcrowding, and net contact previously associated with the prototype brailing process (Tuohy et al., 2020). In contrast with the earlier prototype design, the upstream-positioned pot was altered to passively funnel fishes one-by-one against the ebb current into an upstream-positioned live well without brailing en masse or necessitating a dip-net (Video 1). Using underwater video cameras or observation above the water column, the free-swimming catch could be identified within the live well to species and adipose fin-clip status, allowing for selective removal of hatchery-origin fishes and passive release of non-target fishes through a submerged exit door (Tuohy et al., 2020). This method was defined as the "passive operation."

In efforts to assess the effectiveness of fish trap modifications, post-release survival of sockeye salmon (*Oncorhynchus nerka*) and coho salmon (*Oncorhynchus kisutch*) from passive operations was estimated and compared to that of brailing operations in side-by-side studies in 2019 (Tuohy et al., 2020). Demonstrating significant improvements in bycatch survival and 100 % post-release survival for both sockeye salmon and coho salmon (Tuohy et al., 2020), passive operations were expanded to allow for effective capture during all tides with construction of a double-ended fish trap in Clifton Channel, OR in 2021 (Video 2). This modified trap was designed to fully eliminate the brailing technique from fishing operations.

Although data from prior studies has indicated that passive operations with fish traps may have little to no effect to released salmonid bycatch (Tuohy et al., 2020; Cox and Sippel, 2020), bycatch survival rates are known to vary depending on the species encountered, the timing of seasonal gear operation, and water quality conditions (among other factors) (Davis, 2002; Raby et al., 2015a, 2015b). For these reasons, stock-specific post-release survival studies and data collection have been encouraged by fisheries management agencies for most commercial gears that may impact ESA-listed species within a specific season in the Columbia River. Therefore, we conducted additional studies of two passively operated fish traps between 2019 and 2021 to further evaluate bycatch survival rates for coho salmon and fill existing data gaps for spring-run and summer-run Chinook salmon in the lower Columbia River. We hypothesized that survival estimates for passive operations with fish traps would continue to exceed that of brailing operations from the prototype fish trap design, nearing 100 %. Given that wild populations of spring-run Chinook salmon and coho salmon are listed under the ESA (constraining or impeding commercial gill net and alternative gear fisheries in the Columbia River), accurate and precise estimates of bycatch impacts are paramount to fisheries management and the recovery of these ESA-listed species (NMFS, 2018). Bycatch survival results for both Chinook salmon and coho salmon are presented together within this publication to ensure peer-review and summary of the outlying data from our fish trap studies conducted on the lower Columbia River.

2. Materials and methods

2.1. Study location

Two fish traps were studied between 2019 and 2021 in the lower Columbia River where fish traps were commonly used prior to a ban of fixed fishing gear in Washington State and Oregon in 1934 and 1948, respectively (Fig. 1) (Washington State Session Laws, 1935; State of Oregon, 1948). In 2019–2020, pilot research of passive capture operations occurred at rkm 67 on the lower Columbia River in the Cathlamet Channel (Wahkiakum County, Washington). This trap occupied the same location as used in the studies of Tuohy et al. (2020). In 2021, research of passive capture operations occurred at a new site near rkm 55 in the Clifton Channel (Clatsop County, Oregon) (Fig. 1). At these locations, the maximum depth at high-tide toward the riverward-end of



Video 2. A modified fish trap in Clifton Channel, OR operates to capture and release salmonids passively during all tidal stages in 2021.A video clip is available online. Supplementary material related to this article can be found online at doi:10.1016/j.fishres.2022.106495.

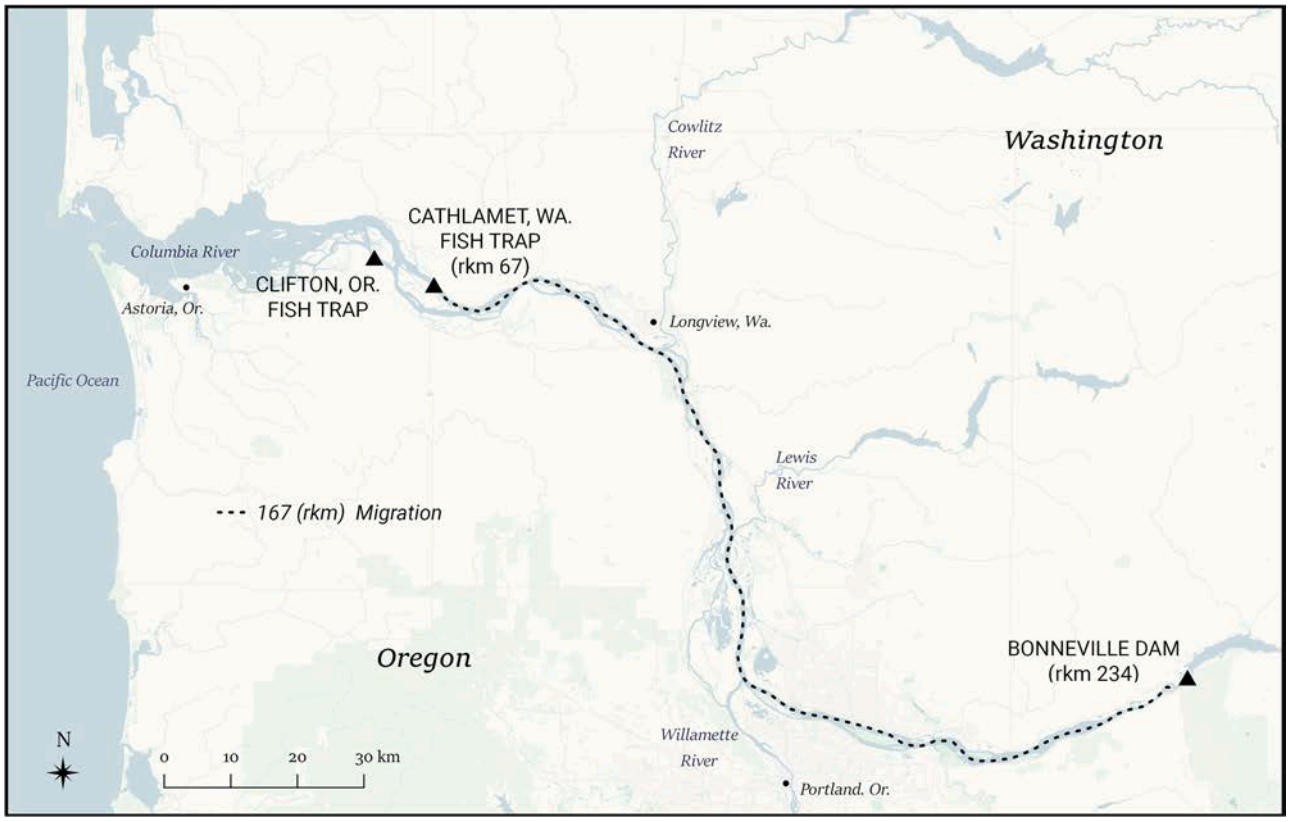


Fig. 1. Research occurred at two fish trap sites in the lower Columbia River: (1) Cathlamet, WA (rkm 67); and (2) Clifton, OR (rkm 55). Mark-recapture research evaluated Chinook salmon survival from the Cathlamet, WA fish trap to Bonneville Dam (rkm 234) located 167 km upriver. [Intended for color reproduction].

the trap ranged from 6 m to 9 m. Daily tidal flux ranged from 1.5 m to 2.8 m.

2.2. Fish trap design

For studies of spring-run and summer-run Chinook salmon survival in 2019, the Cathlamet Channel fish trap (Fig. 2a) was used to evaluate potential survival benefits of passive capture operations relative to prototype brailing operations (similar to concurrent studies by Tuohy et al., 2020 for sockeye salmon). As described in detail within Tuohy et al. (2020), this fish trap consisted of a lead (~90 m; 7.94 cm stretch mesh), jigger (~10 m; 7.94 cm stretch mesh), and heart (23-m length; 20-m maximum width; 6.35 cm stretch mesh) (Christensen Net Works, Everson, Washington). It was equipped with one pot (6 × 6 × 9 m; 6.35 cm stretch mesh) and two live wells (2.74 × 0.61 × 0.76 m) (Fig. 2a): one attached at the upstream side of the heart compartment (allowing for effective passive capture during ebb tides), and the other positioned riverward to retain the ability of the prototype fish trap design to brail fishes (Tuohy et al., 2019). This multi-operational fish trap allowed for pilot studies of passive operations and side-by-side

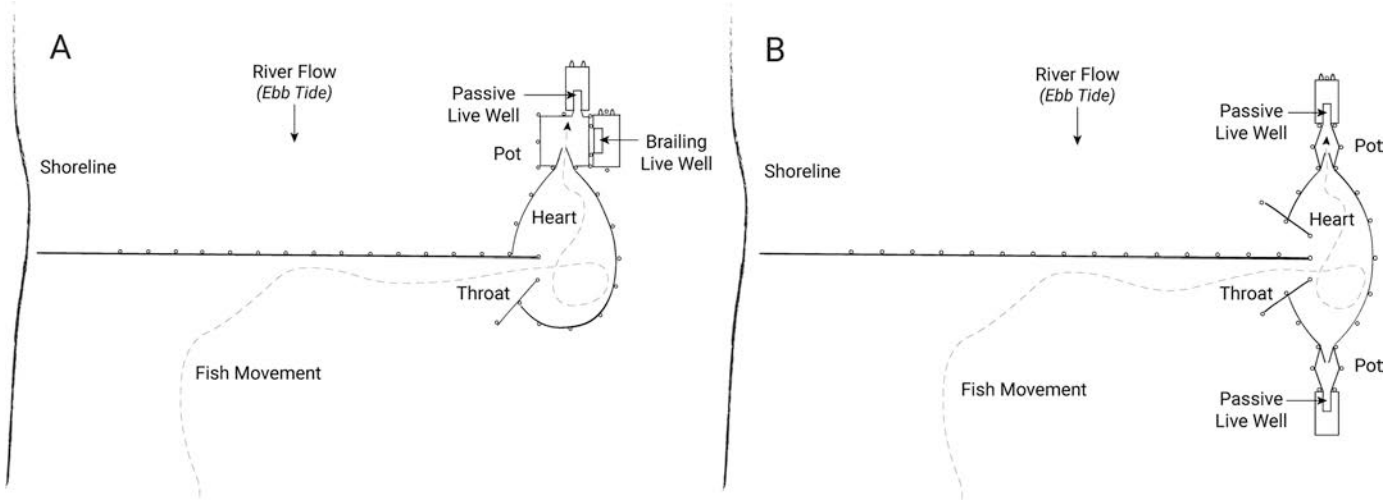


Fig. 2. Bycatch survival was evaluated at two separate fish trap sites. The Cathlamet, WA fish trap (A) was equipped with only one pot, from which fishes could be passively captured on the ebb tide or brailed in order to compare bycatch post-release survival effects from each treatment. The Clifton, OR fish trap (B) was equipped with two pots to allow for passive capture operations during all tides.

comparison to prototype brailing operations (Fig. 2a). Beyond survival investigations for spring-run and summer run Chinook salmon, this trap was further used for study of coho salmon survival, specifically for passive operations in 2020.

For studies of coho salmon in 2021, the Clifton Channel fish trap was used to estimate survival from passive operations. This fish trap was similar in design to that described by Tuohy et al. (2020), consisting of a lead (~90 m; 7.94 cm stretch mesh), jigger (~10 m; 6.35 cm stretch mesh), and heart (27-m length; 20-m maximum width; 6.35 cm stretch mesh) (Christensen Net Works, Everson, Washington) (Fig. 2b). The design embraced the same passive capture operation piloted by Tuohy et al. (2020) during the final moment of capture from the pot to live well; however, the Clifton Channel site was equipped with two pots (~7 m long × 4.3 m wide × 6 m deep; 6.35 cm stretch knotless mesh) located at both upstream and downstream ends of the heart (Fig. 2b). Abandoning brailing methods altogether, the upstream and downstream pots were designed specifically to passively ramp and funnel fishes against ebb and flood tides, respectively, to attached live wells positioned centrally at the apex of each pot compartment (Fig. 2b). Depending on the tide, operators would deploy the upstream or downstream pot toward the riverbed to allow for capture of fishes migrating against the tidal current from the heart. Once within the pot compartment, free-swimming fishes were guided volitionally against the current toward the apex of the pot to the live well.

Mirroring Tuohy et al. (2020), each live well was aluminum framed with 3.81-cm knotless-nylon mesh walls to enable fresh river water to constantly flow through the trough. The live well was equipped with two parallel rectangular chambers (2.74 × 0.61 × 0.76 m) and a mesh pivot capture door near the entrance of the live well from the pot. Operators could open or close the capture door of the live well to passively entrap migrating fishes in one chamber while enabling the adjacent chamber to occupy. Within the shallow live well, the free-swimming catch could be identified to species and adipose fin-clip status (indicating hatchery and wild origins) with underwater video cameras (Splashcam Deep Blue) or by observation from above the water surface. In a commercial setting, hatchery fishes identified by a clipped adipose-fin could be dip-netted from the live well for selective harvest; wild-origin salmonids and bycatch species could be passively released though a submerged exit door without handling or air exposure (Fig. 3). However, for this study it was necessary for operators to wade within the live well to restrain the catch for data collection purposes.

2.2.1. Chinook salmon survival study design

Research for spring-run and summer-run Chinook salmon was conducted in the lower Columbia River between May 5 and July 2, 2019 to fill existing data gaps for these Chinook salmon runs and provide an estimate of adult salmonid post-release survival for passively operated fish traps. Mark-recapture studies for estimation of Chinook salmon survival had been encouraged by resource managers; therefore, a tagging methodology was pursued for the species.



Fig. 3. Wild-origin coho salmon and other bycatch species could be passively captured with the modified fish trap, identified with underwater video cameras, and released though a submerged exit door without entanglement, brailing, human handling, or air exposure. Photo by Conrad Gowell. [Intended for color reproduction].

Similar to concurrent studies of sockeye salmon post-release survival (Tuohy et al., 2020), trap operators began a fishing event by deploying the pot compartment from its suspended position above the water column toward the river bottom. Pot tunnels were then opened, enabling the capture of free-swimming fish from the pot compartment for data collection. In capturing the catch for this mark-recapture tagging experiment, fishes were either (1) exposed to brailing en masse via the bunt of the pot net, or (2) passively captured and unexposed to brailing. It must be noted that greater effort was made to sample via passive capture operations (rather than brailing) to provide a more robust survival estimate for the newly developed fishing technique. During all operations, investigators documented the beginning set time, tidal stage (ebb, flood, and slack), water temperature (°C; Extech), presence of marine mammals, and the method of capture (exposed to brailing or unexposed to brailing). Tunnel doors remained open to fish passage until a pause or cessation of fishing was desired.

When a fish was captured through any means, the catch was restrained by hand or rubberized dip-net for data collection. Although commercial fisheries using the passive operation with the gear-type are designed to eliminate fish handling and air exposure, restraining the catch by hand or dip-net remained necessary for conducting the survival study. Wading within the live well, biologists or fishers enumerated, measured (fork-length (FL)), and identified all specimens by species and adipose fin-clip status. All salmonids (regardless of their adipose fin-clip status) were scanned for PIT-tags with a Biomark HPR Lite reader (Biomark, Boise, Idaho). If existing PIT-tags were detected, codes were recorded using P4 software (PSMFC, 2017); these salmonids were then allowed to passively migrate through the live-well exit door for detection upriver. All Chinook salmon lacking an existing PIT-tag (100 % of those encountered) and > 400 mm FL were tagged in the peritoneal cavity with a 12.5-mm, 134.2- kHz, full-duplex PIT-tag using a MK-25 Rapid Implant Gun (Biomark). These fish were then scanned to record PIT-tag information and a 1 mm caudal fin clip tissue sample was secured for future genetic processing by the Columbia River Inter-Tribal Fish Commission (CRITFC) Hagerman Genetics Laboratory. With all data collected, each fish was passively released through the live-well exit door for upriver detection at Bonneville Dam (rkm 234). Any fish that showed no signs of life at capture or release was noted as an immediate mortality.

2.2.2. Chinook salmon survival analysis

To determine where each PIT-tagged Chinook salmon was likely to migrate post-release from the fish trap, genetic samples were processed by CRITFC (Hess et al., 2021). Using a combination of Genetic Stock Identification (GSI) and Parentage Based Tagging (PBT) methods, Hess et al. (2021) assigned each PIT-tagged Chinook salmon to one of 19 established Columbia River Basin population reporting groups. With genetic assignment results paired with each PIT-tagged Chinook salmon, the sample was filtered for individuals genetically assigned to upper-basin population reporting groups originating above Bonneville Dam PIT-tag arrays (rkm 234). For the sample collected in this study, upper-basin reporting groups consisted of the Klickitat River spring-run (KLICKR), the Hells Canyon spring-run (HELLSC), the South Fork Salmon River spring-run (SFSALM), the upper Salmon River spring-run (UPSALM), and the upper Columbia River summer-/fall-run (UCOLSF). Lower-basin reporting groups consisted of the Columbia Rogue (YOUNGS), the West Cascade spring-run (WCASSP), and the Willamette River spring-run (WILLAM) (Hess et al., 2021). All PIT-tagged Chinook salmon genetically assigned to these lower-basin reporting groups were removed from the analysis given their tendency to remain below Bonneville Dam PIT-tag arrays. In regard to the accuracy of genetic assignment methods in identifying spring-run and summer-run Chinook salmon originating from these defined upper-basin population groups in

the Columbia River, it must be noted that the confidence of assignment to the pooled upper-basin reporting group was nearly 100 % (Hess et al., 2021).

Given the PIT-tagged Chinook salmon sample that had genetically assigned to upper-basin reporting groups, we used an unpaired single release–recapture method to estimate the joint probability of survival and detection for Chinook salmon released from each treatment group between the fish trap site (rkm 67) and Bonneville Dam (rkm 234). Bonneville Dam was selected as the final detection point primarily due to the fact that significant tribal gill net fisheries occurred upriver in the zone 6 fishery between Bonneville Dam and McNary Dam (with potential to bias unpaired survival estimates low above Bonneville Dam). Secondly, PIT-tag arrays at Bonneville Dam are known to have detection efficiencies for PIT-tagged adult salmon nearing 100 % (WDFW, 2014). Lastly, Vander Haegen et al. (2004) and Ashbrook (2008) had evaluated post-release survival of spring Chinook salmon from gill nets and tangle nets using Bonneville Dam as a final detection point. However, it is worth noting that our analysis of survival to Bonneville Dam occurred over a greater migration distance with the fish trap capture and tagging location located ~146 km downriver. In further contrast with relative survival studies of Vander Haegen et al. (2004) and Ashbrook (2008), our analysis was unpaired and lacked the ability to control for confounding factors such as tag loss, upriver predation, sport fisheries, and handling/tagging mortality effects. This was due to the fact that an insufficient sample of adult Chinook salmon ($n = 4$) that had been previously tagged in the juvenile life-stage was redetected at PIT-tag arrays in the lower river during the May 5 - July 2 study period to function as a viable control group. Furthermore, no other control sourcing method for capture and tagging of fishes in the adult life-stage appeared lower-impact than passive operations with the commercial fish trap within the study region. Therefore, the unpaired analysis of post-release survival in this study was inherently conservative, with the survival estimate prone to negative bias.

Upriver detection histories for PIT-tagged spring-run and summer-run Chinook salmon in 2019 were downloaded on November 19, 2019, from the Columbia Basin PIT-Tag Information System (PTAGIS), which provides public access to all PIT-tag detection data throughout the Columbia River Basin. It must be noted that one additional PIT-tagged Chinook salmon (Code: 3DD.003C06B8DA; passive treatment, tagged on June 16) that failed to upload to the PTAGIS database was detected at Bonneville Dam on June 24. Given interrogations of the tagged sample 167 km upstream at Bonneville Dam, the observed detection rate was directly estimated by a binomial proportion (p = # detected/# total tagged) with associated binomial variance. Observed detection was used as a proxy for post-release survival assuming Bonneville Dam PIT-tag arrays had detection efficiencies of 100 %. Similar to other Columbia River alternative fishing gear survival studies (WDFW, 2014; Tuohy et al., 2019), cumulative survival (representing the total estimated mortality effect from fish trap capture and release processes) was calculated for pooled hatchery and wild-origin Chinook salmon as the product of immediate survival at release from the gear (S_0 = # survived/# encountered) and post-release survival to Bonneville Dam (S_1). The 95 % profile likelihood confidence interval was estimated through Program USER (Skalski and Millspaugh, 2006; http://www.cbr.washington.edu/analy sis/apps/user). In the case of no observed mortality, a lower one-tailed interval estimate of survival was calculated using the method in Skalski (1981).

2.2.3. Coho salmon survival study design

The net pen holding studies conducted in 2020–2021 were similar in design to those conducted by Buchanan et al. (2002), Takata and Johnson (2018), and Tuohy et al. (2020) in which coho salmon were captured with a commercial gear and released into captivity to directly observe mortalities over a set period of time. This methodology of estimating post-release survival was selected for four primary reasons: (1) coho salmon mostly spawn in tributaries of the lower Columbia River below mainstem dam PIT-tag arrays; (2) technologies to detect PIT-tags or radio tags below Bonneville Dam are insufficient to meet model assumptions for release-recapture (WDFW, 2014); (3) previous alternative gear studies specific to coho salmon in the lower Columbia River have mostly relied upon a net pen holding methodology to estimate post-release survival (Takata and Johnson, 2018); and (4) resource managers had encouraged use of the net pen holding methodology for coho salmon, specifically.

Mirroring Takata and Johnson (2018) in the timeframe of study in the lower Columbia River, net pen holding studies were conducted from late September through October 2020 when commercial coho salmon fisheries commonly occur. Our studies observed coho salmon survival from the passive trapping process over 2 d and 4 d post-release periods in water temperatures ranging from 16.7 °C to 19.3 °C—conditions warmer than that of Takata and Johnson (2018) for evaluation of tangle nets. At the recommendation of management agency representatives, the study period in 2021 was shifted earlier than any prior coho salmon net pen holding study conducted in the lower Columbia River to evaluate 6 d post-release survival of the species in adverse water quality conditions in early September. It must be noted that study investigators anticipated confounding mortality effects from prolonged confinement in nearly lethal water quality conditions exceeding 20 °C (EPA, 2003, 2021; Donaldson et al., 2011).

On research days in each year of study, trap operators deployed the pot of the gear to the river bottom and opened the tunnel doors to initiate the soak period. Observers noted the set time, water temperature (ºC; Extech), and presence of marine mammals. With the soak period initiated, the pot and live well of the modified fish trap was monitored to determine fish entrance and occupancy. Once a live well chamber was occupied by one or more fishes, operators passively trapped the catch through closure of the capture door. Captured fishes were enumerated, measured (FL), noted for capture/release conditions ("lively," "lethargic," or "no signs of life"; Takata and Johnson, 2018), and identified by species and adipose fin-clip status. After all data were collected, salmonids were released to resume the upriver migration unless criteria were met for inclusion in coho salmon net pen holding studies.

During collection of net pen holding samples, adult coho salmon (> 47 cm FL) captured with the modified trap were restrained by hand and transferred individually with a rubberized dip net to a designated temporary holding chamber of the live well until a sample of approximately 29–44 fish was retained. With the desired sample size achieved after a 4–12 h collection period, investigators sealed outlets to all pot tunnels. Coho salmon were once again restrained by hand, enumerated, identified by origin (adipose fin clipped or unclipped), measured (FL), noted for capture condition, and transferred from the live well by hand or dip-net to the sealed pot compartment (now functioning as a net pen holding chamber with dimensions similar to Takata and Johnson, 2018). Once the last fish was released into the net pen, investigators initiated holding periods of 0–2 d (S_1), 2–4 d (S_2), and 4–6 d (S_3). With the holding study underway, a biologist was stationed on site to note the date, time, water temperature (°C; Extech), and presence of marine mammals. As in previous studies (Takata and Johnson, 2018), coho salmon that exhibited significant predator-induced injuries or previous damage from gill nets were excluded from the holding study.

2.2.4. Coho salmon survival analysis

Post-release survival of pooled hatchery-origin and wild-origin coho salmon was estimated by holding and observing three trial groups (sample size mean = 35, min = 29, max = 38) for a 4-d period in 2020 and five trial groups (sample size mean = 40, min = 38, max = 44) for a 6-d period in 2021. To determine fish mortalities during the holding periods, samples were checked at least once daily at regular intervals from above and below the water surface (via snorkel/free-dive and underwater video survey). At the end of the holding period, all fish in the pen were enumerated, measured (FL), identified for species type and adipose fin-clip status, noted for condition ("lively," "lethargic," or "no

signs of life"), and released to resume the upriver migration.

At the conclusion of each research season, data from the trial groups were pooled within each defined post-release period—0–2 d (S_1), 2–4 d (S_2), and 4–6 d (S_3). Post-release survival in each period was directly estimated by a binomial proportion ($p = \#$ survived/# total) with associated binomial variance. Cumulative survival ($S_0{}^* S_1{}^* S_2{}^* S_3$) was calculated as the product of immediate survival (S_0) and post-release survival ($S_1{}^* S_2{}^* S_3$) with the 95 % profile likelihood confidence interval estimated through Program USER (Skalski and Millspaugh, 2006). In the case of no observed mortality, a lower one-tailed interval estimate of survival was calculated using the method in Skalski (1981). For these post-release survival studies, it must be noted that potentially confounding mortality effects from factors such as net pen confinement, environmental stressors, natural mortality, and research processes (e.g., fish handling and dip-netting on two occasions to restrain fish during data collection and transfer to the holding pens) were not controlled.

3. Results

3.1. Chinook salmon

Between May 5 and July 2, 2019, at the Cathlamet, WA fish trap site, a total of 146 spring and summer-run Chinook salmon (71.2 % adipose fin-clipped) were genetic sampled and PIT-tagged for a mark-recapture analysis. In efforts to restrain the catch in the live well for genetic sampling and tagging, 114 were captured through passive operations with the fish trap and 32 fish were captured via brailing with the bunt of the pot net. Of the total tagged and genetic sampled population, 80 were classified by capture date as spring-run (< 15 June) and 66 were summer-run (> 15 June). During all gear operations, tagging, and genetic sampling, zero Chinook salmon adult or jack immediate mortalities occurred, resulting in an immediate survival estimate of $\widehat{S}_0 = 1.000$ (95 % CI: $S \geq 0.982$) for returning adults and jacks. Water temperatures ranged from 13.4 °C to 19.2 °C (mean = 16.3 °C). On three separate occasions, a California Sea Lion (*Zalophus californianus*) was observed within the vicinity of the trap site for periods less than ~10 min; no fish predation was observed by the study investigators during these incidents.

Stock composition of the sampled Chinook salmon population was estimated through a combination of GSI and PBT by Hess et al. (2021), resulting in genetic stock assignments for 142 PIT-tagged Chinook salmon to defined Columbia River Basin population reporting groups (Table 1). For the PIT-tagged Chinook salmon that were captured through passive operations with the fish trap and paired with genetic assignment data ($n = 110$), 88 fish (80.0 %) were assigned to upper-basin reporting groups above Bonneville Dam (i.e., SFSALM, UPSALM, and UCOLSF) and 22 fish (20.0 %) were assigned to lower-basin reporting groups below Bonneville Dam (i.e., WCASSP and WILLAM) (Table 1). Of the PIT-tagged Chinook salmon captured via brailing operations and paired with genetic assignment data ($n = 32$), 19 fish (59.4 %) were assigned to upper-basin reporting groups above Bonneville Dam (i.e., UCOLSF, HELLSC, and KLICKR) and 13 fish (40.6 %) were assigned to lower-basin reporting groups below Bonneville Dam (i.e., YOUNGS, WCASSP, and WILLAM) (Table 1).

Given the Chinook salmon samples that were PIT-tagged and successfully paired with upper Columbia River Basin genetic assignment data for passive operations ($n_{\text{passive}} = 88$) and brailing operations ($n_{\text{brailing}} = 19$), detection rates for each group were determined at PIT-tag arrays at or above Bonneville Dam (Table 2). For upper-basin Chinook salmon exposed to passive operations with the fish trap, observed detection was 1.000 (95 % CI: $S \geq 0.970$). For upper-basin Chinook salmon exposed to brailing operations, observed detection was 0.947 (95 % CI: $0.788 \leq S \leq 0.997$) (Table 2). The one fish that was not detected at Bonneville Dam from the brailed sample (assigned to UCOLSF) did not appear to have evaded detection based upon data from arrays positioned upriver of Bonneville Dam. Given the observed detection results, detection differed between passive and brailed samples at the $\alpha = 0.05$ level ($|Z| \geq 2.162$, $P = 0.03$). For the two treatment groups, mean migration time over the total 167 km distance from the fish trap to Bonneville Dam was estimated at 6.5 d (95 % CI: $5.7 \leq M \leq 7.3$) for the passively captured treatment group and 7.3 d (95 % CI: $5.6 \leq M \leq 9.0$) for the brailed treatment group.

3.2. Coho salmon

Between September 25 and October 15, 2020, a 4-d net pen holding study was conducted at the Cathlamet, WA fish trap site for coho salmon captured using passive operations. During the research period, water temperatures ranged from 16.7ºC to 19.3ºC (mean = 18.1ºC). Encountering 2209 adult coho salmon in the fall 2020 fishing season, there were zero adult immediate mortalities resulting in an immediate survival estimate of $\widehat{S}_0 = 1.000$ (95 % CI: $S \geq 0.999$). A total of 105 coho salmon (71.4 % adipose fin-clipped) were held in captivity post-release from the commercial gear in three separate trial groups (Table 3). No mortalities occurred within 0–2 d, nor did any mortalities occur between 2 and 4 d for post-release survival estimates of $\widehat{S}_1 = 1.000$ (95 % CI: $S_1 \geq 0.975$) and $\widehat{S}_2 = 1.000$ (95 % CI: $S_2 \geq 0.975$), respectively (Table 4). All coho salmon encountered during the fish collection process for the 2020 holding study were lively and vigorous upon capture and release after 4 d, with zero fish appearing lethargic. However, the snout and caudal fins of all fish appeared moderately abraded upon release after 4 d of confinement in the net pen environment.

In 2021, a 6-d net pen holding study was conducted at the Clifton, OR fish trap site for coho salmon captured using passive operations. This

Table 1
Spring-run and summer-run Chinook salmon were genetically assigned to Columbia River Basin population reporting groups above and below the PIT-tag array at Bonneville Dam by Hess et al. (2021). Upper-basin reporting groups consisted of the Klickitat River spring-run (KLICKR), the Hells Canyon spring-run (HELLSC), the South Fork Salmon River spring-run (SFSALM), the upper Salmon River spring-run (UPSALM), and the upper Columbia River summer-/fall-run (UCOLSF). Lower-basin reporting groups consisted of the Columbia Rogue (YOUNGS), the West Cascade spring-run (WCASSP), and the Willamette River spring-run (WILLAM).

Upper or lower-basin genetic assignment	Genetic reporting group	Passive treatment	Brailed treatment
Lower-basin	YOUNGS	0	1
(below Bonneville Dam)	WCASSP	2	1
	WILLAM	20	11
Total tagged and assigned below Bonneville Dam:		**22**	**13**
Upper-basin	KLICKR	0	1
(above Bonneville Dam)	HELLSC	0	2
	SFSALM	1	0
	UPSALM	1	0
	UCOLSF	86	16
Total tagged and assigned above Bonneville Dam:		**88**	**19**

Table 2
The spring-run and summer-run Chinook salmon sample size, PIT-tag detections, observed detection rate at Bonneville Dam, and the associated 95 % profile likelihood confidence interval (in parentheses) are shown for passively captured and brailed treatment groups.

Category	**Passive treatment**	**Brailed treatment**
Detected at Bonneville Dam	88	18
Total tagged and assigned to populations above Bonneville Dam	88	19
Observed detection rate	**1.000 (0.970 – 1.000)**	**0.947 (0.788 – 0.997)**

Table 3
Coho salmon mortalities were observed over 0–2 d, 2–4 d, and 4–6 d net pen holding periods in the fall of 2020–2021. The observation date, sample size, fish mortalities, and mean water temperature are shown for each trial group.

Year	Trial group	Dates	Mean water temperature (°C) and 95 % confidence interval	0–2 d		2–4 d		4–6 d	
				n	Mortalities	*n*	Mortalities	*n*	Mortalities
2020	1	25 Sep–29 Sep	18.6 (18.5–18.7)	38	0	38	0	–	–
	2	4 Oct– 8 Oct	18.4 (18.3–18.5)	38	0	38	0	–	–
	3	11 Oct– 15 Oct	17.2 (17.1–17.3)	29	0	29	0	–	–
	Total	25 Sep– 15 Oct	18.1 (17.9–18.2)	105	0	105	0	–	–
2021	1	3 Sep– 9 Sep	20.4 (20.2–20.5)	38	1	37	0	37	0
	2	9 Sep– 15 Sep	20.3 (20.2–20.5)	39	0	39	1	36	3
	3	16 Sep– 22 Sep	19.3 (19.1–19.4)	38	0	38	0	38	1
	4	23 Sep– 29 Sep	18.7 (18.5–18.8)	44	0	44	0	44	1
	5	29 Sep– 5 Oct	17.9 (17.8–18.1)	41	0	41	0	41	0
	Total	3 Sep– 5 Oct	19.3 (19.1–19.5)	200	1	199	1	196	5

Table 4
Immediate and post-release survival of coho salmon was estimated in 2020 and 2021. Associated 95 % confidence intervals are provided in parentheses.

Year	Survival estimate and 95 % confidence interval				
	Immediate	(>0–2 d)	(2–4 d)	(4–6 d)	Cumulative
2020	1.000 (0.999–1.000)	1.000 (0.975–1.000)	1.000 (0.975–1.000)	–	1.000 (0.975–1.000)
2021	0.999 (0.997–0.9998)	0.995 (0.978–0.9997)	0.995 (0.978–0.9997)	0.974 (0.946–0.991)	0.964 (0.947–0.968)

study was conducted earlier in the fall fishing season than prior years, with fish collection dates occurring as early as a sufficient sample of coho salmon could be collected between September 3 and September 29. Throughout the net pen holding experiment, water temperatures ranged from 17.4°C to 20.9°C (mean = 19.3°C). Encountering 1790 adult coho salmon over the 2021 fishing season, two adult immediate mortalities occurred due to predator-induced injury. Based upon the freshness of the wounds, investigators assumed these injuries occurred in the vicinity of the trap site, resulting in an immediate survival estimate of $\widehat{S}_0 = 0.999$ (95 % CI: $0.997 \leq \widehat{S}_0 \leq 0.9998$).

A total of 200 coho salmon (90.5 % adipose fin-clipped) were held in captivity post-release from the commercial gear for a 0–2 d duration in five separate trial groups (Table 3). One mortality occurred during the 0–2 d holding period for a post-release survival estimate of $\widehat{S}_1 = 0.995$ (95 % CI: $0.978 \leq \widehat{S}_1 \leq 0.9997$) (Table 4).

With one mortality occurring during the 0–2 d holding period, a total of 199 coho salmon were held in captivity for the 2–4 d holding period in five separate trial groups (Table 3). Similar to the 0–2 d holding period, one mortality occurred between 2 and 4 d of confinement for a survival estimate of $\widehat{S}_2 = 0.995$ (95 % CI: $0.978 \leq \widehat{S}_2 \leq 0.9997$) (Table 4).

Given the two total mortalities that occurred within the 0–2 d and 2–4 d holding periods and removing two fish from the sample due to pinniped predation within the holding pen, a total of 196 coho salmon were held in captivity for the 4–6 d holding period in five separate trial groups (Table 3). Between 4 and 6 d of confinement, five mortalities occurred (Table 3). From these results, 4–6 d survival was estimated at $\widehat{S}_3 = 0.974$ (95 % CI: $0.946 \leq \widehat{S}_3 \leq 0.991$). From these findings, we estimated total post-release survival (i.e., $S_1 * S_2 * S_3$) in 2021 to be 0.965 (95 % CI: $0.948 \leq \widehat{post-release} \leq 0.969$). Incorporating immediate survival, cumulative survival was estimated at 0.964 (95 % CI: $0.947 \leq \widehat{cumulative} \leq 0.968$) (Table 4).

Similar to prior years of study, all coho salmon encountered during the fish collection process for the holding study were lively and vigorous upon capture with no signs of physical injury related to the commercial gear. Those that survived the 6 d holding period to release also appeared lively and vigorous despite considerable abrasion to the snout and caudal fins from prolonged confinement in the net pen environment. Cause of death for the mortalities within this study could not be determined from autopsy but likely were the result of the pooled effect of natural mortality, confinement in the net pen environment during adverse water temperature conditions (> 20 °C), and potential stressors from passive capture and research processes.

4. Discussion

Research findings over these three years of study at two separate fish trap sites further suggest that recently developed commercial fish trapping techniques can allow for selective harvesting of hatchery produced fish (and other abundant fish runs) while achieving nearly 100 % post-release survival of ESA-listed adult salmonids. Using mark-recapture and net pen holding techniques to estimate post-release survival of coho salmon and Chinook salmon (both spring-run and summer-run stocks), results for each species and methodology mostly validate the findings of prior survival studies for sockeye salmon, coho salmon, fall-run Chinook salmon, and summer-run steelhead from passive operations with the gear (Tuohy et al., 2020; Cox and Sippel, 2020) (Table 5). Evaluating detections of PIT-tagged spring-run and summer-run Chinook salmon that were genetically assigned to population reporting groups above Bonneville Dam (Hess et al., 2021), observed detection of the passively captured and released treatment group at Bonneville Dam was 1.000 (95 % CI: $S \geq 0.970$) over a 6.5 d, 167 km migration. Given

Table 5
Stock-specific post-release survival estimates and 95 % confidence intervals are shown for all studies relevant to passive operations with fish traps between 2017 and 2021 (Cox and Sippel, 2020[a]; Tuohy et al., 2020[b]).

Salmonid stock	Study period	Water temperature (°C)	Study methodology	Survival estimate and 95 % confidence interval
Summer steelhead	Aug-Sep, 2017	18.7 – 22.3	Paired mark-recapture[a]	1.000 (0.783 – 1.000)
Fall Chinook	Aug-Sep, 2017	18.7 – 22.3	Paired mark-recapture[a]	1.000 (0.752 – 1.000)
Spring/Summer Chinook	May-Jul, 2019	13.4 – 19.2	Unpaired mark-recapture	1.000 (0.970 – 1.000)
Sockeye	May-Jul, 2019	14.4 – 19.2	Paired mark-recapture[b]	1.000 (0.974 – 1.000)
Coho	Sep-Oct, 2019	12.1 – 19.2	Unpaired net pen holding (2 d)[b]	1.000 (0.978 – 1.000)
Coho	Sep-Oct, 2020	16.7 – 19.3	Unpaired net pen holding (4 d)	1.000 (0.975 – 1.000)
Coho	Sep-Oct, 2021	17.4 – 20.9	Unpaired net pen holding (6 d)	> 0.965 (0.947 – 0.968)

that this unpaired analysis lacked a control group to adjust for confounding factors such as tag loss and mortality effects from research handling and tagging, upriver predation, fisheries, and the natural environmental baseline, the study methodology for survival estimation was inherently conservative and prone to negative bias. Therefore, the survival estimate of 1.000 from this study of spring-run and summer-run Chinook salmon supports the conclusion that actual survival was at or near 1.000. Although there may seem to be sample size limitations, the fact that 88 of 88 of the PIT-tagged sample that had assigned to upper-basin populations were detected at Bonneville Dam in the absence of a control group (Table 2) is highly persuasive and corroborates the findings of prior studies for passively operated fish traps that estimated survival at 1.000 (Table 5; Tuohy et al., 2020; Cox and Sippel, 2020).

Mark-recapture post-release survival findings for the passively operated fish trap are further supported by the net pen holding results for coho salmon in 2020–2021. Similar to Tuohy et al. (2020) that estimated coho salmon post-release survival from passive operations with fish traps at $\widehat{S}_1 = 1.000$ (95 % CI: $S_1 \geq 0.978$) over 0–2 d in 2019, we estimated 0–2 d post-release survival at $\widehat{S}_1 = 1.000$ (95 % CI: $S_1 \geq 0.975$) in 2020 and $\widehat{S}_1 = 0.995$ (95 % CI: $0.978 \leq \widehat{S}_1 \leq 0.9997$) in 2021. Similarly, over 4 d of confinement, we estimated post-release survival at $\widehat{S}_2 = 1.000$ (95 % CI: $S_2 \geq 0.975$) in 2020 and $\widehat{S}_2 = 0.995$ (95 % CI: $0.978 \leq \widehat{S}_2 \leq 0.9997$) in 2021. These survival results for coho salmon are equivalent to the mark-recapture results for spring-run and summer-run Chinook salmon from 2019.

Although findings for 4–6 d net pen holding deviate from the conclusions of all other studies for passively operated fish traps with post-release survival estimated at $\widehat{S}_3 = 0.974$ (95 % CI: $0.946 \leq \widehat{S}_3 \leq 0.991$), it must be noted that the net pen holding methodology lacked a control group to adjust for confounding mortality factors including confinement in nearly lethal water quality conditions, the natural environmental baseline, and research processes (e.g., dip-netting, fish handling, and other stressors unique to the study and absent from commercial processes). Based upon the environmental conditions experienced during the 2021 holding study, it is likely that the few mortalities that occurred between 4 and 6 d of captivity were primarily due to the prolonged effects of confinement in sublethal to lethal water quality conditions and abrasion in the holding pen. During the holding period for trial group two when the majority of the long-term mortalities occurred (Table 3), water temperatures consistently neared or exceeded thresholds identified as potentially lethal for fall runs of salmon in the Columbia River (20–22 °C; Coutant, 1970; Becker, 1973; EPA, 2003; EPA, 2021), with the mean temperature during captivity estimated at 20.3 °C (95 % CI: 20.2 °C $\leq \widehat{temp} \leq$ 20.5 °C). In the captive net pen environment, fishes in the study could not find temperature refugia available in the wild and remained subject to adverse water quality conditions (> 20 °C) known to increase fish susceptibility to disease, parasites, stress, and mortality (Fryer and Pilcher, 1974; Groberg et al., 1978; Richter and Kolmes, 2005).

In addition to the likely mortality effects from adverse water quality conditions, the mortality effects of prolonged net pen confinement on wild fish survival are well-established in the scientific literature (Portz et al., 2006; Donaldson et al., 2011; Raby et al., 2015a, 2015b). Donaldson et al. (2011) demonstrated that sockeye salmon held in confinement for 1 d resulted in substantial physiological stress and significantly higher mortality than fish unexposed to net pen confinement. Raby et al., 2015a, 2015b drew similar conclusions for coho salmon, determining that physiological stress and the time-specific rate of mortality was higher for fish held in net pens for 1 d than fish tagged and immediately released. Based upon the evidence, it is clear that wild adult salmon experience severe physiological stress from prolonged periods of net pen confinement that can increase the likelihood of mortality from various factors, including lethal water quality conditions. This may be the reason that virtually all holding studies used to set official gear mortality rates have been conducted over 1–3 d holding periods (Raby et al., 2015a, 2015b). Considering that few known post-release mortality studies for coho salmon have been conducted over a period of 6 d or longer (Takata and Johnson, 2018) and no known commercial fishery mortality study to date has ever held salmon in net pens where water temperatures commonly exceeded 20 °C, it is likely that coho salmon post-release survival results from 2021 were biased low and the true survival effect from passive operations with the fish trap exceeded that of 0.974 during the 4–6 d holding period.

While these post-release survival studies generally validate the findings of previous studies conducted for passively operated fish traps (Table 5), Chinook salmon survival results also corroborate the findings of Tuohy et al. (2020) and Cox and Sippel (2020) in supporting the hypothesis that bycatch survival from passively operated fish traps exceeds that of prototype brailing operations. Although the sample size for the brailed treatment group was limited ($n = 19$) and results for the treatment should be viewed with caution, the observed detection rate of 0.947 (95 % CI: $0.788 \leq S \leq 0.997$) at Bonneville Dam was similar to Cox and Sippel's (2020) survival estimate of $S = 0.935$ (95 % CI: $S \geq 0.648$) for upper-basin fall-run Chinook salmon released from brailing operations. For passive operations with the fish trap, our analysis of PIT-tagged spring-run and summer-run Chinook salmon demonstrated that the joint probability of survival and detection over 167 km to Bonneville Dam was 1.000 (95 % CI: $S \geq 0.970$), exceeding that of brailing operations ($|Z| \geq 2.162$, $P = 0.03$). Once again, this conclusion mirrors that of Cox and Sippel (2020) that compared brailing vs. passive operations and similarly estimated survival of upriver-basin fall-run Chinook salmon from passive operations with fish traps at 1.000 (95 % CI: $S \geq 0.752$) = 0.95). The same significant difference in survival was found by Tuohy et al. (2020) in an analysis of brailing vs. passive operations for sockeye salmon. By addressing the primary physical and physiologically factors known to impact bycatch survival (Donaldson et al., 2014; Raby et al., 2015a, 2015b), it appears that use of passive operations with fish traps provides survival benefits to encountered salmonid bycatch stocks. Nevertheless, statistical differences in survival between treatment groups from this study must be viewed with caution given the small sample size collected for the brailed treatment group.

4.1. Conclusions

The primary strength of this research is the simplicity of the methods and the strikingly high bycatch survival results achieved for all methods

of fish trap operation despite the inherent negative biases within the statistical analyses. Various studies relevant to passively operated fish traps have now been conducted demonstrating bycatch survival at or near 1.000 (Tuohy et al., 2020; Cox and Sippel, 2020; Table 5); however, there is perhaps no evidence as simple and persuasive as that from these three unpaired mark-recapture and net pen holding studies conducted at two separate fish trap sites across three seasons in the lower Columbia River. With the inability to control for well-known confounding mortality factors, post-release survival was 1.000 for spring-run and summer-run Chinook salmon in 2019; for coho salmon, post-release survival was estimated at 1.000 and 0.965 in 2020 and 2021, respectively. Given these estimates of post-release survival and the collective evidence from other prior studies of passively operated fish traps (Table 5), it is evident that the fishing practice may allow for selective harvesting of targeted fish stocks while minimizing bycatch mortality of ESA-listed adult salmonids in Pacific Northwest fisheries. Furthermore, the results demonstrate that passively operated fish traps may provide increased opportunities for low-impact salmonid population monitoring and serve as a zero-mortality control group to fill data gaps for other poorly understood commercial or recreational fishing gears used within the Columbia River and elsewhere throughout the region. Ultimately, findings of these studies may be applied to improve management of Pacific Northwest salmon fisheries, inform the implementation of alternative gear fisheries, and protect the diversity and abundance of ESA-listed wild salmonids for recovery.

CRediT authorship contribution statement

Adrian M. Tuohy: Conceptualization, Methodology, Funding Acquisition, Resources, Project Administration, Investigation, Data Curation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Aaron T. Jorgenson:** Conceptualization, Methodology, Project Administration, Investigation, Data Curation, Validation, Writing – review & editing, Visualization. **John R. Skalski:** Supervision, Software, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

All data may be downloaded through the Wild Fish Conservancy webpage (https://wildfishconservancy.org/the-fish-trap-project/fish-trap-research/) by scrolling downward and clicking on the “Data” tab. All PIT-tag information can be accessed through the PTAGIS webpage (www.ptagis.com) using the code “CPN” and name “Cathlamet Pound Net.

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Glossary

CRITFC: Columbia River Inter-Tribal Fish Commission
ESA: Endangered Species Act.
GSI: Genetic stock identification methods for genetic assignment.
HELLSC: Hells Canyon spring-run.
KLICKR: Klickitat River spring-run.
PBT: Parentage based tagging methods for genetic assignment.
SFSALM: South Fork Salmon River spring-run.
TAC: U.S. v. Oregon Technical Advisory Committee.
UCOLSF: Upper Columbia River summer-/fall-run.
UPSALM: Upper Salmon River spring-run.
WCASSP: West Cascade spring-run.
WILLAM: Willamette River spring-run.
YOUNGS: Columbia Rogue.

PLOS ONE

RESEARCH ARTICLE

Population growth is limited by nutritional impacts on pregnancy success in endangered Southern Resident killer whales (*Orcinus orca*)

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Abstract

The Southern Resident killer whale population (*Orcinus orca*) was listed as endangered in 2005 and shows little sign of recovery. These fish eating whales feed primarily on endangered Chinook salmon. Population growth is constrained by low offspring production for the number of reproductive females in the population. Lack of prey, increased toxins and vessel disturbance have been listed as potential causes of the whale's decline, but partitioning these pressures has been difficult. We validated and applied temporal measures of progesterone and testosterone metabolites to assess occurrence, stage and health of pregnancy from genotyped killer whale feces collected using detection dogs. Thyroid and glucocorticoid hormone metabolites were measured from these same samples to assess physiological stress. These methods enabled us to assess pregnancy occurrence and failure as well as how pregnancy success was temporally impacted by nutritional and other stressors, between 2008 and 2014. Up to 69% of all detectable pregnancies were unsuccessful; of these, up to 33% failed relatively late in gestation or immediately post-partum, when the cost is especially high. Low availability of Chinook salmon appears to be an important stressor among these fish-eating whales as well as a significant cause of late pregnancy failure, including unobserved perinatal loss. However, release of lipophilic toxicants during fat metabolism in the nutritionally deprived animals may also provide a contributor to these cumulative effects. Results point to the importance of promoting Chinook salmon recovery to enhance population growth of Southern Resident killer whales. The physiological measures used in this study can also be used to monitor the success of actions aimed at promoting adaptive management of this important apex predator to the Pacific Northwest.

Competing interests: The authors have declared that no competing interests exist.

1. Introduction

The Southern Resident killer whales (SRKW; *Orcinus orca*) represent the southern population of the fish-eating ecotype inhabiting the northeast Pacific Ocean [1]. From late May through October, the three SRKW pods, termed J, K and L, frequent the inshore waters of Washington State and British Columbia, commonly known as the Salish Sea. Following a near 20% decline in their population during the late `90's, the population was listed as endangered under the Canadian Species at Risk Act in 2001 [2] and the U.S. Endangered Species Act in 2005 [1]. Only 78 individuals (J pod = 24 individuals; K pod = 19 individuals; L pod = 35 individuals) remain in the current population as of December, 2016 [3]. Reduced availability of their preferred prey, threatened and endangered Chinook salmon, appears to be at the core of the SRKW decline [4±7], although exposure to toxicants [8], and pressure from vessel disturbance may also contribute to these cumulative effects [9].

Reduced fecundity appears to be a particularly important contributor to the SRKWs failure to recover [4]. The rate of successful pregnancy in the wild population is unknown since, to date, pregnancy is only confirmed by observation of a newborn calf. SRKW typically give birth every 5.3 years [10]. However, holding age structure and survivorship constant, fecundity rates of SRKW (0.21) are significantly lower than those of Northern Resident (0.26;) [11] or Southeast Alaskan Resident killer whales (0.27) [12], neither of which are listed as at risk. Assuming a median peak fecundity rate of 0.21, the 31 potentially reproductive females in the SRKW population should have had 48 births between 2008±2015. Yet, only 28 births were recorded during that period. The 7 adult females in K pod have not had a birth since 2011, and just two births since 2007. The 24 females in the remaining two pods (J and L) have averaged < 1 birth per pod since 2011, with no births in 2013, but had 7 births in 2015. One of the two offspring born in 2014 died [3]. This study addresses causes of the low reproductive rate in SRKWs in an effort to recommend management decisions that can enhance population growth and long-term sustainability of this endangered population.

We examine determinants of pregnancy success and failure in the SRKWs from 2008 through 2014 based on hormone measures of pregnancy occurrence and health as well as physiological stress from genotyped feces. SRKW fecal samples are located with high efficiency by specially trained detection dogs, with detection rates over five times that by trained human observers [5,13,14]. Progesterone and testosterone collectively provide reliable indices of pregnancy occurrence, timing and health in killer whales. Concentrations of both P4 and T increase several-fold during gestation, although the increase is more gradual for T. Both hormones sharply decline to pre-conception levels around parturition [15,16]. We develop and validate a noninvasive endocrine measure of pregnancy occurrence and loss in the killer whales using metabolites of progesterone (P4) and testosterone (T) excreted in their feces.

Fecal glucocorticoid (GC) and thyroid (T3) hormone metabolite measures are used to monitor nutritional and disturbance stress within and between years. These two endocrine systems work closely together to regulate energy availability and utilization to meet nutritional, growth and thermoregulatory demands [17]. GCs rapidly rise in response to poor nutrition, cold temperature and disturbance stressors, mobilizing glucose to provide energy to deal with the immediate emergency [18,19]. GC concentrations over time are particularly informative for distinguishing nutritional from boat stress since abundances of both Chinook and whale-watching boats have very similar temporal patterns. Chinook and boat abundance are both relatively low in spring, peak in mid- to late August and then decline. Yet, the GC signal from nutritional stress should be lowest when fish abundance is at its peak while highest when boat density is at its peak [5].

Thyroid hormone (triiodothyronine, T3), on the other hand, produces a more conservative response to nutritional and thermal stress, functioning by adjusting metabolism. It is also

important to promote fetal brain growth during gestation [20]. While T4 is the most abundant thyroid hormone, it is directly converted to T3, which has many times the biological activity of T4 [20,21]. T3 levels are relatively slow to change when food shortages are first encountered, allowing the body to use all available fuel to search for food. If poor food conditions persist, T3 abruptly declines, lowering metabolism to prevent the body from exhausting its remaining fuel stores [21±24]. T3 may also be blunted under good food conditions when a low metabolism is needed to increase growth (e.g., to accumulate blubber stores in fall, in preparation for the relatively lean winter; [20]). In dolphins, T3 is lower in failed versus successful pregnancies at all stages of gestation [25]. T3 is relatively unresponsive to disturbance stress.

This study uses temporal patterns in P4 and T to predict pregnancy outcomes among the SRKWs and T3, GC and the T3/GC ratio to index the importance of nutritional and other stressors in their reproductive decline.

1.1 SRKW natural history

Mean reproductive maturity (age at first conception) in female SRKWs occurs at 9.8 years of age in captivity 12.1 years in the wild [10,26]. Maximum fecundity (probability of becoming pregnant in a single estrous cycle) of SRKW occurs between ages 20±22, increasing quickly during the first four years after sexual maturity, slowly declining from age 22 to 39, and then precipitously declining thereafter [4,10]. Gestation is approximately 18 months, making the prior year's salmon availability particularly important to fecundity [11,27].

During our late May through October study period, the SRKWs primarily feed on Chinook salmon, increasingly dominated by Fraser River Chinook (FRC) returning to spawn in nearby rivers [28,29]. SRKWs generally spend the remainder of the year outside the Salish Sea, moving up and down the Pacific Coast, from CA to Southeast AK [6]. K and L pods tend to spend more time further south than does J pod in winter, while J pod frequents the Salish Sea more than does K and L pods in summer and winter. Nutritional demands on SRKW are presumed to be greatest in winter when their salmonid prey are more widely dispersed, smaller in size and other non-salmonid prey appear to be a larger fraction of the diet [6,29,30]. Thermoregulatory demands may also influence nutritional demands during winter. SRKW then transition to spring, eventually subsisting on a diminishing number of spring/summer run adult Chinook salmon approaching river mouths inside and outside the Salish Sea until the Fraser River Chinook (FRC) runs peak in mid- to late-August.

Temporal patterns in fecal GC and T3 concentrations [5], combined with radio-tagging data [28], suggest that early spring interior race Columbia River Chinook (CRC) runs are also important to SRKW nutrition. The CRC run increases from mid-March to the end of May based on estimates at the Bonneville dam [31] and have some of the highest fat content of any adult salmon to support their extremely long freshwater spawning migration [32,33]. Foraging on the fat rich Columbia River Chinook in early spring was hypothesized to replenish the killer whales after the long winter and sustain them until the temporally and quantitatively variable mid to late August peak in Fraser River Chinook (FRC) occurs (S1 Fig). T3 concentrations in fecal samples collected between 2007 and 2009 were consistently at their highest when the SRKW first arrived in the Salish Sea in late spring [5]. Presumably, this occurred because the whales arrived after feeding on the fat rich Columbia River Chinook. SRKW were detected twice as frequently at the Columbia River in early spring than expected by chance [28]. This argument is further supported by increases in serum thyroid stimulating hormone, T4 and T3 in fasting humans and rats in response to leptin injections [20]. With FRC runs still quite low, T3 levels then fell precipitously. GC concentrations when the SRKWs first arrive in the Salish Sea in late spring were also relatively high, further reflecting the comparatively low FRC

abundance at that time, and consistent with the precipitous decline in T3 shortly following SRKW arrival [5].

2. Methods

2.1 Ethics statement

Fecal samples were collected in United States waters under National Marine Fisheries Service permits 532-1822-00, 532±1822, 10045 and 17344. Samples were collected in Canadian waters under Marine Mammal License numbers 2008±16, 2009±08, 2010±09 and 2012±08, as well as Species at Risk Act permits numbered 91, 102, 109 and 155. Sample collection methods were approved by the University of Washington's Institutional Animal Care and Use Committee (IACUC) under protocol 2850±08.

2.2 Scat (fecal) sampling using detection dogs

Scat sampling occurred in the Salish Sea between late May and October, from 2008±2014, coinciding with the time the SRKWs frequent the study area. Whenever possible, we aimed to evenly sample each pod by starting at the front of the pod's direction of travel, continuing to sample until the pod passes and then returning again to the front of the pod.

Scat samples are located by detection dogs trained to locate SRKW scat floating on the water's surface [5,13,14]. The use of detection dogs greatly increases sample size due to their remarkable ability to smell SRKW scats at distances up to one nautical mile away, even in fast moving currents. The detection dog rides on the bow of the boat, driven perpendicular to the wind, beginning at least 200 yards downwind from an area where the whales have just traveled. As the boat approaches the edge of the scent cone emanating from the sample, the dog's behavior suddenly changes from resting to actively perched far over the bow of the boat, anticipating its reward for sample detection. As the boat passes through the center of the scent cone, where the odor is strongest, the dog leans heavily over the windward side of the boat, following the strongest scent, informing the handler to direct the boat driver to turn into the wind. Subtle cues by the dog, relative to wind direction, allow the driver to stay on the scent line until the sample is reached. The dog typically becomes restless, often whining at that point because the scent surrounds the boat and thus no longer has a clear direction. If at any time the boat travels out of the scent cone, the dog changes position and looks back to where the scent was strongest. The handler then directs the driver to circle back into the scent cone until the dog's change in behavior once again alerts the handler it has redetected the scent.

As soon as the sample is visually located, a 1-liter polypropylene beaker fastened to a 3±6 foot pole is used to scoop the sample by skimming the surface just under the sample. The first sample out of the water is presented to the dog, which is followed immediately by the toy reward and a few minutes of play. Meanwhile, the crew continues to scoop all remaining sample pieces from the water's surface. The majority of water is carefully poured off the sample, and the sample pieces are collected into a 50 mL polypropylene tube, centrifuged, and the remaining seawater is decanted. The sample is placed on dry ice until stored frozen at -20ÊCthat evening and remains at that temperature until processed in the lab. Fecal samples range in size from 0.5 to 300 mls, but a typical sample collection volume is 2 mls. Fortunately, the consistency of SRKW scat makes the hormones fairly evenly distributed even in small samples (Ayres and Wasser, unpublished data).

2.3 Fecal DNA and hormone measures

Once thawed for hormone extraction, the homogenized sample is swabbed for DNA using a synthetic tip. The swab is then kept frozen at -20ÊCuntil being genotyped for species, sex, pod,

and individual identification by NOAA NW Fisheries Science Center [34]. 76% of all individuals are currently genotyped to the individual, and 88% of all adult females. Fecal hormone metabolites of glucocorticoid (GC), thyroid (triiodothyronine, T3), testosterone (T) and progesterone (P4) are extracted using methods described in [21] and measured using assays in Wasser et al. [35] (P4), [36] (GC), [21] (T3)] and Vellosa et al. [37] (T). Briefly, each sample is thawed once and centrifuged (2,200 rpm for 20 minutes), allowing any excess salt-water to be decanted. Samples are lyophilized (48 hours in a Labconco FreeZone Freeze Dry System), thoroughly mixed and up to 0.1g weighed, transferred to a 50 ml polypropylene screw-top tube and extracted once in 15ml of 70% ethanol using a Multi-Tube Pulse Vortexer (Terre Haute, IN). Extracts are then stored at -20^0 C until assayed for hormone concentrations. Hormone concentrations are expressed per gram dry weight to control for inter-sample variation due to diet and variable moisture [38]. Wasser et al. [38] showed that expressing fecal hormones per gm dry weight controls for diet related changes in fecal bulk. Because fecal hormones are hydrophobic, removing all water from the sample removes the majority of variation in fecal bulk, significantly improving the blood-fecal hormone correspondence (see also [5] for killer whales). Samples smaller than 0.02 g dried weight were excluded from analysis to avoid inflation effects of low sample mass on hormone concentrations [39].

Radioimmunoassay was performed to measure fecal hormone metabolites using ^{125}I corticosterone RIA kits (#07±120103; MP Biomedicals, Costa Mesa, CA) and MP Biomedicals' Total T3 coated tube RIA kits (#06-B254216) for GC metabolites and T3, respectively. The T3 assay was previously validated for killer whales [21]. The GC assay [36] was validated for killer whales in Ayres et al [5]. Fecal pools as well as commercial controls from each assay kit were used to assess inter-assay coefficients of variation. Commercial T3 controls were prepared as previously described [21]. P4 and T were measured using an in house 3H progesterone RIA assay using antibody CL425 [35,40], and an in-house 3^H testosterone RIA assay using antibody #250 [37,40]. All other hormone assays were validated in the present study.

All five hormone assays exhibited parallelism; slopes of serially diluted SRKW fecal extracts were not significantly different from the slopes of the standard curves (GC: $F_{1,7} = 0.41$, $p = 0.54$; T3: $F_{1,9} = 2.89$, $p = 0.12$; P4: $F_{1,10} = 0.80$, $p = 0.3925$; T: $F_{1,9} = 3.65$, $p = 0.09$). Fifty percent binding of the radioactively labeled hormone occurred at target dilutions of 1:60 for GC, 1:30 for T3,1:60 for P4 and 1:10 for T metabolites. All five hormones also exhibited good accuracy at their target dilutions (GC: slope = 1.2, $r^2 = 0.98$; T3: 1.09, 1.00; P4: 1.07, 0.98; T: 0.68, 0.99), indicating that substances in SRKW fecal extract do not interfere with hormone binding. Inter-assay coefficients of variation were 7.8% for T3, 7.6% for GC; 17% for P4, and 19% for T. Intra-assay coefficients of variation (calculated as the percent of the mean divided by the standard deviation) were 1.9% for T3, 3% for GC, 3.1% for P4; and 3.2% for T. Antibody cross-reactivities are published in Wasser et al ([35], P4; [36], GC; [21], T3) and Velloso et al ([37], T).

2.4 Pregnancy assignment

All whales are photo-identified each day they are observed in the study area, making it unlikely that a newborn would be missed if present when the population is being observed [3]. This enabled us to establish temporal pregnancy profiles using fecal P4 and T concentrations for all pregnant females that subsequently gave birth, approximating gestational age at the time of sample collection based on the estimated birth date of the female's calf. All birth dates in our study (Table 1) were estimated by two independent observers from the Center for Whale Research, respectively with 40 and 30 years experience, using close range photographs taken of each calf at the time of first observation. Features used to assess calf age included: shape of

Table 1. Sex, date of first observation, estimated age, birthdate and survival status for each calf whose mother was sampled during her pregnancy or lactation of that calf.

	Calf Data						Mother of Calf data		
Year	Calf ID	Calf Sex	Date Calf was ®rst photographed	Assigned Calf Birthday	Estimated age of Calf	Calf age at death	Mother of Calf	Birth year of Mother	Age of Mother
2007	J42	F	5/2/2007	5/2/2007		Alive	J16	1972	35
2008	K42	M	6/3/2008	4/3/08	1±3 mo	Alive	K14	1977	31
2008	L111	F	8/12/2008	7/30/2008	2 wk	<1 month	L47	1974	34
2009	L112	F	2/6/2009	1/24/2009	2 wk	3 years	L86	1991	18
2009	J44	M	2/6/2009	1/1/2009	1 mo +	Alive	J17	1977	32
2009	J45	M	3/3/2009	2/15/2009	2 wk	Alive	J14	1974 (died 2016)	35
2009	L113	F	10/10/2009	10/1/2009	1±2 wk	Alive	L94	1995	14
2009	J46	F	11/11/2009	10/28/2009	2 wk	Alive	J28	1993 (died 2016)	16
2010	J47	M	1/3/2010	12/9/2009	< 1 mo (12/5 no calf)	Alive	J35	1998	12
2010	K43	F	2/21/2010	1/31/2010	3 wk	Alive	K12	1972	38
2010	L115	M	8/6/2010	7/31/2010	1 wk	Alive	L47	1974	36
2010	L116	M	10/13/2010	10/3/2010	1±2 wk	Alive	L82	1990	20
2010	L117	M	12/6/2010	11/30/2010	1 wk	Alive	L54	1977	33
2010	L114	U	2/21/2010	2/16/2010	< 1 wk	4 months	L77	1987	23
2011	K44	M	7/6/2011	7/3/2011	3 days (No calf 3 days prior)	Alive	K27	1994	17
2011	L118	F	2/10/2011	1/20/2011	3 wk?	Alive	L55	1977	34
2011	J48	U	2/17/2011	1/29/2011	$\leq$ 3 wk	<1 month	J16	1972~	39
2012	J49	M	8/6/2012	8/6/2012	1 day, saw 1st day	Alive	J37	2001	11
2012	L119	F	5/29/2012	5/15/2012	2 wk	Alive	L77	1987	25
2013	unk	U	1/7/2013	1/7/2013	1 day	<1 month	J28	1993	20
2014	J50	F	12/23/2014	12/15/2014	2 wk? (12/12 no calf)	Alive	J16	1972~	42
2015	L123	M	11/7/2015	10/15/2015	< 1 Mo (10/11 no calf)	Alive	L103	2003	12
2015	J53	F	10/24/2015	10/14/2015	1±2 wk (10/03 no calf)	Alive	J17	1977	38
2015	L122	M	9/7/2015	8/24/2015	2 wk	Alive	L91	1995	20
2015	J52	M	3/30/2015	3/16/2015	2 wk (no calf 02/18)	Alive	J36	1999	16
2015	L121	M	2/25/2015	2/18/2015	~ 1 wk	Alive	L94	1995	20
2015	J51	M	2/12/2015	2/5/2015	1 wk	Alive	J41	2005	10

Maternal age at time of sampling is also included.

? = best guess.

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cranial crest (lumpy at birth), flopped over dorsal fin (apparent in first 1±2 days), fetal folds, fattening after first month, jaundice coloration, skin molting at 3±5 months, date of previous observed photo of pregnant females without a calf. The Center for Whale Research (unpublished data) developed these criteria by compiling a time-stamped folder of known-age calf photos that illustrate these age-dependent morphological differences.

A fecal P4 concentration threshold was then established to indicate pregnancy by comparing P4 concentrations across all known sex and reproductive classes, and demonstrating that all gestating SRKW females, subsequently confirmed to have been pregnant by a live birth, surpassed this threshold and sustained it until the end of their 18 month gestation period (see also

[15]). No samples from genotyped males, or from lactating, non-cycling, immature or post-reproductive females approached this P4 threshold. Comparisons of T concentrations were similarly used to separate pregnancies into early and late stages of gestation. T rises during pregnancy, albeit more slowly than P4. By mid-gestation, T concentrations in pregnant females are comparable to, if not higher than those observed only in adult males (but without a comparable rise in P4) [16] (see also results). Thus, high P4, low T samples were classified as from females in early gestation and high P4, high T samples were classified as from females in mid- to late-gestation. All samples from genotyped adult females at or above these P4 and T concentrations were classified as pregnant. Pregnancies were classified as successful if the female was subsequently observed with a live birth before 18 months from the time of sample collection. Otherwise, the pregnancies were classified as unsuccessful, representing a spontaneous abortion or an unobserved perinatal mortality.

2.5 Statistical analyses

All statistical analyses were performed using the software, JMP (SAS Institute, 2010). Log-transformed values were used for all hormone analyses. A general linear model (GLM) was used to distinguish reproductive and non-reproductive groups of each sex based on P4, T, T3, GC and T3/GC concentrations. Differences between groups were then tested using a chi-square contrast test.

The abundance and timing of Fraser River Chinook (FRC) was determined from 2008± 2014 by Albion Test Fishery CPUE data (Catch Per Unit Effort, [41]), collected on a daily basis by an independent observer during spring, summer, and fall months. All correlations between hormone concentrations and fish abundance used Albion Test Fishery CPUE data lagged by 12 days from the time a sample was collected; the 12 day lag was derived from estimates of Chinook swim time from the study area to the test fishery, which was also in agreement with the lag time that resulted in the best fit model between prey abundance and nutritional hormones [5,8]. The CPUE data were $\log_{10}$ transformed to achieve normality. Early spring Columbia River Chinook abundance was also estimated from daily counts at the Bonneville dam [31] by calculating the area under the curve from Julian Day 100 to 140.

Vessel counts were taken every half hour (within 5 minutes of the half hour). Any vessels outside the 5 minute grace period were not counted. All boats within 0.5 mile of the killer whales were recorded by type (commercial whale watch, recreational, cargo, ferry, commercial fishing, enforcement, research, monitoring, and kayak or paddleboard) and activity (e.g., transiting, whale watching, fishing (lines in the water), acoustic, enforcing). A second (B) count was taken when a second nearby whale group was present (1±2 miles away) but outside of our initial count area, providing that the vessels and their activity could be clearly identified.

The correspondence between fish abundance and Julian date (i.e., the consecutive day of the year, ranging from 1 to 365) and vessel abundance and Julian date, across years, was established with a GLM, which allowed us to then use Julian date as proxies for fish and boat abundance in subsequent analyses. A GLM was used to separately predict T3 and GC by Julian date for all sampled individuals. The relation between early spring Columbia River salmon abundance and subsequent T3 and GC concentrations during that same year was also tested in those regressions. Finally, GLM was used to separately predict T3, GC and the T3/GC ratio, using Julian date as a polynomial and pregnancy type as independent variables. GC was included as a covariate whenever predicting T3, and vice versa, since both hormones respond to other in the regulation of energy balance. For T3, this was done by fitting T3 by GC, saving the residuals, and then using the residuals of that analysis in the final regression. For GC, the

residuals for GC fit by T3 were used. In all cases, forward stepwise model selection was used to identify the best model in our GLM analyses, based on Akaike's Information Criterion (AIC).

Raw Data are provided in S1 Appendix.

3. Results

In total, there were 348 samples from known (genotyped) individuals, in the final analytic dataset representing 79 unique whales (Supplemental Information-raw data), including 11 successful and 24 unsuccessful pregnancies (Table 2). Each year included a representative sampling by pod, sex and reproductive class.

3.1 Changes in fish abundance, vessel density, T3 and GC concentrations over time

Based on delta AIC, the Albion Test Fishery Abundance of FRC, measured in CPUE, was best predicted by a 4th order polynomial using Julian date (i.e., consecutive day of the year, $P < 0.0001$) across years (Fig 1A), with a peak in CPUE at day 228 (Aug 16). CPUE significantly declined across years, when examined as a continuous variable ($P < 0.0001$). The lowest FRC CPUE occurred in 2013, followed by 2012 (for both, $p < 0.0001$ compared to all prior years, and $p < 0.004$ compared to 2014) and then 2014 ($p < 0.04$ compared to 2008±2011) (see also S1 Fig). Vessel density was similarly predicted by a 4th order polynomial using Julian date ($p < 0.0001$) with a peak at day 222 (Fig 1B). Vessel density significantly increased across years, when examined as a continuous variable ($P < 0.0001$).

We next separately predicted T3 and GC concentrations based on Julian date (Fig 1C and 1D, respectively), given the close association of Julian date with both fish and vessel abundance. Spring Columbia River Chinook (CRC) abundance was also included as a covariate in these analyses since the relatively slow responding T3 was hypothesized to still be influenced by spring CRC abundance at the time of SRKW early summer arrival in the Salish Sea. T3 concentration was best predicted by a 5^{th} order polynomial of Julian date ($p < 0.0001$) and was also positively correlated with CRC ($p < 0.0001$). For all years of study, T3 was at its peak

Table 2. Pod composition and samples per unique successful and unsuccessful pregnancy from genotyped females per year.

	SRKW Pod			Reproductive Age Class				Unsuccessful Pregnancy+: unique whales/ total samples		Con®rmed pregnancies+*: unique whales/ total samples	
Year	J	K	L	Juvenile	RM	RF	PRF	Low T	High T	Low T	High T
2008	13	5	7	7	6	7	5	0/0	0/0	1/1	1/1
2009	24	10	14	9	18	13	8	1/2	2/2	0/0	1/2
2010	14	6	12	3	6	13	10	1/1	0/0	1/2	1/1
2011	25	17	23	15	16	24	10	0/0	3/4	2/2	1/1
2012	32	11	8	6	13	24	8	5#/9	1#/2	0/0	0/0
2013	17	7	21	6	12	23	4	4ˆ/4	1ˆ/1	0/0	0/0
2014	36	18	6	19	10	27	4	5/6	1/1	1/4	2/2

RM = reproductive male, RF = reproductive female, PRF = Post-reproductive female.

*Not all samples between years are unique pregnancies

ˆ Includes 2 samples from one pregnancy, one with Low T and one with High T

+ Includes only samples from females with P4 concentrations ≥ 2000 ng/g

Observed birth, reclassi®edat unsuccessful due to early perinatal mortality

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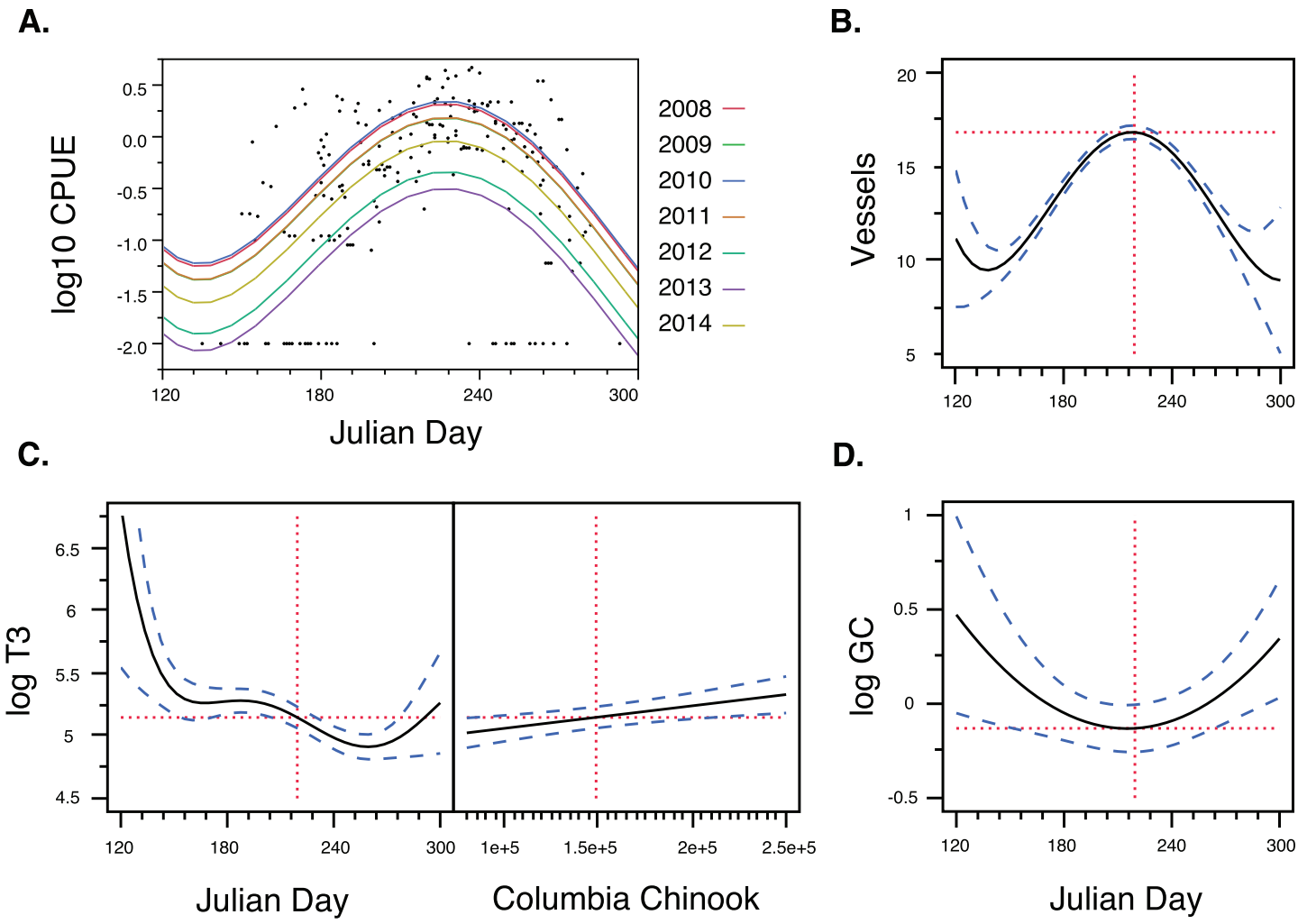


Fig 1. A) Fraser River Chinook (FRC) Salmon Run abundance (CPUE: catch per unit effort), B) mean vessel count (all boats observed with 0.5 m of the whales) plotted by Julian date across years, C) Change in SRKW fecal thyroid hormone (triidothyronine, T3 ng/g dry feces) by Julian date (left panel) and early spring Columbia River Chinook abundance (right panel), and D) Change in SRKW fecal glucocorticoid (GC ng/g dry feces) hormone concentration by Julian date. Dashed blue lines represent the standard error surrounding each curve. Vertical red line in left panel, Fig C indicates the mean peak in FRC abundance and the mean peak in boat abundance in Fig B and D.

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when the SRKWs arrived in early summer, presumably after feeding on the early spring CRC. T3 sharply declined shortly thereafter, presumably because FRC abundance was still low, plateauing around the time that FRC CPUE begins to rise. T3 concentrations then slightly declined again in September, just after the FRC peak.

GC concentration was best predicted by the quadratic of Julian date ($p = 0.004$), showing the U-shaped pattern indicative of nutritional stress, with the trough at day 220, near the FRC peak. GC was not correlated with CRC, supporting the hypothesis that the GC response reflects more immediate conditions compared to T3.

3.2 Pregnancy occurrence and loss indices

Twelve females sampled during pregnancy were subsequently confirmed to give birth (37% of detected pregnancies) by photo-identification between 2008 and 2015. However, one of those females (J28) was subsequently reclassified as a High T unsuccessful pregnancy because her

calf died immediately post-partum.) In all samples, P4 was well above the 2000 ng/g pregnancy threshold by 2.5 months gestation, and remained so for the next 15.5 months until parturition. One sample collected on a confirmed pregnant female during her first month of gestation had P4 levels below the 2000 ng/g threshold (Fig 2A). By contrast, no male, or immature, non-cycling, lactating or post-reproductive female whale ever approached that P4 threshold (Table 3). The majority of samples from confirmed pregnant females were well above 18,000 ng by 10 months gestation. All samples from confirmed pregnant females exhibited a precipitous decline below 2000 ng/g P4 immediately following parturition (Fig 2A).

T concentrations of all samples from confirmed pregnant females clearly remained below 50 ng/g until mid-gestation (Fig 2B). Thus, pregnancy samples (i.e., samples above the 2000 ng/g P4 threshold) were divided into low ($\leq$ 50 ng/g) and high ($>$ 50 ng/g) T groups, respectively, corresponding to early, and mid-to-late stages of gestation (Fig 2A and 2B). The only other age-sex class that showed significantly elevated T concentrations, above the 50 ng/g threshold, was adult males, but their P4 concentrations never approached 2000 ng/g (see Table 3). T was above the 20 ng/g by 2.5 months gestation in all confirmed pregnant females, with the majority above 100 ng/g by 10 months gestation (Fig 2B). Low T confirmed pregnant females had a mean fecal P4 of 6206 ng/g ± 2565) and a mean T concentration of 21 ng/g ± 5.8, whereas High T confirmed pregnant females had a mean fecal P4 $>$ 25587 ng/g ± 5116) and a mean T concentration of 215 ng/g ± 43 (Table 3). With the exception of one early lactation sample, testosterone concentrations declined well below the 50 ng/g threshold after parturition (Fig 2B). Multiple scat samples were obtained from the same pregnancy event in 4 of the 11 pregnancies and three lactation events; all multiple samples exhibited these same P4 and T patterns over time.

None of the post-reproductive females were ever recorded to be pregnant nor did they show any sign of ovarian activity (Table 3). These results support the assertion that the ᵃpost-reproductiveº adult females (>40 years of age) in this population have undergone reproductive senescence [42].

Samples from genotyped reproductive age adult females with P4 concentrations above the 2000 ng/g pregnancy threshold that were not followed by a live calf within the 18-month gestation period were assumed to be from females that experienced a spontaneous abortion (in utero mortality), or early perinatal death prior to calf's first observation, collectively termed an unsuccessful pregnancy (UPg). Among the females classified as reproductive adults, we characterized 24 unique unsuccessful pregnancy (UPg) events from 12 different females with genotyped samples collected between 2008±2014Ðup to 69% of all confirmed pregnancies (Table 2). All samples from the 22 apparent UPg's had significantly elevated progesterone concentrations well above 2000 ng/g. Yet, no observations of those females over the next 18 months included a new calf. As with confirmed pregnancies, the presumed UPg samples were separated into two distinct groups: one with T concentrations above 50 ng/g feces (mean T = 198.6±40; P4 = 37,425±12,820), hereafter termed ᵃhigh T UPgº samples (7 unique females, 7 presumed late spontaneous abortions and one early perinatal loss), and the other with T concentrations below 50 ng/g feces (mean T = 11.3±3.2; P4 = 6618±2014), termed ᵃlow T UPgº samples (4 females, 16 presumed early spontaneous abortions; Table 2; Fig 3A). Multiple samples from 6 of the 24 unsuccessful pregnancy samples (4 low T, 2 high T, plus 1 low T that transitioned to high T) were all within the pregnancy range (i.e., P4 $<$ 2000 ng/g). Thirty three percent of the UPg samples (8 out of 24) identified here were high T UPg (up to 23% of all recorded pregnancies). The high T UPg samples were likely from the second half of gestation, based on their high P4 and T concentrations relative to temporal profiles for those hormones in whales with a confirmed pregnancy (see Fig 2).

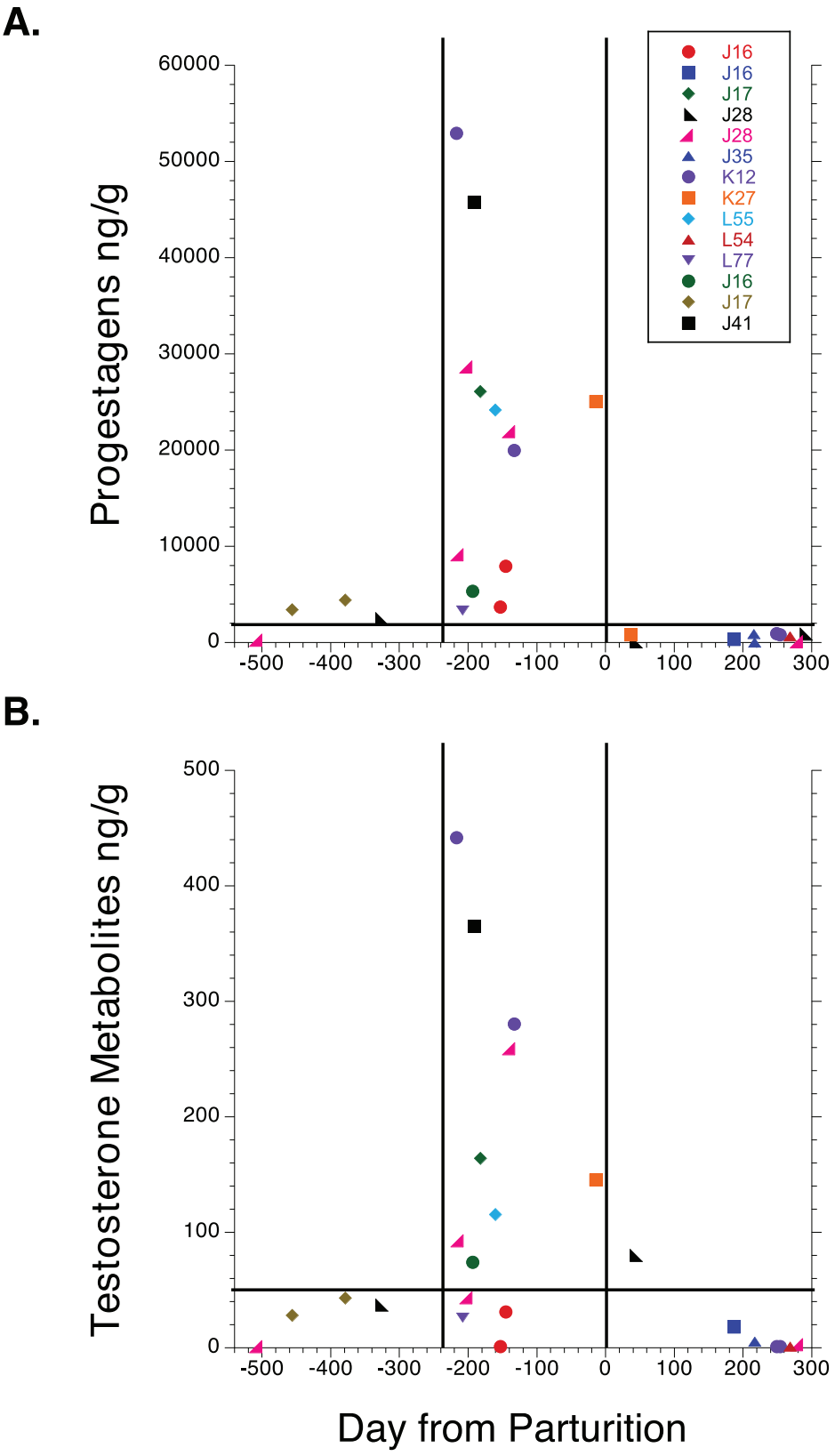


Fig 2. A) Progesterone (P4) and B) testosterone (T) concentrations across gestation and lactation, for all successful pregnancies (Pg), subsequently confirmed by observed births. Each unique pregnancy

is indicated by its own symbol, along with the associated female's ID. The vertical dashed black line in Fig A and B indicate estimated day of parturition. The 2000 ng pregnancy threshold is indicated by the horizontal dashed red line in Fig A, as is the 50 ng/g T cut-off for High and Low T samples in Fig B. The left vertical line in red indicates the Julian day where both P4 and T show sharp elevations.

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T3 and GC concentrations also varied across all sex, age and reproductive classes (Table 3). T3 was highest in juvenile and pubescent individuals compared to adults, with the exception of Low and High T successful pregnant and low T UPg females. All of those individuals also had a relatively high T3/GC ratio (> 0.3), indicative of relatively good nutrition (Table 3). By contrast, T3 in the High T UPg samples was comparable to that of non-pregnant adults (Table 3), and notably lower than the concentrations from successful pregnant and low T UPg females (Fig 3B). These High T UPg samples also had the highest GC concentrations of any reproductive class, was significantly higher than the GC concentrations in High T successful pregnancies. The T3/GC ratio in High T UPg females was lower than that of another other reproductive class (Table 3), indicative of nutritional stress (Table 3), and nearly 7 times lower than that among High T successful pregnancies. Indeed, the T3/GC ratio in High T successful pregnancies was higher than that for any other reproductive class, with the exception of lactating females (Table 3, Fig 3B).

3.3 Changes in T3 and GC concentrations relative to fish abundance over time across pregnancy groups

T3 and GC concentrations, along with the T3/GC ratios were separately compared among High T successful pregnant and UPg samples, across Julian date. (Low T samples were not included in these comparisons because their T3 and GC concentrations were not significantly different from those of confirmed pregnant females.) All three dependent variables were best predicted by a 3rd order polynomial of Julian date ($p < 0.01$). Similar to the overall population trend, T3 concentrations were highest in early summer, followed by a precipitous decline.

Table 3. Mean hormone concentration (ng/g dry feces) and (standard error) by sex and reproductive class for each hormone measured during the study.

	Reproductive Hormones				
Sex and Reproductive Class	**Thyroid (T3)**	**Glucocorticoid (GC)**	**Progesterone**	**Testosterone**	**T3/GC Ratio**
Juv F	248.40 (40.06)	610.73 (200.17)	794.40 (268.84)*b,k,u,C,J*	3.38 (1.14)*a,j,v,F*	0.69 (.24)*a,f*
Juv M	229.98 (26.98)*a,f*	501.03 (158.82)	800.96 (73.99)*a,j,t,B,K,O*	30.11 (7.84)*a-i*	0.44 (.05)*b,f*
Pub F	264.19 (47.49)*d,i*	955.08 (286.02)	305.90 (95.0)*g,q,y,F,H,J-N*	3.80 (1.90)*h,p,y,D,H*	0.70 (.31)*d*
Pub M	230.99 (29.34)*e*	1244.21 (310.87)	258.11 (42.15)*h,r,z,G,I,O-R*	19.32 (6.08)*q,A-E*	0.71 (.35)
Ad M	167.07 (10.63)*a-e*	1073.14 (114.92)	579.57 (38.14)*I,s,H-I*	126.67 (17.73)*I,r,u,w,z,E-H*	0.32 (.044)*e,f*
Ad F no-calf	169.97 (14.13)	1004.21 (135.15)	651.83 (68.28)*d,m,w,A,D,M,Q*	5.12 (1.60)*c,l,x,B*	0.35 (.057)
LoT Conf	250.78 (35.63)*c,h*	1127.81 (233.66)	6205.89 (2564.93)*g,o,B-G*	21.28 (5.78)*n,x-z*	0.37 (.14)
LoT Upg	252.56 (27.06)*b,g,i*	1288.23 (228.05)	6618.20 (2014.13)*e,n,t-z*,A	11.32 (3.2)*e,m,s-u*	0.82 (0.46)
HiT Conf	218.05 (45.6)	1057.31 (477.75)*a*	25587.17 (5116.49)*a-i*	215.34 (42.87)*f,t,v,w*	1.11 (.42)*c,e*
HiT Upg	177.1 (26.98)	1787.20 (467.83)*a*	37425.73 (12819.62)*j-s*	197.95 (39.7)*d,j-r*	0.16 (.035)*a-d*
Lactating	165.02 (24.70)*f-i*	1094.36 (270.03)	650.12 (84.68)*c,l,v,C,L,P*	22.71 (13.33)*b,k,s,A,G*	2.05 (1.59)
Post-Reprod F	199.01 (19.82)*j*	1039.2 (133.11)	662.30 (66.62)*f,p,x,y,E,N,R*	7.88 (1.89)*c,o,C*	0.36 (.068)

Signi®cantdifferences between means in any two cells within the same column are indicated by the same italicized letter in both cells.
F = female, M = male, Juv = juvenile; Pub = pubescent, Ad = adult, T = testosterone, Conf = con®rmed pregnant female by subsequent observation of a live calf; UPg = unsuccessful pregnancy.

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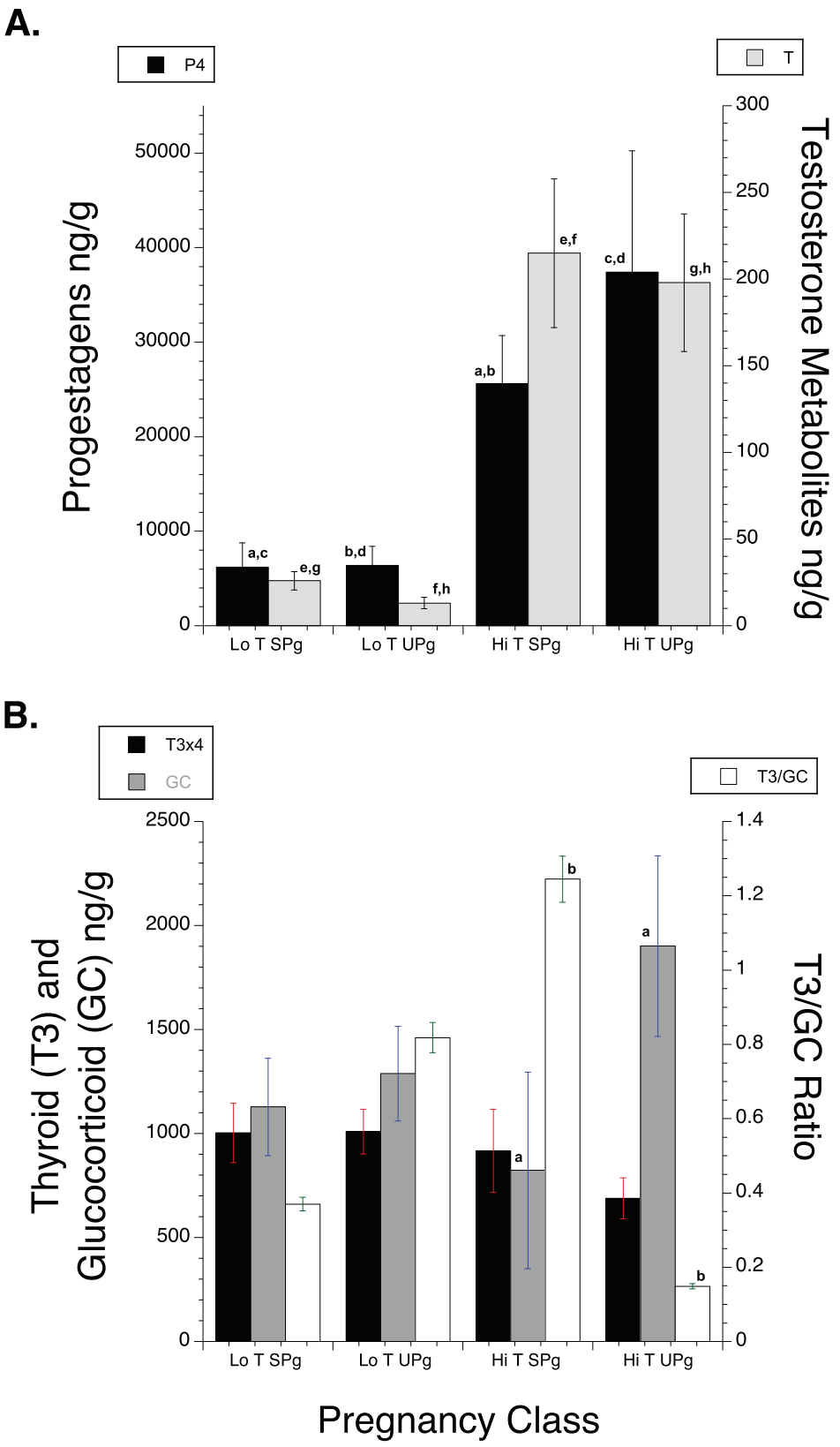


Fig 3. A) Mean P4 and T concentrations and B) mean tri-iodothyronine (T3) and glucocorticoid (GC) concentrations, along with the T3/GC ratio, for Low and High T successful (SPg) and unsuccessful

pregnancies (UPg). Corresponding values for all sex and reproductive classes of SRKWs, including significant differences between classes, are presented in Table 3. Note: T3 Concentrations are multiplied by 4 in Fig B to scale its concentrations to those of GC in order to present a double Y graph for 3 related metrics, each with different value ranges. Bars with the same letter are significantly different from each other.

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However, the initial T3 decline was longer in duration than that observed for the overall population, lasting until day 190. T3 concentrations in the pregnant females then increased until day 250 (Fig 4A), which was near the time when the FRC run reached it back (Fig 1A). While the pattern was the same in High T successful and unsuccessful pregnancies, T3 in High T UPg samples remained significantly lower than that in High T successful pregnant females ($p = 0.004$), consistent with relatively higher nutritional stress in the High T UPg females (Fig 4A). Change in GC concentrations among pregnancy females were the exact opposite of T3, showing a steep rise until day 190 followed by a decline until day 250, and significantly higher in High T UPg compared to High T successfully pregnant females ($p < 0.002$) throughout this period (Fig 4B). Change in the T3/GC ratio followed the same pattern as T3, also remaining significantly higher in HighT successful pregnancies ($p< 0.003$) (Fig 4C).

4. Discussion

Reproductive failure in response to conditions that jeopardize offspring survival has been described as an adaptive response if conditions are likely to improve in the foreseeable future. This environmentally-mediated loss most commonly occurs early in reproduction (conception and early pregnancy) when the cost of suppression (e.g., lost time and energy; impacts on maternal health) is relatively low [43,44]. However, failure at later stages of reproduction is expected when cues indicating poor fetal or neonatal conditions present themselves late in the reproductive event. The longer the span between conception and birth the more likely later suppression is to occur. Premature birth is a relatively low risk way to suppress reproduction because the reproductive failure occurs post-partum with reduced chance of infection. However, its occurrence should still depend on when harsh conditions present themselves. If fetal demise occurs or environmental conditions become especially harsh (e.g., risk of sepsis from starvation induced ketoacidosis during pregnancy; [45]), spontaneous abortion is expected. Thus, spontaneous abortion, premature birth, still birth, and perinatal and neonatal mortality are all part of a continuum of reproductive suppression that present with harsh conditions, on balance with risk of reproductive loss at that stage of reproduction [44,46].

SRKWs have an 18 month gestation period and their nutritional health depends on the relative timing of multiple, seasonal fish runs (e.g., spring CRC and summer FRC), as well as food availability in between those periods, each of which vary markedly between years (S1 Fig). The increasingly common occurrence of SRKW births outside the typical winter calving period may well be an indication of the increased unpredictability of diminishing fish runs along with the corresponding high rate of late reproductive loss in SRKWs, including more costly late spontaneous abortions. The SRKWs had a 69% pregnancy failure rate during our study and an unprecedented half of those occurred at later stages of reproduction when the energetic cost of failure and physiological risk to the mother was relatively high. Temporal patterns in T3 and GC hormone profiles suggest that the SRKWs are experiencing periodic nutritional stress, partly caused by variation in the relative timing and strength of seasonal FRC and CRC runs (Fig 1). This nutritional stress is significantly associated with unsuccessful pregnancies in SRKWs (Figs 3 and 4), impairing the potential for population recovery through low recruitment as well as risk to the health and survival of the limited number of reproductive-age females.

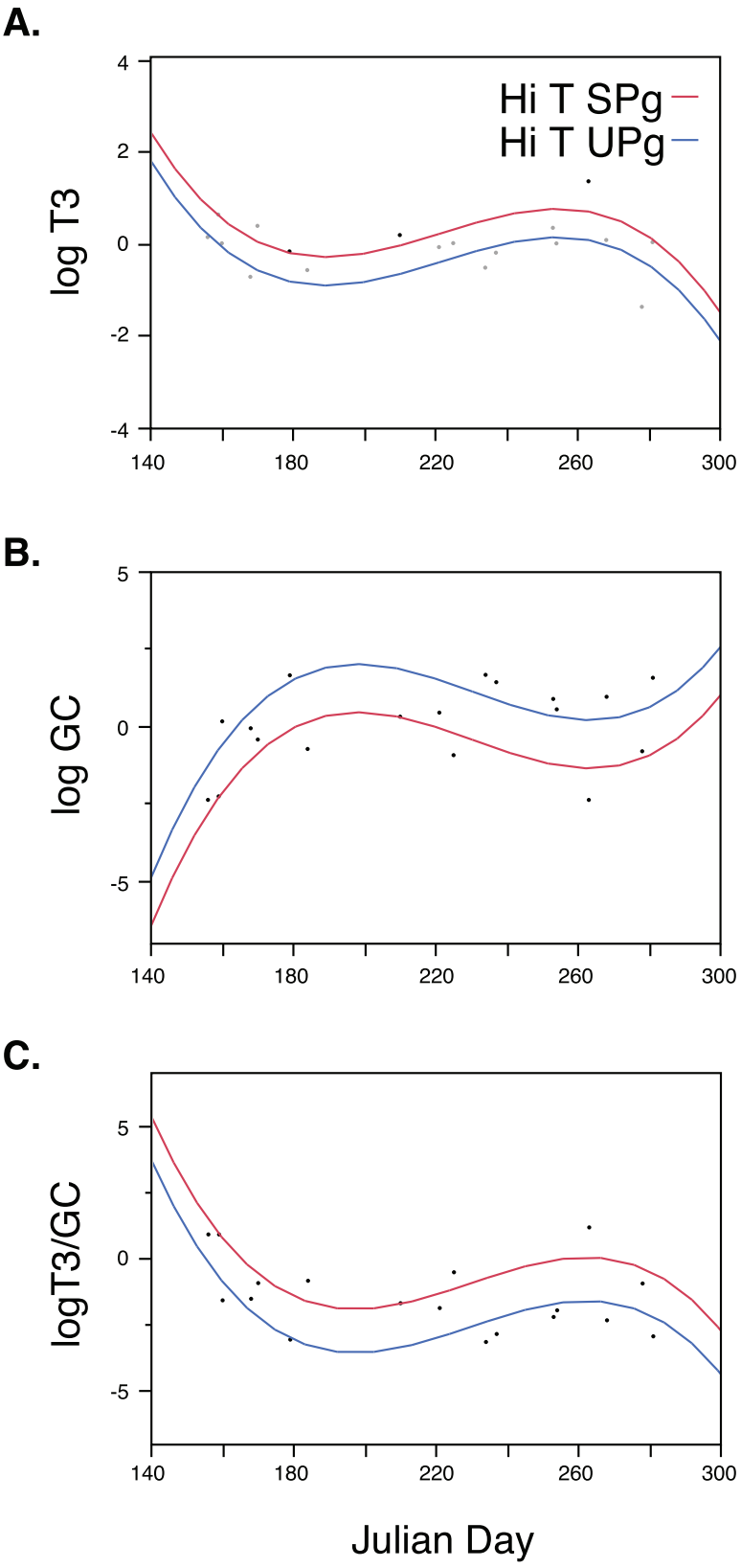


Fig 4. A) T3 and B) GC concentrations, along with (C) the T3/GC ratio, by Julian day for High T successful pregnancies (SPg) versus High T unsuccessful pregnancies (UPg).

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High T (mid-to-late gestation) females with successful pregnancies in our study had significantly higher T3 and lower GC concentrations, as well as a substantially higher T3/GC ratio over time, compared to High T unsuccessful pregnancies (Figs 3 and 4). This indicates that successfully pregnant females arrived in the Salish Sea in significantly better nutritional condition, and remained so compared to UPg females that experienced pregnancy loss some time after mid-pregnancy. West et al [25] similarly found significantly higher total T3 concentrations among adult females in successful compared to unsuccessful pregnancies at all stages of gestation among captive dolphins.

Only 4 detected pregnancies between 2011±2013 resulted in live births when Fraser River Chinook and early spring Columbia River Chinook runs were both exceedingly low. Just one of those births occurred in 2013, when both FRC and CRC abundances were at their lowest, and that animal died almost immediately post-partum. By contrast, there were up to 9 early gestation (Low T) and 5 mid to late gestation (High T) unsuccessful pregnancies detected during that same 3 year period, with almost half of these early-term and one of the mid to late term unsuccessful pregnancies occurring in 2013. That trend reversed in 2014, with relatively high CRC returns and early onset of FRC returns in 2014 and 2015 (S1 Fig, Appendix) that was followed by 8 new births between December of 2014 and October 2015; however, up to 6 unsuccessful pregnancies still occurred that year, five of which occurred early in gestation (Low T Upg).

High T UPg samples were either from late spontaneous abortions (also known as intrauterine fetal demise), or undocumented perinatal or neonatal deaths where the infant disappeared prior to first observation. The lack of observed perinatal or neonatal deaths when most successful births during our study were observed within 2 weeks of parturition (Table 1), led us to estimate that a substantial portion of the High T UPg samples represented late spontaneous abortions. Although the negative effect of these later reproductive losses on SRKW population growth is roughly the same, infection from a failed or incomplete abortion likely poses a greater risk of removing a reproductive female from the breeding population. At least one SRKW stranding was confirmed to be a pregnant female with infection from a retained fetus listed as the cause of maternal death (J32, December 2014).

Reproductive loss among women during the well-documented 1945 Dutch Famine may exemplify the kinds of impacts expected in response to severe nutritional stress among SRKWs, since: both humans and SRKWs have relatively long interbirth intervals (gestation length and extended lactation amenorrhea), starvation was acute and the Dutch Famine outcomes were not biased by interventions from modern health care [44,47,48]. The Nazis closed off the borders of Holland between October 1944 and May 1945, causing massive starvation over a 5±8 month period, with good food conditions before and after. There was a one-third decline in the expected number of births among confirmed pregnant woman during the under-nutrition period. Conceptions during the hunger period were very low. However, women who conceived during the hunger period had higher rates of abortion, premature and stillbirths, neonatal mortality and malformation. Nutrition had its greatest impact on birth weight and length for mothers experiencing hunger during their second half of gestation, when the fetus is growing most rapidly [47].

Many of the unsuccessful pregnancies in our study were based on single genotyped samples, and it is possible that pregnancy failure rates could be somewhat overestimated. For example, we cannot rule out that some portion of the singleton Low T samples were actually from post-ovulatory luteal phase females that did not produce a detectable conception. Some low T samples could also be from pseudo-pregnancies, although those are rare, have only been reported in captivity [49], and could be an artifact of captive husbandry where males and females are housed separately. It is unlikely that any post-ovulatory luteal phase samples were misclassified

as High T UPg samples because both P4 and T concentrations in the High T samples were all well above those expected for luteal phase samples (Table 3, Fig 2). Moreover, Robeck et al [15,16] clearly distinguished luteal phase samples from pregnant samples by 4 weeks of gestation. This is consistent with our findings from Fig 2, indicating pregnancy detection among females by 100 days of gestation. Given the above, we consider only a small portion of the 8 singleton, low T UPg samples with P4 above the 2000 ng/g pregnancy threshold to be possibly misclassified as early abortions. However, the consistency of these patterns on multiple endocrine and temporal measures, across years, strengthens the assertion that pregnancy failure is a major constraint on killer whale population growth, triggered by insufficient prey.

The rise in fecal P4 concentrations that we observed among successful pregnancies was somewhat delayed compared to that observed in serum from captive killer whales [15]. This could suggest that our estimated birth dates, and hence our projected conception dates, actually occurred earlier than expected, increasing the likelihood that some perinatal mortalities were misclassified as late spontaneous abortions. However, the delayed P4 peak in feces of pregnant SRKWs compared to Robeck et al [15] most likely resulted from differences in the P4 metabolites measured in feces versus serum. The predominant P4 metabolite measured by our antibody is 5α-DHP [35]. Using an EIA version of the P4 antibody we used in our study, Robeck et al [15] found that 5α -DHP did not become the predominant progesterone metabolite in captive killer whale serum until 161±360 days of gestation, and remained secondarily so from 361 days gestation to term. Fecal progesterone metabolites spiked around mid-pregnancy in our study, consistent with the time when 5α -DHP predominated in serum [15]. It is also noteworthy that our testosterone antibody [37,40] followed a similar temporal pattern in SRKW to that described for captive whales by [16]. That also supports the reliability of our projected conception dates and occurrences of spontaneous abortion.

Exposure to persistent organic pollutants (POPs)Ðlipophilic compounds with established adverse health effectsÐin response to food stress add yet another cumulative risk of fetal demise and/or perinatal and neonatal mortality. Lundin et al. [8,50] showed that POPs, namely PCBs, DDTs, and PBDEs, increase in circulation in SRKWs when Fraser River Chinook abundance is lowest, presumably due to increased fat metabolism in response to nutritional stress. Mobilization of contaminants into circulation also occurs during the energetic demands of lactation, with an estimated 70±90% lactation transfer of maternal toxicant burden in primiparous females [51]. High POP burden has specifically been associated with disruption of reproduction success and reduced calf survival in marine mammals [52±55]. Most notably, Lundin et al. [8] found increased Persistent PCBs, the group of PCBs considered more persistent and more toxic [56], in the female whales classified with UPg's (73%; 95% CI, 61±85) compared to all other female reproductive groups (range 43±56%). Further evidence in support of the occurrence of UPg in this population is the unexpected inverse in bioaccumulation of POPs with age in ªnulliparousº mature females (3 of 4 nulliparous whales had an unsuccessful pregnancy defined by fecal hormone measures). This occurrence is likely explained by toxicant offloading from an undocumented pregnancy or neonate loss.

Both poor nutrition and increased POP loads have each been demonstrated to suppress T3, which negatively impacts fetal brain growth [22,57,58]; immunosuppression may also occur, increasing risk of infection [53,59±61]. Salmon are the Southern Resident killer whales predominant prey and main source of toxic exposures [62,63]. This relation of reduced food supply and increased exposure to lipophilic POPs could be similarly impacting coastal Native American communities that depend on this same seasonal salmon resource and also appear to be experiencing high rates of reproductive loss [64,65].

Results of the SRKW study strongly suggest that recovering Fraser River (FRC) and Columbia River Chinook (CRC) runs should be among the highest priorities for managers aiming to

recover this endangered population of killer whales. SRKW are suffering significant reproductive loss due to lack of Chinook prey and associated effects (e.g., release of lipophilic toxins into circulation). The FRC run is a major prey source for the SRKW population during summer and early fall, and appears to be key to providing the needed reserves to carry the whales through the subsequent winter [6]. The early spring CRC runs likely serve to replenish energetic reserves expended during the previous winter as well as help sustain the whales until the occurrence of the subsequent late summer peak in the FRC runs. The relative importance of the early spring Columbia River Chinook run likely became all the more critical to the SRKWs as historic FRC runs that peaked earlier in summer became depleted from overfishing and habitat destruction [6]. Other species, including people, also appear to be impacted by these conditions.

Without steps taken to remedy the situation, we risk losing the endangered SRKW, an extraordinarily important and iconic species to the Pacific Northwest. Since strengthening relevant Chinook runs should significantly decrease physiological stress and increase pregnancy success rates in SRKW during the same year that fish runs increase, the physiological indices used in this study could also provide rapid assessment tools for guiding adaptive management of SRKW populations. Historical and modern dependence on fish as an essential food source for coastal communities with limited resources, in conjunction with growing food shortages and increased risk of toxicant exposure, has international implications.

Supporting information

S1 Fig. Timing and abundance of Columbia River (orange) and Fraser River (blue) Chinook runs based on DART (2015) and Albion Test fisheries (Catch Per Unit Effort, Albion 2015), respectively (see also Lundin 2015).
(TIFF)

S1 Appendix. Raw data.
(XLSX)

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What is the Seventh Generation Principle?

May 30, 2020

The Seventh Generation Principle is based on an ancient Haudenosaunee (Iroquois)* philosophy that the decisions we make today should result in a sustainable world seven generations into the future. This extremely prescient philosophy is currently somewhat overused as a "green" marketing ploy to sell everything from dish soap to cars.

The first recorded concepts of the Seventh Generation Principle date back to the writing of The Great Law of Haudenosaunee Confederacy, although the actual date is undetermined, the range of conjectures place its writing anywhere from 1142 to 1500 AD. The Great Law of Haudenosaunee Confederacy formed the political, ceremonial, and social fabric of the Five Nation Confederacy (later Six). The Great Law of Haudenosaunee Confederacy is also credited as being a contributing influence on the American Constitution, due to Benjamin Franklin's great respect for the Haudenosaunee system of government, which in itself is interesting from the perspective that the United States formed their Constitution not on the principles of European governments, but rather on that of a people considered "savages".

The Seventh Generation Principle today is generally referred to in regards to decisions being made about our energy, water, and natural resources, and ensuring those decisions are sustainable for seven generations in the future. But, it can also be applied to relationships - every decision should result in sustainable relationships seven generations in the future.

Relationships today between Indigenous Peoples and non-Indigenous peoples should be forged with the Seventh Generation Principle in mind. Through my workshops, Working Effectively with Indigenous Peoples®, I strive to provide an understanding of the background to the existing relationship between Indigenous Peoples and non-Indigenous Peoples so that future relationships will be positive for many generations to come. It is my life's ambition to provide tools and suggestions on how to live and work with Indigenous Peoples with the goal that in the future, workshops on how to relate to one another will no longer be necessary... which means I could retire and go fishing!

*Terminology note:
Called the Iroquois Confederacy by the French, and the League of Five Nations by the English, the confederacy is properly called the Haudenosaunee Confederacy meaning People of the long house. The confederacy was founded by the prophet known as the Peacemaker with the help of Aionwatha, more commonly known as Hiawatha. The exact date of the joining of the nations is unknown and said to be time immemorial making it one of the first and longest-lasting participatory democracies in the world.

Does size matter? A bioeconomic perspective on optimal harvesting when price is size-dependent

Fabian Zimmermann, Mikko Heino, and Stein Ivar Steinshamn

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Abstract: Body size is a key parameter influencing demographic characteristics of fish populations as well as market value of landed catch. Yet in bioeconomic modelling, body size is often an overlooked biological and economic parameter. Here we evaluate how size-dependent pricing influences optimal harvest strategies in a model parameterized for two pelagic fisheries, those targeting Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*), in Norway. In our model, positively size-dependent pricing clearly shifts optimal harvest strategies towards lower harvest rates and higher mean body size of caught fish. The results are relatively insensitive to biological (e.g., natural mortality) and economic details of the model (e.g., discount rate or demand function). These findings show that size-dependent pricing influences optimal harvest strategies aiming at maximum economic yield and, hence, requires more attention in resource economics and in fisheries management.

Résumé : La taille corporelle est une variable clé qui influence certaines caractéristiques démographiques des populations de poissons ainsi que la valeur marchande des débarquements. Néanmoins, la taille corporelle est souvent une variable biologique et économique négligée dans les modèles bioéconomiques. Nous évaluons ici comment la fixation des prix en fonction de la taille influence les stratégies de récolte optimale dans un modèle paramétrisé pour deux pêches pélagiques, celles qui ciblent le hareng atlantique (*Clupea harengus*) et le maquereau bleu (*Scomber scombrus*) en Norvège. Dans notre modèle, une fixation positive des prix en fonction de la taille fait déplacer les stratégies de récolte optimale vers des taux de récolte plus faibles et vers une taille moyenne plus grande des poissons récoltés. Les résultats sont relativement insensibles aux détails biologiques (par ex., la mortalité naturelle) et économiques (par ex., le taux d'escompte ou la fonction de demande). Ces résultats montrent que la fixation des prix en fonction de la taille influence les stratégies de capture optimale qui recherchent un rendement économique maximal et qu'ainsi elle mérite plus d'attention dans l'étude économique des ressources et la gestion des pêches.

[Traduit par la Rédaction]

Introduction

It is common that price of fish depends on their size; typically, large individuals fetch a higher price per kilogram than small individuals of the same species. When present, such size dependence should be considered when evaluating harvest strategies (Hilborn and Walters 1992). While size-dependent pricing is occasionally included in bioeconomic models, it is very rare that the consequences of size-dependent pricing per se have been studied in any detail. We are aware of only few studies where this question has been touched; Gallagher et al. (2004) and Holland et al. (2005) showed that for Oregon ocean shrimp (*Pandalus jordani*) and rock lobster (*Jasus edwardsii*), respectively, size-related pricing indeed influences management strategies. Similarly, Tahvonen (2009) demonstrated in a generic age-structured model how equilibrium revenue and stock size are affected by size-dependent pricing. More typically, size-dependent pricing has been either overlooked, acknowledged but not analyzed (Anderson 1989), or taken as an extrinsically determined model component that is kept fixed in the analysis (e.g., Thunberg et al. 1998; De Leo and Gatto 2001; Katsukawa 2005). Some studies also acknowledge other biological factors influencing price (e.g., seasonal changes in fish quality; Larkin and Sylvia 1999). Size-dependent pricing is also important in aquaculture (Bjørndal 1988; Asche and Guttormsen 2001). Thus, we have all reasons to expect that the size dependency of the price is widespread and highly relevant for optimal utilization of fish stocks.

Here our aim is to quantify how size-dependent pricing influences optimal harvest strategies. We use Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) as case studies. Specifically, we focus on the Norwegian

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spring spawning herring stock and the northeast Atlantic mackerel stock, following the stock definitions used in the management (ICES 2010). Herring and mackerel are of major importance for the fisheries of several European countries, with a total catch of about 1.7 and 0.7 million tonnes, respectively, in 2009 (ICES 2010). Moreover, herring and mackerel are key species in the northeast Atlantic pelagic ecosystem (Skjoldal et al. 2004), making their sustainable management even more important.

We utilize an age-structured, discrete-time population model with size-dependent harvesting. Price data are based on Norwegian market data for herring and mackerel. For simplicity we assume that the relationship between size and price is linear; this allows us to smoothly vary the strength of size dependency, in contrast with earlier studies that only considered a limited set of fixed pricing scenarios (Gallagher et al. 2004; Holland et al. 2005) The cost of harvesting is output-regulated and depends on yield. In the optimization, the main target is to maximize the net present value over a long time scale with discount rates on an efficient market level, while high discount factors are used to emulate an open-access situation. We show how optimal fishing mortality and resulting mean individual mass in the catch depends on the size dependency of pricing. We also estimate the shadow cost (i.e., the opportunity costs for applying a suboptimal harvest regime and the lost margin of benefit due to ignoring the size dependency of pricing).

Materials and methods

Biological model

The biological model is based on an age-structured population dynamics model with annual time steps. Sexes are combined because male and female life histories are similar in herring and mackerel (the parameters and their values are listed in Appendix Table A1).

There are n discrete age classes, denoted by N_a with $a = 1, 2, \ldots, n$, and there is no senescence. The last age class is a so-called plus-group representing all fish n years of age or older. Population dynamics is then described by

$$N_a(t+1) = \begin{cases} r[\mathrm{SSB}(t)] & \\ s_a N_{a-1}(t) & \text{if} \\ s_n[N_{a-1}(t) + N_a(t)] & \end{cases} \quad \begin{cases} a = 1 \\ 1 < a < n \\ a = n \end{cases}$$

where SSB is the spawning stock biomass, r(SSB) is the stock–recruitment function, and s_a is age-specific survival probability defined below.

The connection between age and size is defined through the von Bertalanffy growth model $l(a) = L_\infty (1 - \mathrm{e}^{-ka})$, where L_∞ is the asymptotic length and k is the growth coefficient. Furthermore, we assume an allometric mass–length relationship $w(l) = vl^u$, where v is the length–mass coefficient and u is the allometric exponent.

Reaching maturity is based on the age of the individual and defined by the age-maturity ogive $o(a) = \left[1 + \mathrm{e}^{-(a - a_{50})/a_{\mathrm{width}}}\right]^{-1}$, where a_{50} is the age where 50% of the individuals have reached maturity and a_{width} is the coefficient describing width of the maturity envelope. Mature individuals constitute the spawning stock, and SSB is defined as $\mathrm{SSB} = \sum_a w_a o_a N_a(t)$. For herring, recruitment follows the Beverton–Holt stock–recruitment model as defined by (Fiksen and Slotte 2002), $r(\mathrm{SSB}) = \frac{b_1\,\mathrm{SSB}}{b_2 + \mathrm{SSB}}$, where b_1 is asymptotic maximum recruitment and b_2 determines how fast the asymptote is approached. For mackerel, we use the hockey-stick recruitment model estimated by ICES (2010), implying that below a threshold $\mathrm{SSB}_{\max}$ recruitment is a linear, increasing function of SSB, $r(\mathrm{SSB}) = b_3\mathrm{SSB}$, whereas above the threshold recruitment is assumed to be constant, $r(\mathrm{SSB}) = r_{\max}$.

The fishing mortality is assumed to be length-dependent. Catchability usually increases with size until levelling off at some intermediate size, a relationship usually described by a sigmoid curve. However, in our study stocks, no such levelling off can be detected between fishing mortality (mean fishing mortality at age from 1984–2009; ICES 2010) and length-at-age (from the growth model described above); for mackerel, the three-parameter sigmoid model fails to converge, whereas for herring the inflection point in the resulting fit is far outside the range of observed lengths. Within the range of observed lengths, a two-parameter power function and the sigmoid function predict similar fishing mortalities for mackerel, but the power function gives a lower Akaike information criterion (AIC) (difference = 2.0) than the sigmoid function. The relationship between fishing mortality and length is therefore most parsimoniously described as a power function for both stocks. Here we normalize length relative to mean catch length $\bar{l}$, such that

$$(1) \qquad F_a = F[l(a)] = F_0(l/\bar{l})^\eta$$

where F_0 is fishing mortality at mean catch length and η is a selectivity parameter that determines the strength of length dependency; the function is convex for $\eta > 1$. The equation was fitted to fishing mortality at age data from (ICES 2010), transforming age into length using the von Bertalanffy model described above. Mean catch length $\bar{l}$ used in the normalization was estimated through back calculation of mean catch mass based on mass at age in the International Council for the Exploration of the Sea (ICES) catch from 2009 (ICES 2010).

The natural mortality M is based on the values used in the stock assessment (ICES 2010). The survival probability s is determined by the total mortality Z, which is the sum of fishing mortality F and natural mortality M: $s_a = \mathrm{e}^{-Z_a} = \mathrm{e}^{-(F_a + M_a)}$

The link between the biological and economic part of the model is the catch equation $H_a = N_a(1 - \mathrm{e}^{-Z_a})F_a/Z_a$, where H_a is catch numbers at age. Total catch in terms of biomass, or yield, is catch numbers times the mean age-specific individual mass, $Y = \sum_a H_a w_a$.

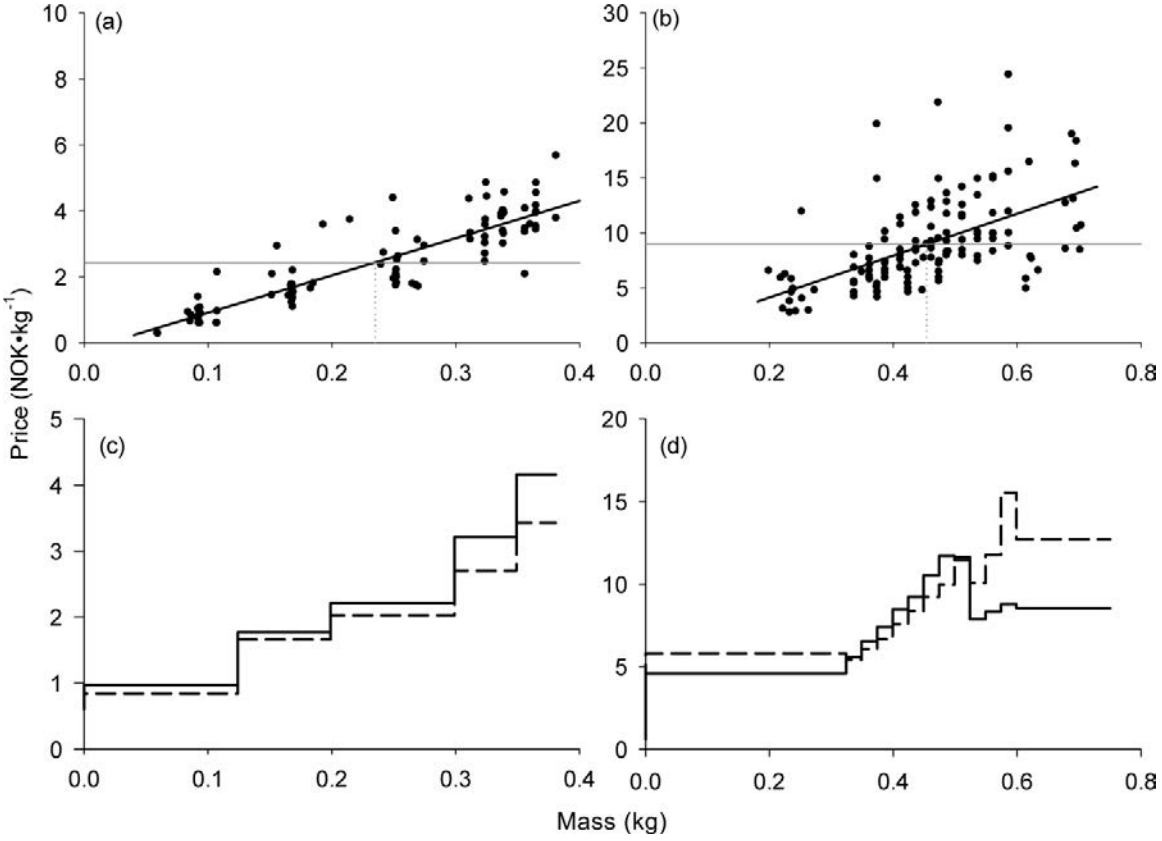
Economics

We assume that the relationship between size and price can be expressed as a simple linear function of mass, such that we can easily change the strength of size dependence. To make the parameters easily interpretable, we standardize mass relative to the mean observed individual catch mass over all age classes, $\overline{w}$. Furthermore, we standardize the price–mass coefficient relative to the observed coefficient,

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Fig. 1. Linear mass–price functions (solid lines) estimated from real price data (dots) and step functions based on price per mass categories for herring (*a*, *c*) and mackerel (*b*, *d*). The actual price slopes β_0 are 2.43 (herring) and 8.97 Norwegian krones (NOK)·kg^{-1} (mackerel). For reference, the case with constant price ($\beta = 0$; grey line) is also shown. The pivot point of these lines corresponds to the observed mean individual catch mass, $\overline{w}$ (dotted line) and price per kilogram for this mass, $p_{\overline{w}}$. The price data are annual mean prices per mass class from Norwegian spring spawning herring and northeast Atlantic mackerel in 2000–2010 provided by the Norwegian Fisheries Directorate (Per Sandberg, Fiskeridirektoratet, Postboks 185 Sentrum, 5804 Bergen, Norway, personal communication, 2011). We use annual catch mass distributions (ICES 2010) to transform mass classes into mean mass of each mass class (*a*, *b*). Step functions (*c*, *d*) represent prices per mass class in 2009 (dashed line) and 2010 (solid line).



β_0. The price function is then $p(w) = p_{\overline{w}} + \beta\beta_0\left(\frac{w-\overline{w}}{\overline{w}}\right)$, where the intercept $p_{\overline{w}}$ is the price per unit biomass for $\overline{w}$, the observed slope β_0 gives the price increase when individual mass is increased by $\overline{w}$, and β is the relative deviation from the observed slope. $\overline{w}$ thus acts as the pivot point in this function. The parameters $p_{\overline{w}}$ and β_0 of the price function (Fig. 1) were estimated with linear regression using data provided by the Norwegian Fisheries Directorate (Per Sandberg, Fiskeridirektoratet, Postboks 185 Sentrum, 5804 Bergen, Norway, personal communication, 2011). The data comprise total annual yield and value per mass class in 2000–2010 as registered by the sales organizations. Average prices per mass class are derived from these data. To obtain mean mass for each mass class, we assumed that mass at age in the catch is normally distributed, with mean taken from ICES (2010) and a coefficient of variation of 30%. We then multiplied the age-specific mass distributions with catch numbers at age (ICES 2010) to obtain total mass distribution in a given year, which allows estimating the mean mass for a certain mass class as well as the overall mean mass $\overline{w}$. Mean price $p_{\overline{w}}$ was derived from the data from the Norwegian Fisheries Directorate.

We also considered constraining the influence of size on price. As the minimum price, we used the minimum price set by the Norwegian pelagic fish sales organization, which was 0.60 Norwegian krones (NOK)·kg^{-1} for both herring and mackerel in 2010 (Norges Sildesalgslaget 2011). As the maximum, we used the highest mean price in 2010, which was 4.16 NOK·kg^{-1} for herring and 11.7 NOK·kg^{-1} for mackerel.

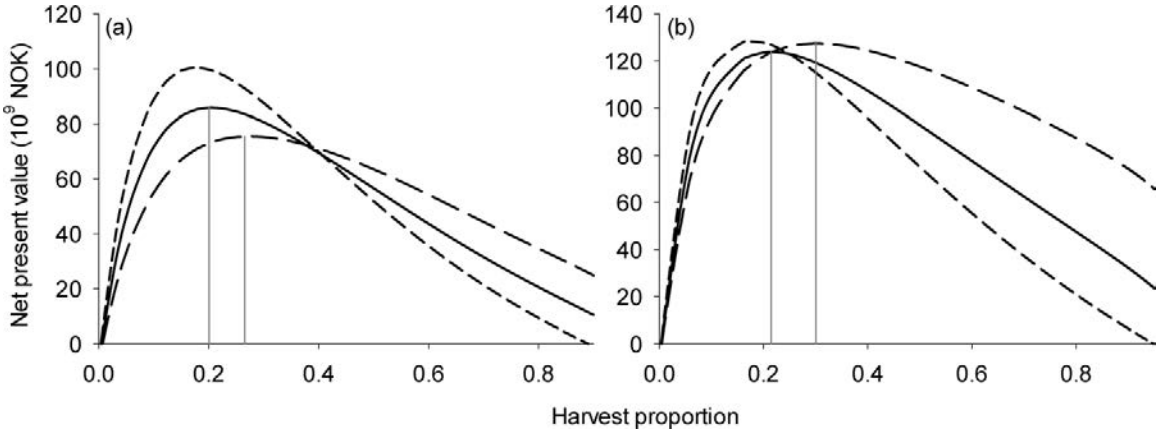
The total revenue is the sum of the annual yield times the mass-dependent price for each age class, $R_t = \sum_a p(w_a)Y_a$. The cost function is derived from the model of Touzeau et al. (2000). To avoid potential complications due to the non-linearity of this cost curve, a simplified cost function with a linear relationship between yield and cost based on a linear regression of the cost function of Touzeau et al. (2000), $C_t = C_0 + \upsilon Y_t$, has been used. Here the intercept C_0 represents fixed costs, and the term υY_t represents variable costs. The net revenue is then $\Pi_t = R_t - C_t$. With d denoting discount rate, the net present value (NPV) is the sum of annual discounted net revenues:

$$\text{NPV} = \sum_0^t \frac{\Pi_t}{(1+d)^t} \quad (2)$$

We tested a demand function estimated from Norwegian yield and price data in 2000–2009. However, the resulting fit

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Fig. 2. Net present value (NPV) for herring (*a*) and mackerel (*b*) fisheries as a function of harvest proportion under the current pricing regime (solid line), no size-dependent pricing ($\beta = 0$; long dashed line) and a twofold price slope ($\beta = 2$; short dashed line). The distance between vertical grey lines illustrates the difference in the NPV-maximizing harvest strategies in the presence and absence of size-dependent pricing. Discount rate (d) is equal to 0.05. Harvest proportion is calculated from the mean fishing mortality over reference ages as defined by ICES (ages 5–14 years for herring, 4–8 years for mackerel; ICES 2010).



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was poor because of the lack of information about willingness to pay outside the narrow range of actual production volumes and because of other factors influencing the price. Sensitivity analysis showed no significant influence on the results, and therefore demand effects were not considered further in this study. However, because of this and the simple cost function used, we emphasize that we do not expect the model to give precise quantitative predictions, even though the results shown are qualitatively robust.

Simulations

The model was run over 1000 years, an essentially infinite time horizon unless discount rate is very low ($d < 0.01$). The first 200 years were used to establish prefishing equilibrium. Fishing started from the virgin stock at year 200, causing the stock to decline towards a new equilibrium. It is assumed that size selectivity of the fisheries is fixed, but that the managers can adjust the overall level of fishing mortality such that NPV of the stock is maximized. Harvest strategies in our model are therefore defined through the parameter F_0, fishing mortality at mean catch length. The optimal F_0 was identified using the function "optimize" in R (R Development Core Team 2010).

Results

The effect of size-dependent pricing is to shift harvest rate that maximizes NPV towards lower values (Fig. 2). Comparing the harvest strategy optimized for size dependency of the current pricing regime and one without any size dependency, the shadow cost of omitting the size dependency in the current pricing regime is found to be about 3.3% for herring and 3.8% for mackerel relative to the optimal NPV (discount rate $d = 0.05$). Shadow costs define here the difference in NPV between the optimal harvest strategy with the current, size-dependent price regime and the one that would be optimal when we assume no size-dependent pricing (i.e., the opportunity cost of ignoring size dependency in price).

With increasing effect of size on price (increasing β), the mean fishing mortality that maximizes NPV decreases and the corresponding mean individual size increases (Fig. 3); for herring the effect is almost linear within the considered range, whereas for mackerel the effect is levelling off for strong size dependence. Mean fishing mortalities (age groups 4–8 for mackerel and 5–14 weighted by stock numbers for herring) yielding maximum NPV (with discount rate $d = 0.05$) are 0.146 year^{-1} in the current pricing regime ($\beta = 1$) compared with 0.189 year^{-1} without size-dependent pricing for herring and 0.242 year^{-1} compared with 0.357 year^{-1} for mackerel. For reference, the latest stock assessments estimated fishing mortalities at 0.154 year^{-1} for herring and 0.233 year^{-1} for mackerel (ICES 2010). In our model, the decrease in mean fishing mortality between no size dependency and a realistic size-dependent pricing is about 23% for herring and 32% for mackerel, and the mean catch mass increases by about 6% and 8%, respectively. The patterns remain similar if the initial stock states are changed from the pristine levels to lower population abundances estimated in the latest stock assessments (ICES 2010).

The discount rate has no influence on the qualitative effect that size-dependent pricing has on optimal fishing mortality and the corresponding mean size (Fig. 3), even when very high discount rates emulating an open-access situation are considered (Fig. 4). Nevertheless, the discount rate has a considerable quantitative effect on the optimal fishing mortality; the optimal value increases almost threefold between the extreme cases of no discounting and a very high discount rate of one, mimicking an open-access situation. As theory suggests, the biggest effect on optimal fishing mortality is found on low to intermediate discounting levels.

Because natural mortality is an important parameter in age-structured models, we investigate its influence further. For both species, changing natural mortality results in changes in optimal fishing mortality and, to a somewhat lesser extent, in the resulting mean catch mass (Fig. 5). These changes are opposite for the two species; higher natural mortality leads to higher optimal fishing mortality for mackerel but lower optimal fishing mortality for herring. These effects are slightly more pronounced for low β; an increasing β

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Fig. 3. The influence of relative price slope β on optimal fishing mortality (black) and the resulting mean individual mass (grey) in the catch of herring (*a*) and mackerel (*b*) with respect to different discount rates *d*. Discount rate takes values $d = 0.05 \pm 0.05$ ($d = 0$ long dashed line; $d = 0.1$ short dashed line; $d = 0.05$ solid line). Optimal strategy is the one maximizing the net present value of a pristine stock. Strength of size dependence of price is expressed as the relative price slope β, with $\beta = 1$ corresponding to the current price dependence shown in Fig. 1, and $\beta = 0$ corresponding to no price dependence. Fishing mortality is the mean fishing mortality over reference ages as defined by ICES (ages 5–14 years weighted by stock numbers for herring, 4–8 years for mackerel; ICES 2010).

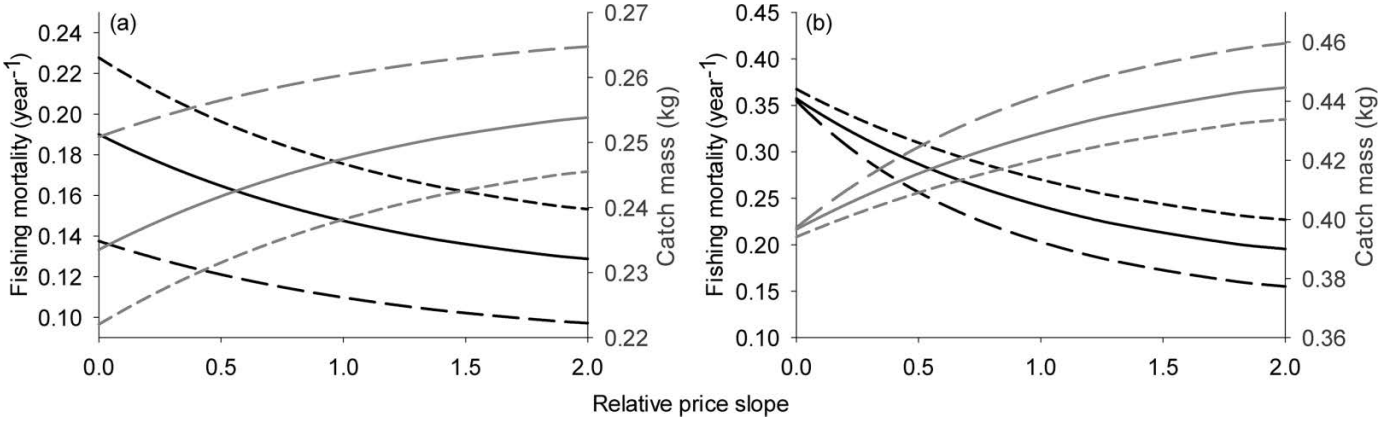
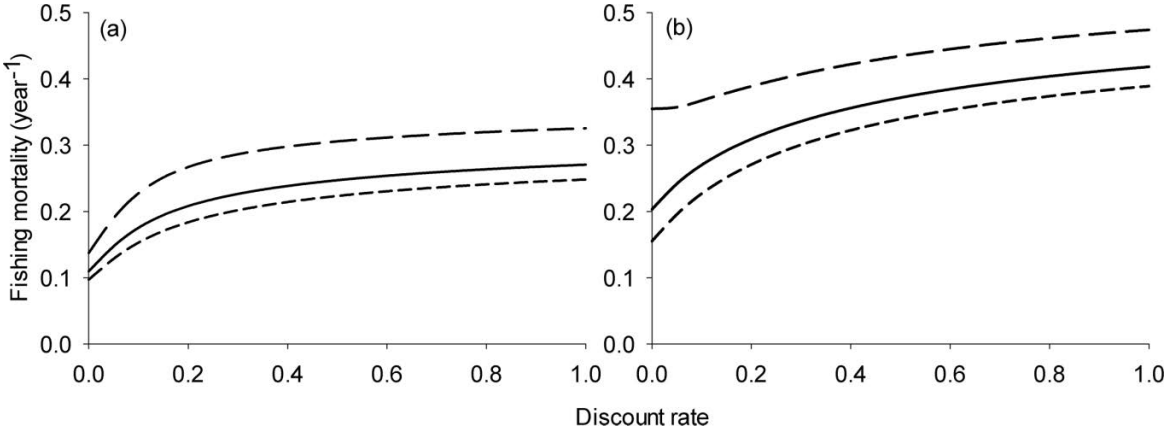


Fig. 4. Mean fishing mortality optimized for net present value in herring (*a*) and mackerel (*b*) fisheries under the assumptions of discount rates between 0 and 1. The solid line shows results for the real size dependence of pricing. The envelope with dashed lines shows the case of no size dependency (long dashed) and doubled slope (short dashed). Optimal strategy is the one maximizing the net present value of a pristine stock. Fishing mortality is the mean fishing mortality over reference ages as defined by ICES (ages 5–14 years weighted by stock numbers for herring, 4–8 years for mackerel; ICES 2010).



tends to dampen the influence of changing natural mortality. The qualitative difference between the species is caused by the age-dependent natural mortality in herring; assuming a constant natural mortality for herring leads to mackerel-like results. For catch masses, the influence of changing natural mortality is qualitatively the same for both species; mean catch mass is increased (decreased) by higher (lower) natural mortality.

Comparing the continuous price function with the empirical step functions either in 2009 or 2010 given in Fig. 1 shows that the differences are negligible; optimization with discrete price classes displays the same shift between constant price and size dependency and similar quantitative results. The same applies when applying minimum and (or) maximum price caps. Additionally, optimal fishing mortality depends on the selectivity parameter η, but the effect is minor and does not influence the qualitative pattern (Fig. 6).

Discussion

The size of fish is a key parameter from biological as well as technical and economic perspectives. In terms of biology, size is closely linked with growth, maturation, reproductive output, and survival. Avoidance of growth overfishing — catching fish too small, before a cohort has realized its growth potential — has been a crucial part of fisheries management since Beverton and Holt (1957). Using minimum size restrictions and mesh size regulations as management tools to protect the productivity of a fish stock reflects this idea. Likewise, the fishing industry has a strong interest in fish size both to optimize the industrial utilization and to serve consumer preferences. Ultimately, these market incentives are a key driver for size-dependent pricing. Yet the connection between price and body size is an understudied issue in fisheries economics. This is surprising given that size-

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Fig. 5. Mean fishing mortality (black) that maximizes net present value (NPV) in herring (*a*) and mackerel (*b*) fisheries and the corresponding mean catch mass (grey) as functions of the relative price slope. The lines represent the default natural mortality M_a (solid) and M_a decreased (long dashed) or increased (short dashed) by 20%. The discount rate is $d = 0.05$. Optimal strategy is the one maximizing the NPV of a pristine stock. Strength of size dependence of price is expressed as the relative price slope β, with $\beta = 1$ corresponding to the current price dependence shown in Fig. 1 and $\beta = 0$ corresponding to no price dependence. Fishing mortality is the mean fishing mortality over reference ages as defined by ICES (ages 5–14 years weighted by stock numbers for herring, 4–8 years for mackerel; ICES 2010).

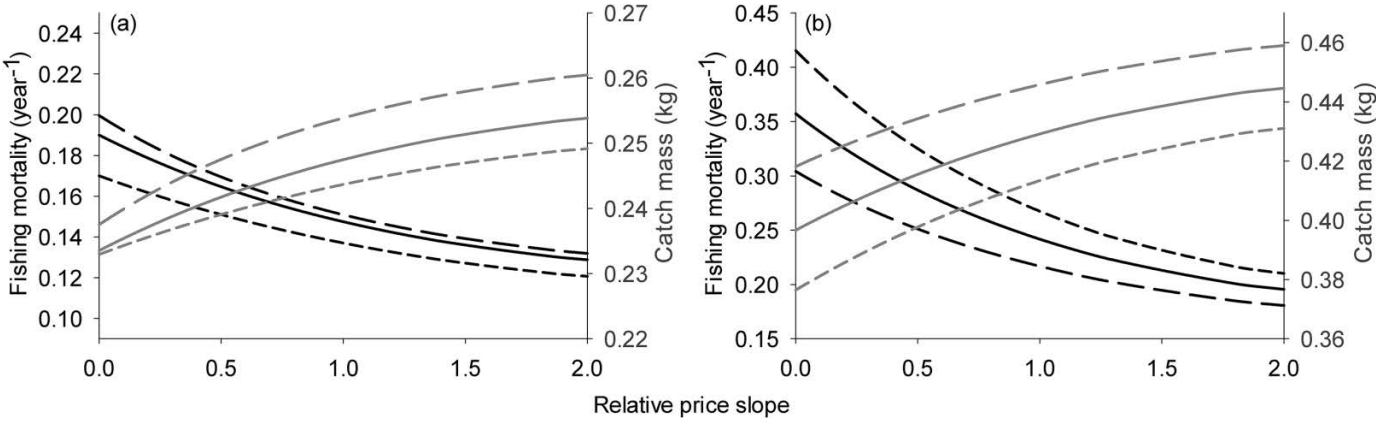
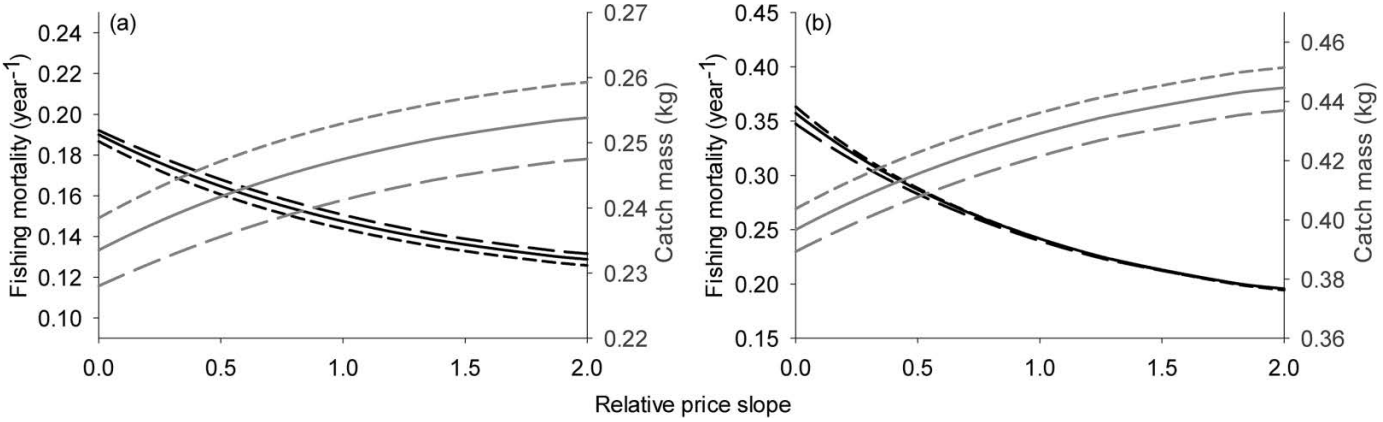


Fig. 6. Mean fishing mortality (black) optimized for net present value (NPV) in herring (*a*) and mackerel (*b*) fisheries and the corresponding mean catch mass (grey) as functions of the relative price slope. The lines represent the default selectivity parameter η (solid line) and η decreased (long dashed line) or increased (short dashed line) by 20%. The discount rate is $d = 0.05$. Optimal strategy is the one maximizing the NPV of a pristine stock. Strength of size dependence of price is expressed as the relative price slope β, with $\beta = 1$ corresponding to the current price dependence shown in Fig. 1 and $\beta = 0$ corresponding to no price dependence. Fishing mortality is the mean fishing mortality over reference ages as defined by ICES (ages 5–14 years weighted by stock numbers for herring, 4–8 years for mackerel; ICES 2010).



dependent pricing is ubiquitous and that its role in rational harvest management has in theory been acknowledged for a long time (Hilborn and Walters 1992). While a number of studies on capture fisheries have included size-dependent pricing, the majority of these have only considered a single scenario, without studying the effects of size-dependent pricing per se (e.g., Helser et al. 1996; Thunberg et al. 1998; Katsukawa 2005). A few studies have included a small number of alternative size-dependent pricing scenarios when analysing specific fisheries (Gallagher et al. 2004; Holland et al. 2005). There are also a few generic models that have included size-dependent pricing (Anderson 1989; Tahvonen 2009). While Anderson (1989) did not elaborate on the importance of size-dependent pricing, Tahvonen (2009) showed with a concrete example how positively (or negatively) size-dependent pricing leads to equilibrium revenues to be maximized at a higher (or respectively lower) stock biomass level. The topic has also been discussed outside fisheries economics. For example, price of fish produced in aquaculture is size-dependent, and this has consequences for optimizing the production cycle (Bjørndal 1988; Asche and Guttormsen 2001).

Our goal here was to demonstrate the importance of size-dependent pricing for economically optimal harvest strategies using simple age-structured models parameterized for two important pelagic fish stocks. The results confirm our expectations; fishing pressure maximizing economic yield in terms of revenue and NPV depends on the applied size-based pricing regime, with implications for mean size of fish in the catches and equilibrium stock abundance. The results reveal potential for overestimation of future profits and rent dissipation due to the application of suboptimal harvest strategies when ignoring size-dependent pricing; the effect in the examples studied here is nevertheless quantitatively modest. However, the effect on the resultant harvest strategy is appreciable. Considering that in most commercially important fish stocks

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the price is size-dependent, the insights presented here call for broader utilization of size-dependent pricing in economic modelling.

When the size–price relationship is monotonic and positive, maximum economic yields are obtained through higher stock sizes and smaller catches than when such size dependence is absent. In other words, positive size–price relationships imply that lower fishing mortalities optimize the NPV. It is acknowledged that catches below maximum sustainable yield typically maximize the resource rent (Clark 2006; Grafton et al. 2007; Tietenberg and Lewis 2008). Our results suggest that this effect might even be stronger than maximum economic yield estimates ignoring size-dependent pricing would suggest. Therefore, taking positively size-dependent pricing into account would result in lower harvest rates, which would not only ultimately increase society's direct economic benefits from fisheries, but also reduce the negative effects fisheries might have on the ecosystems. This is in accord with the precautionary approach to fisheries management, calling for more conservative harvest policies that lead to an increased overall stock abundance. This would enhance population resilience, harvest productivity, and efficiency.

Our results resonate with calls to save the big fish for the sake of improved biological sustainability (Birkeland and Dayton 2005; Francis et al. 2007; Diekert et al. 2010). This statement may seem counterintuitive, since we emphasize the high market value of large-sized fish. However, we have focused on a single-owner fishery where the manager adopts a long time perspective, avoiding the short-sighted temptation of targeting the large fish. In our model, the opportunity cost of choosing a suboptimal harvest strategy can only be mitigated by reducing the overall fishing mortality, therefore allowing more fish to reach large sizes and, ultimately, leaving more big fish in the sea.

We emphasize that in general, mesh size regulations and other means of modifying size-dependent catchability can be important levers of optimizing the harvest, even though we did not consider them here. Our model applies to pelagic fisheries where effective regulation of size-dependent catchability is difficult; gears like purse seines are weakly size-selective, and pelagic fish have low survival after slipping through meshes or being strangled in a net. However, demersal fish are often more robust and have better chances of surviving if slipping through meshes or sorting grids or if discarded after the capture. Mesh size regulations can therefore be a means to ensure that enough fish have chance to grow to the most valuable size classes. In such cases, economic implications of considering size-dependent pricing are likely larger than what we have found for herring and mackerel here.

We have used the simplest possible price function, a linear relationship between price and mass, as the default price function. While this is a good approximation for herring and mackerel, more complex relationships occur in some fisheries (Thunberg et al. 1998). There is also some evidence that the price premium for larger size disappears for very large mackerel, a situation that may not be uncommon if very large fish have lower flesh quality, higher concentrations of contaminants, or are less suited for industrial processing. Similarly, if small-sized fish are destined to fish meal production instead of human consumption, their precise size may become unimportant. We therefore also tried constraining the price between certain minimum and (or) maximum levels, but this did not change the results in any essential way (the bulk of the harvest comes from medium-sized fish). Additionally, our price function implies continuously increasing effect of size on price, whereas real markets commonly operate with discrete mass classes. While using the real mass classes should give more precise results, our simulations suggest that a linear function is a good approximation. Moreover, market mass classes often vary over time and space. For these reasons we consider a linear approximation justified here.

Our study has several general limitations. We rely on a single-species approach and focus in the steady state scenario without environmental oscillations. Size structure in the model is determined by the age structure using a static age–length relationship. In reality, size structure of the harvestable stock is determined by intra- and inter-specific interactions (availability of resources and presence of predators). In particular, density-dependent body growth (e.g., Lorenzen and Enberg 2002) might counter the increase in average size that is expected to occur when fishing is reduced and therefore influence management strategies (Helser and Brodziak 1998). A major source of uncertainty is natural mortality. This is modelled as constant (mackerel) or age-dependent (herring); both assumptions are crude approximations of reality, but unfortunately data for more realistic choices are not available. Also, our economic model is rather simplistic, apart from inclusion of size-dependent price. We assume a simple yield-determined cost function and absence of market feedbacks on price. Our initial explorations suggested that considering effort-dependent costs or demand curves is not important for the questions addressed here. Moreover, developing a more detailed bioeconomic model for mackerel would have been a major task on its own, whereas for herring, more detailed information exists (e.g., Touzeau et al. 2000; Sandberg 2006). Finally, the model does not account for practical challenges in balancing stakeholder interests nor policy implementation and enforcement; in reality, suboptimal management due to political and social pressures and illegal fishing are more a rule than an exception (Beddington et al. 2007; Agnew et al. 2009; Mora et al. 2009).

Another angle worth discussing is that of fisheries-induced adaptive changes. Statistical, experimental, and modelling approaches are giving increasing support to the hypothesis that fishing causes evolutionary shifts in life-history traits (Jørgensen et al. 2007; Dunlop et al. 2009; Sharpe and Hendry 2009). Because these changes typically involve reduced adult body size (Heino 1998; Enberg et al. 2011), size-dependent pricing is relevant also when trying to estimate the possible economic impacts of fisheries-induced evolution.

To conclude, this study has highlighted that size-dependent pricing has important implications for fisheries management. Because markets usually value large fish more than small fish, harvest strategies should consider how the harvest influences size structure of the catch: the higher the harvest pressure, the lower the mean size of fish. Therefore, harvest policies that aim at maintaining harvest of large-sized fish lead to lower harvest levels than those that ignore the quality of the catch; ultimately, this might lead to more sustainable harvest and increased economic benefits from the fisheries.

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We encourage further explorations into consequences of size-dependent pricing on fisheries management, both in the direction of further generalizations and towards more detailed studies on specific fish stocks and fisheries.

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Appendix A

Table A1. List of parameters and their values.

Parameter	Definition	Unit	Value	
			Herring	Mackerel
n	Maximum age class[a]	year	15	12
M_a	Natural mortality[a]	year^{-1}	$\begin{cases} 0.9 \\ 0.15 \\ 0.5 \end{cases}$ for $a = \begin{cases} a \leq 2 \\ 2 < a < n \\ n \end{cases}$	0.15
b_1	Asymptotic recruitment[b]	—	1.9×10^{11}	—
b_2	Steepness of recruitment function[b]	kg	5.1×10^{9}	—
b_3	Initial slope of recruitment function[a]	kg^{-1}	—	1.811
r_{max}	Maximum recruitment[a]	—	—	4.252×10^{9}
L_∞	Asymptotic length[c]	mm	370	418
k	von Bertalanffy growth parameter[c]	year^{-1}	0.26	0.43
v	Length–mass coefficient[c]	kg·mm^{-u}	2.32×10^{-5}	3.4×10^{-3}
u	Length–mass exponent	—	2.81	3.24
a_{50}	Age at 50% maturity[a]	year	4	3
a_{width}	Width of maturity envelope	year	0.3	0.2
η	Selectivity parameter[a]	—	4.3	3.3
β_0	Price function slope[d]	NOK·kg^{-1}	2.43	8.97
$\overline{w}$	Mean catch mass[a,d]	kg	0.235	0.454
C_0	Fixed costs[e]	NOK	3.4×10^{5}	3.4×10^{5}
υ	Cost function slope[f]	NOK·kg^{-1}	0.7	0.7

[a]ICES 2010.

[b]Fiksen and Slotte 2002.

[c]Jennings and Beverton 1991.

[d]Norwegian Directorate of Fisheries (P. Sandberg, Fiskeridirektoratet, Postboks 185 Sentrum, 5804 Bergen, Norway, personal communication, 2011).

[e]Touzeau et al. 2000.

[f]Froese and Pauly 2009.

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Energy content of Pacific salmon as prey of northern and southern resident killer whales

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ABSTRACT: Recovery of depleted species is difficult, but it can be especially complex when the target species interacts strongly with other depleted species. Such is the case for northern and southern resident killer whales *Orcinus orca* which are listed as 'endangered' under the US Endangered Species Act (ESA) and Canada's Species at Risk Act. These resident killer whales prey heavily on Pacific salmon *Oncorhynchus* spp., including several 'evolutionarily significant units' also listed under the ESA. In response to concerns that a depleted prey base may affect killer whale recovery, we analyzed proximate composition and calculated caloric content of Pacific salmon to evaluate the importance of salmon species, population, body size, and lipid levels in determining their energy content as prey for killer whales. We sampled all 5 species of Pacific salmon, but emphasized Chinook salmon, a predominant prey of killer whales. Energy density (kcal kg^{-1}) was highly correlated with lipid content, whereas total energy value (kcal $fish^{-1}$) was determined primarily by fish mass and secondarily by lipid content. These salmon energetics data can be used to provide better precision and estimates on the caloric value of prey to killer whales. To facilitate application of these results to the co-management of salmon and killer whales, we produced a simple relationship that uses fish length to predict total energy of Chinook salmon as prey where population-specific energy densities and fish masses are lacking. Benefits to killer whales from possible salmon fishery closures, or other activities that affect prey availability, will depend on the salmon species and populations involved.

KEY WORDS: Pacific salmon · Energy content · Resident killer whale prey

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INTRODUCTION

The preservation and rebuilding of threatened and endangered species is a world-wide concern, as many species and distinct population segments have declined precipitously in the past decades (Hutchings & Reynolds 2004, Schipper et al. 2008). Rebuilding plans for single species are always challenging, but they are especially so when the target species interacts strongly with other listed species (Williams et al. 2011). For example, in the northeastern Pacific Ocean, killer whales *Orcinus orca* exist as 3 sympatric ecotypes, commonly known as resident, transient, and offshore forms, each of which has a distinct diet (Krahn et al. 2002, Ford et al. 2010a). Residents feed on fish and especially Pacific salmon *Oncorhynchus* spp., whereas transient killer whales feed primarily on marine mammals (Ford 1998). The offshore killer whales are distributed along the outer coast and also eat fish, but they appear to specialize in sharks and other large fishes (Ford et al. 2000, Dahlheim et al. 2008). Krahn et al. (2004) described several populations of eastern North Pacific resident killer whales, including northern and southern resi-

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dent killer whales (NRKW and SRKW, respectively). The NRKW population is found mostly in coastal waters near the middle of Vancouver Island and north to southeastern Alaska, whereas the SRKW population is found primarily farther south, off the southern half of Vancouver Island and in the inland waters of Washington state (Ford et al. 2010b), although there is some overlap in distribution (summarized in Hilborn et al. 2012).

From 1996 to 2001, the SRKW population declined 20% (from 97 whales to 78), and was listed as endangered under both the Endangered Species Act (ESA) in the United States (NMFS 2005) and the Species at Risk Act (SARA) in Canada (Fisheries and Oceans Canada 2008). The NRKW population also declined during the late 1990s, and was designated as threatened under the SARA (Fisheries and Oceans Canada 2008). Many factors may have contributed to these declines, including vessel and noise disturbances (Holt et al. 2009, Lusseau et al. 2009) and exposure to high levels of persistent organic pollutants (POPs) obtained through their diet (Ross et al. 2000, Rayne et al. 2004, Krahn et al. 2007, 2009). Reduction in populations of the whales' prey has also been hypothesized as a contributing factor in reduced reproduction (Ward et al. 2009) and population declines (Ford et al. 2010a,b).

NRKW and SRKW feed primarily on Pacific salmon, and Chinook salmon *O. tshawytscha* are the predominant prey during the summer and early fall (Ford 1998, Ford & Ellis 2006, Ford et al. 2010a,b, Hanson et al. 2010). They also capture older (i.e. larger) than average Chinook salmon (Ford & Ellis 2006) and likely consume both wild and hatchery salmon (Hanson et al. 2010). Other salmon species are sometimes consumed, but much less frequently than would be expected based on their abundance in coastal waters. Chinook salmon achieve the largest body size of the Pacific salmon, commonly reaching 10 to 15 kg, but are currently (and likely also in the past) the least numerous (Quinn 2005). It has been hypothesized that NRKW and SRKW focus their foraging efforts on Chinook salmon to maximize energy intake (Ford & Ellis 2006). Other possible explanations may be a difference in the whales' ability to detect Chinook salmon (Au et al. 2004) or to catch larger versus smaller fish, or a constraint of their culturally inherited foraging strategies (Ford et al. 2010a).

The abundance of Pacific salmon and especially Chinook salmon has been declining in the southern portion of their range for decades (Nehlsen et al. 1991, Fisher 1994, Slaney et al. 1996, Yoshiyama et al. 1998, Gustafson et al. 2007), resulting in the listing of numerous 'evolutionarily significant units' of Pacific salmon as threatened or endangered under the US Endangered Species Act. While naturally produced salmon have declined in many areas, hatchery production has supplemented many populations (Barnett-Johnson et al. 2007 [Central Valley], NMFS 2008b [Columbia River Basin], PMFC 2011 [Puget Sound]) and may contribute a large fraction of the salmon prey base returning to watersheds within the range of SRKW individuals. In addition to declines in abundance, some evidence suggests that Chinook salmon have declined in body size (Ricker 1981, Bigler et al. 1996). A combination of the decreasing abundance and body size of the primary prey of SRKW could significantly reduce the prey base below levels necessary to meet the energetic requirements of resident killer whales, potentially affecting their persistence and recovery (NMFS 2011).

A better understanding of the variation in caloric content among salmon populations is needed to improve estimates of the available prey base, enhancing the integration of killer whale conservation with salmon management. For example, Williams et al. (2011) noted that the predictions of the total prey requirement of the SRKW population could vary by a factor of 2.3, depending on the values used for whale body size; a factor of 2.9, depending on whether all or none of the diet is composed of Chinook salmon; and a factor of 1.7, depending on whether the caloric values used for Chinook salmon were for 'calorie-rich' or 'lean' fish. Estimating the energetic values of Chinook salmon as prey is complicated by the great diversity in body size and fat content among populations (Healey 1991), but improving the accuracy and precision of this parameter is far more tractable than estimating the body size of the whales or the percent of their diet that is composed of Chinook salmon.

In many large river systems, Chinook salmon breed in discrete locations, and those populations may differ in timing of return from the ocean, body size, and fat content as needed to reach spawning grounds that differ in distance and elevation from the ocean (Ricker 1972, Quinn 2005). Other salmon species also vary in size (Quinn 2005), so additional information on body size and energy density for Chinook salmon and other Pacific salmon is needed to evaluate their value as prey. Currently, most of the energy content data on Pacific salmon are based on fillets (Gilhousen 1980), whereas whales eat whole fish, and the available data are limited in geographic range.

The goal of this study was to determine the energy content of Pacific salmon as prey for resident killer whales using proximate composition and fish mass

data. We conducted a coast-wide study to assess the energetic content (kcal kg^{-1} and kcal $fish^{-1}$) of Chinook salmon over the geographic range in which they would be routinely encountered by NRKW and SRKW. Major population-complexes of sockeye *O. nerka*, coho *O. kisutch*, pink *O. gorbuscha*, and chum salmon *O. keta* were also sampled to compare energetic content among Pacific salmon species. Specifically, we (1) quantified differences in energy content among 5 salmon species, (2) tested for differences in energy content among Chinook salmon populations, and (3) evaluated the influence of lipid content and fish size in determining energy density (kcal kg^{-1}) and total energy value (kcal $fish^{-1}$). Additionally, to facilitate application of the results to the co-management of Chinook salmon and killer whales, we produced a simple predictive relationship between fish length and total energy value for use when population-specific energy density and body mass information are not available. The results of this study can be used to better assess the energetic value of the prey base available to resident killer whales, a necessary first step in evaluating the potential effects on killer whales of possible salmon fishery closures, or of other activities that affect the availability of salmon species and populations.

MATERIALS AND METHODS

Sampling design and locations

We sampled whole bodies of the 5 species of Pacific salmon caught in marine waters or slightly upriver from the mouths of major rivers, at the beginning of their upriver migration, from northern British Columbia to central California (Fig. 1) during summer and early fall (Table 1), encompassing the spatial and tem-

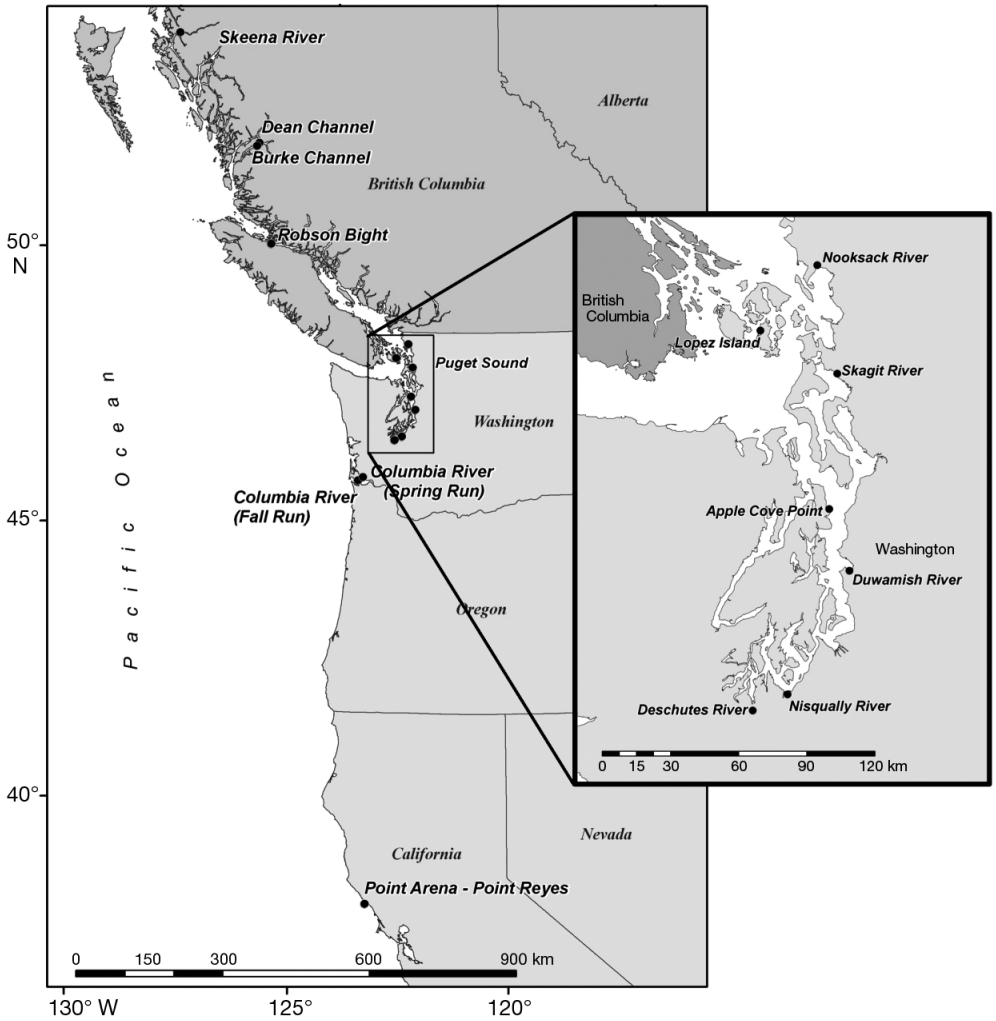


Fig. 1. *Oncorhynchus* spp. Sampling locations for Pacific salmon

Table 1. *Oncorhynchus* spp. Sampling details of Pacific salmon collected for proximate analyses. Proximate samples were composites of 1 to 3 (usually 3) fish of the same gender. All samples were of mature salmon, with the exception of Chinook salmon from Apple Cove Point (Puget Sound blackmouth)

Species	Collection region	Site description	Population-complex	Sample year	Sample month(s)	No. of fish collected	No. of proximate samples
Chinook	Northern British Columbia coast	Lower Skeena River	Skeena River	2004	Jun, Jul	28	10
	Johnstone Strait	Robson Bight	Fraser River	2004	Aug	30	10
	Puget Sound	Lower Nooksack, Duwamish, and Nisqually Rivers	Puget Sound	2000	Aug, Sep	32	11
		Apple Cove Point	Puget Sound blackmouth	2003, 2004	Nov	37	13
	Columbia River	Lower Columbia River	Columbia River–fall run	2004	Aug	30	10
		Lower Columbia River	Columbia River–spring run	2004	Apr	20	7
	Central California coast	Pt. Arena to Pt. Reyes	Sacramento River	2004	Aug	26	9
Sockeye	Northern British Columbia coast	Lower Skeena River	Skeena River	2003	Jun, Jul	27	9
	Strait of Juan de Fuca	San Juan Channel	Fraser River	2004	Jul, Aug	30	10
Coho	Central British Columbia coast	Dean Channel, North Benedict Arm	Kimsquit River	2004	Aug	30	11
	Puget Sound	Lower Nooksack, Nisqually, and Deschutes Rivers	Puget Sound	2000	Sep, Oct	27	10
		Apple Cove Point	Puget Sound	2003	Nov	9	3
Pink	Northern British Columbia coast	Lower Skeena River	Skeena River	2003	Jun, Jul	31	11
	Puget Sound	Lower Skagit River	Skagit River	2003	Sep	28	10
Chum	Central British Columbia coast	Burke Channel	Kimsquit River	2003	Aug, Sep	30	10
	Puget Sound	Apple Cove Point	Puget Sound	2003	Nov	31	11

poral summer feeding ranges of NRKW and SRKW. Mature Chinook salmon were collected from 5 regions, including coastal marine sites where NRKW and SRKW feed (Zamon et al. 2007, Ford et al. 2010b) or nearby rivers: (1) north-central coast of British Columbia, near the mouth of the Skeena River; (2) Johnstone Strait, near Robson Bight; (3) Puget Sound, near the mouths of the Nooksack, Duwamish, and Nisqually Rivers, and in Puget Sound's main basin (Apple Cove Point); (4) the lower Columbia River (spring and fall runs), and central coast of California, between Pt. Arena and Pt. Reyes (Table 1). Sampling bracketed the peak run-timing for each population, when these species are most abundant in near-shore waters.

Each of the other Pacific salmon species was collected in 2 geographically separated regions, one in the more northern end of the NRKW and SRKW summer feeding range and the other in the center of their range. Sockeye salmon were sampled from the north-central coast of British Columbia, near the mouth of the Skeena River, and from the Strait of Juan de Fuca, near Lopez Island (Fig. 1). Pink salmon were also sampled near the mouth of the Skeena River and in Puget Sound near the mouth of the Skagit River. Coho and chum salmon were sampled from the central coast of British Columbia (Dean and Burke channels) and Puget Sound (both species from Apple Cove Point as well as coho salmon near the mouths of the Nooksack, Nisqually, and Deschutes Rivers).

All fish were randomly sampled from commercial or test-fisheries targeting mature salmon (Table 1), usually 3 times, bracketing the peak of the run. Except for Chinook salmon collected from Johnstone Strait, the Columbia River, and the California coast, the population-complex associated with each sampling site (Table 1) was based on the locations and return time for specific populations. Chinook salmon caught at river mouths in Puget Sound (all mature) were treated as 1 population (i.e. Puget Sound), whereas the marine-caught fish (Apple Cove Point) were immature resident fish, referred to regionally as blackmouth, and were treated as a separate population (i.e. Puget Sound blackmouth). All marine and in-river-caught Puget Sound coho salmon were mature and were treated as 1 population.

The population-complexes of Chinook salmon from Johnstone Strait, the Columbia River, and the California coast were based on genetic analyses that use a coast-wide data set of genotypes at 13 microsatellite loci developed by a consortium of laboratories (Genetic Analyses of Pacific Salmonids [GAPS]; see Seeb et al. [2007]) to identify their origin. Chinook

salmon caught in Robson Bight mostly originated from Fraser River (64 % from South Thompson stock) and are hereafter referred to as the Fraser River population-complex but they also included fish from the east coast of Vancouver Island (14 %) and Puget Sound (14 %). The fall and spring runs of Chinook salmon from the Columbia River were treated as separate populations, consistent with their designation as separate evolutionarily significant units for conservation, and the differences in their size, migration timing, marine distribution, and other features (Myers et al. 1998). Genetic sampling of the Columbia River fish confirmed that the spring population-complex consisted almost exclusively (>94 %) of lower Columbia spring-run fish, and the fall population-complex consisted mostly of mid-Columbia Tule (60 %), lower Columbia fall (25 %), and upper Columbia summer/fall stocks (5 %). Chinook salmon collected off the coast of California were mostly (73 %) from the Sacramento and San Joaquin population-complex, but included a few fish from the northern California Coast (11 %) and from the Oregon coast or the Columbia River (16 %), hereafter referred to as the Sacramento River population.

Sample preparation

Whole salmon were transported on ice to the laboratory where they were measured for fork length (mm) and mass (g wet weight). The fish were then placed in plastic bags and frozen at −30°C until tissues were processed for proximate analyses. Whole bodies of frozen salmon were sawed into 38 mm wide strips, then passed through a meat grinder with a 6.35 mm hole plate, and homogenized for approximately 3 to 5 min in an industrial-size food mixer. Approximately 100 g of homogenized tissue from each fish was stored at −30°C until proximate composition was determined.

Proximate analyses

A total of 446 fish, combined into 155 composite samples, were processed (Table 1). Species–population composite samples were created from tissue of males or females from a collection site and analyzed for proximate composition, including moisture, protein, lipid, and ash content. First, 100 g subsamples of individual fish were dried at 105°C to a constant weight to determine the percentage of solids (ratio of dry mass to wet mass) and the percentage of water (100 − the percent of solids). Composite samples for proximate analyses were then created for each sampling site by combining equal amounts of dried tissue from 2 or 3 randomly selected fish of the same sex.

The lipid content of the dry composite tissue sample was determined gravimetrically on methylene chloride Soxhlet-extracted tissues (AOAC International 2000). Percent nitrogen (N) and protein (N × 6.25) content for composite samples were measured using a FP-2000 nitrogen/protein analyzer (LECO Corporation) by the AOAC official method 968.06 (AOAC International 2000). Ash content was determined by combustion using the AOAC official methods 942.05 (AOAC International 2000). Carbohydrates were not measured because they contribute an insignificant amount of energy (e.g. <0.5 % of the somatic tissue) in salmon tissue (Jonsson et al. 1991, 1997). To determine percent lipid, protein, and ash by wet mass, the proportions of dry tissue composed of lipid, protein, and ash in a sample were multiplied by the average percent of solids from that sample.

Energy content

The kilocalories of lipid and protein tissues were estimated separately for each composite whole body sample by multiplying the lipid and protein wet mass (percent tissue × average mass of fish in the composite) by the average energy equivalents in each tissue type (lipid = 9 kcal g^{-1}, protein = 4 kcal g^{-1}). Total energy (kcal $fish^{-1}$) was then estimated by summing the kilocalories for lipid and protein tissues. The energy density (kcal kg^{-1}) for each composite sample was calculated by dividing the total kilocalories of the composite sample by the average mass of fish in the composite.

Statistical analyses

A 1-way analysis of variance (ANOVA) or Kruskal-Wallis test was used to test for significant differences in fish size (length or mass), proximate values (percent lipids, protein), and energy content (kcal kg^{-1} and kcal $fish^{-1}$) among species groups, and among Chinook salmon population-complexes, depending on whether the data for specific tests met the normality and constant variance assumptions of ANOVA (SigmaPlot v. 11.0, 2011). Holm-Sidak and Dunn's post hoc multiple range tests were run for all significant differences in ANOVA and Kruskal-Wallis tests, respectively.

Variation in energy content by species and population was modeled using stepwise linear regression models (SPSS v. 12.0, 2011) with the general goal of deriving a predictive model to maximize the variation explained with as few factors as possible. Significant independent variables or interactions ($p < 0.05$) were only included in the final model if they explained >4% of the variation in the dependent variable. All final models were re-run with backward steps to confirm the robustness of the results. Data were transformed as needed (ln-normalized values of kilocalories and fish mass and arcsine-square-root-transformed percent lipid values) to meet assumptions of linearity and normally distributed errors.

The total energy of a fish (kcal $fish^{-1}$) results from the combination of its mass-specific energy or energy density, and its mass. These analyses were intended to produce predictive regression models for energy density and total energy using the relatively easily measured independent variables: lipids to predict energy density and fish mass and lipids to predict total energy. Using linear regression, we first determined the relationship between lipid concentration and energy density for: (a) the mature Pacific salmon representing all 5 species combined, and then separately for (b) all 7 populations of Chinook salmon samples combined, including immature fish.

(a) Pacific salmon:

$$\text{kcal kg}^{-1} = \beta_0 + \beta_1(\%\ \text{Lipids}) + \varepsilon$$

(b) Chinook salmon:

$$\text{kcal kg}^{-1} = \beta_0 + \beta_1(\%\ \text{Lipids}) + \varepsilon \quad (1)$$

where β represents the regression parameters (intercept and the slope of the line-of-best fit) and ε represents the error.

Second, we modeled total energy as a function of fish mass and lipids for (a) and (b) as defined earlier in this section.

(a) Pacific salmon:

$$\text{kcal fish}^{-1} = \beta_0 + \beta_1(\text{mass}) + \beta_2(\%\text{Lipids}) + \beta_3(\text{mass} \times \%\text{Lipids}) + \varepsilon$$

(b) Chinook salmon:

$$\text{kcal fish}^{-1} = \beta_0 + \beta_1(\text{mass}) + \beta_2(\%\text{Lipids}) + \beta_3(\text{mass} \times \%\text{Lipids}) + \varepsilon \quad (2)$$

Third, we considered total energy of the fish as the response variable and estimated the contributions of fish mass and (a) species and (b) Chinook salmon population as categorical variables, as well as their interaction. These models used fish species and Chinook populations as easily observed proxies for lipid and energy density, which are much more difficult to measure in the field and are described as:

(a) Pacific salmon:

$$\text{kcal fish}^{-1} = \beta_0 + \beta_1(\text{mass}) + \sum_{i}^{5}\beta_i(S_i) + \beta_3(\text{mass} \quad \%\text{Lipids}) + \varepsilon$$

(b) Chinook salmon:

$$\text{kcal fish}^{-1} = \beta_0 + \beta_1(\text{mass}) + \sum_{i}^{7}\beta_i(P_i) + \beta_3(\text{mass} \quad \%\text{Lipids}) + \varepsilon \quad (3)$$

where S_i is one of 5 Pacific salmon species and P_i is one of 7 Chinook salmon population-complexes.

Furthermore, we omitted lipids in the linear regression models that estimated the contribution of fish mass and species (or Chinook salmon population) to the total energy value, because some species (or populations) exhibited unique lipid and fish mass characteristics. For example, all Chinook salmon were larger and fattier than pink salmon. In addition, in no case was the species (or population) interaction with fish mass significant. Hence, intercept differences were used to describe species-specific (and Chinook salmon population-specific) relationships between total energy and fish mass.

Finally, to facilitate application of the information in this study to the management of Chinook salmon, we used linear regression to model a predictive relationship between fish length and total energy for those situations when fish mass is not available.

Chinook salmon:

$$\text{kcal fish}^{-1} = \beta_0 + \beta_1(\text{fish length}) + \varepsilon \quad (4)$$

RESULTS

Fish size

Species comparisons

Other than the immature blackmouth, the Chinook salmon were significantly longer and heavier (800 mm, 7807 g wet mass) than the other salmon species; they were followed by chum salmon (698 mm, 4303 g) which were also longer but not heavier than coho salmon (631 mm, 3556 g) (Table 2; Kruskal-Wallis on fish lengths, $H = 289.3$, df = 4, $p < 0.001$; Kruskal-Wallis on fish mass, $H = 305.4$, df = 4, $p < 0.001$; Dunn's test). Coho salmon were similar in length but heavier than sockeye salmon (*O. nerka*; 579 mm, 2396 g), but were longer and heavier than pink salmon (*O. gorbuscha*; 538 mm, 1858 g). No other significant differences were observed.

Table 2. *Oncorhynchus* spp. Mean (±SE) and ranges of fork length and fish mass of Pacific salmon species used to estimate energy content. All fish were mature, except the Puget Sound blackmouths. N: total number of fish collected. Significant differences in fork length and fish mass among species are noted by superscripted numbers (1 to 4). Significant differences ($p < 0.05$) in fork length and fish mass among mature Chinook salmon population-complexes are noted by superscripted letters from a to c

Species	Population-complex	N	Fork length (mm)		Mass (g)	
			Mean ± SE	Min–max	Mean ± SE	Min–max
Chinook	Skeena River	28	815 ± 18[a]	655–1010	7786 ± 521.2[a,b]	3772–13766
(*O. tshawytscha*)	Fraser River	30	834 ± 23[a]	615–1344	8655 ± 588.7[a,b]	3062–17055
	Puget Sound	32	786 ± 9.3[a]	686–885	6462 ± 209.7[b,c]	4088–9512
	Puget Sound blackmouth	37	492 ± 18	305–667	1921 ± 186.6	409–4081
	Columbia River (fall run)	30	841 ± 14[a]	609–1000	9891 ± 477.4[a]	3825–15486
	Columbia River (spring run)	20	685 ± 16[b]	570–836	5059 ± 385.8[c]	2449–8686
	Sacramento River	26	800 ± 18[a]	678–987	8215 ± 701.2[b,c]	4077–16063
	All Chinook (mature only)	**166**	**800 ± 7.8[1]**	**570–1344**	**3807 ± 233.3[1]**	**2249–17055**
Sockeye (*O. nerka*)	Skeena River	27	607 ± 8.4	491–682	2689 ± 110.2	1343–3917
	Fraser River	30	553 ± 4.1	518–610	2132 ± 61.5	1601–3051
	All sockeye	**57**	**579 ± 5.7[3,4]**	**491–682**	**2396 ± 71.3[3]**	**1343–3917**
Coho (*O. kisutch*)	Kimsquit River	30	678 ±10.8	575–764	4426 ± 22.7	2220–6521
	Puget Sound	36	592 ± 8.6	490–705	2832 ± 140.5	1582–4526
	All coho	**66**	**631 ± 8.6[3]**	**490–764**	**3556 ± 161.1[2]**	**1582–6521**
Pink (*O. gorbuscha*)	Skeena River	31	535 ± 4.9	492–595	1919 ± 48.8	1570–2597
	Puget Sound	28	540 ± 10.1	385–630	1790 ± 54.2	1161–2353
	All pink	**59**	**538 ± 5.4[4]**	**385–630**	**1858 ± 37.0[3]**	**1161–2597**
Chum (*O. keta*)	Kimsquit	30	714 ± 7.0	642–794	4627 ± 156.0	3122–7046
	Puget Sound	31	681 ± 11	576–825	3793 ± 221.2	2315–6924
	All chum	**61**	**698 ± 6.9[2]**	**576–825**	**4203 ± 145.3[2]**	**2315–7046**

Chinook population-complex comparisons

The average size of Chinook salmon varied from 685 to 841 mm and 5059 to 9891 g, with most of the variation among populations associated with the Columbia River spring population (Table 2; Kruskal-Wallis on fish lengths, $H = 38.52$, df = 5, $p < 0.001$; Kruskal-Wallis on fish mass, $H = 43.99$, df = 5, $p < 0.001$; Dunn's test), being shorter (685 mm) than all other populations and lighter (5059 g) than all populations except Puget Sound and Sacramento fish. The Puget Sound blackmouth were considerably smaller (average = 492 mm, 1921 g) than all other Chinook salmon population-complexes, but they were excluded from the above analysis because they were immature.

Proximate analyses

Species comparisons

The lipid contents of sockeye (11.3%) and mature Chinook salmon (10.5%) did not differ from each other, but they were higher than those of pink (4.8%) and chum (3.1%) salmon (Table 3; Kruskal-Wallis on percent lipid, $H = 89.85$, df = 4, $p < 0.001$; Dunn's test). Coho salmon had an intermediate lipid value (6.8%), which was lower than that of sockeye, not significantly different from that of Chinook or pink salmon, but higher than that of chum salmon. No other significant differences were observed.

Among mature fish, the average percent protein values ranged from 17.8 to 19.6%, varying slightly among species (Table 3; ANOVA, $F = 16.49$, df = 4, $p < 0.001$). The highest average percent protein values were observed in Chinook, sockeye, and coho salmon (19.6, 19.4, and 19.3%, respectively); these did not differ significantly from each other (Holm-Sidak test). The average protein value for chum salmon (18.8%) was significantly lower than that for Chinook but not significantly lower than for sockeye or coho salmon. Pink salmon had significantly less protein (17.8%) than any other species.

Chinook salmon population-complex comparisons

Lipid content also varied among the Chinook salmon population-complexes (Table 3; ANOVA, $F = 34.46$, df = 6, 63, $p < 0.001$). The Columbia River spring run (14.8%) had significantly higher values than any other Chinook salmon populations, except the Skeena River (13.1%). Skeena River fish had similar lipid values to those of Fraser River (12.4%) and Sacramento River populations (12.0%; Holm-Sidak test). Interme-

Table 3. *Oncorhynchus* spp. Means (±SD) and ranges of percent lipid, protein, and moisture of composite samples of Pacific salmon used to estimate energy content. N: number of composite samples. Percent ash ranged from 1.63 to 3.50. Significant differences in lipid and protein contents are noted by superscripted numbers (1 to 4) for species comparisons (mature fish only) and superscripted letters (a to d) for comparisons among Chinook salmon population-complexes. All fish were mature, except the Puget Sound blackmouths

Species	Population-complex	N	Percent lipid		Percent protein		Percent moisture	
			Mean ± SD	Range (min–max)	Mean ± SD	Range (min–max)	Mean ± SD	Range (min–max)
Chinook	Skeena River	10	13.1 ± 1.1^{a,b}	11.6–14.5	18.6 ± 0.6^{c}	17.8–19.6	66.1 ± 1.2	63.7–68.0
(*O. tshawytscha*)	Fraser River	10	12.4 ± 1.6^{b}	9.0–14.5	19.9 ± 0.5^{b}	19.0–20.8	66.1 ± 1.5	64.3–69.6
	Puget Sound	11	6.1 ± 0.9^{d}	5.2–7.6	20.8 ± 0.5^{a}	19.6–21.8	69.9 ± 1.1	68.8–72.2
	Puget Sound blackmouth	13	10.0 ± 2.4^{c}	6.7–14.9	16.8 ± 0.6^{d}	15.7–18.1	70.4 ± 3.0	65.9–74.7
	Columbia River (fall run)	10	6.3 ± 2.0^{d}	3.5–9.7	19.6 ± 0.7^{b}	18.3–20.5	70.8 ± 1.8	67.3–73.7
	Columbia River (spring run)	7	14.8 ± 2.1^{a}	12.6–18.2	18.4 ± 0.4^{c}	17.7–19.1	66.1 ± 0.8	64.5–67.0
	Sacramento River	9	12.0 ± 1.5^{bc}	10.3–14.5	19.7 ± 0.5^{b}	18.7–20.2	64.5 ± 2.1	60.9–67.5
	All mature Chinook	**57**	**10.5 ± 3.7^{1,2}**	**3.5–18.2**	**19.6 ± 1.0^{1}**	**17.1–21.8**	**67.4 ± 2.7**	**60.9–73.7**
Sockeye (*O. nerka*)	Skeena River	9	10.4 ± 1.0	8.3–11.7	20.2 ± 0.6	17.4–19.4	66.4 ± 0.9	64.8–67.9
	Fraser River	10	12.1 ± 2.5	7.9–15.5	18.4 ± 0.6	19.6–21.4	65.6 ± 1.2	63.9–67.3
	All sockeye	**19**	**11.3 ± 2.1^{1}**	**7.9–15.5**	**19.4 ± 1.1^{1,2}**	**17.4–21.4**	**66.0 ± 1.1**	**63.9–67.9**
Coho (*O. kisutch*)	Kimsquit River	11	7.2 ± 0.6	6.5–8.8	19.4 ± 0.9	18.2–21.0	70.2 ± 0.9	68.7–71.8
	Puget Sound	13	6.6 ± 0.5	5.9–7.6	19.3 ± 0.7	18.2–20.6	69.8 ± 0.8	68.6–71.3
	All coho	**24**	**6.8 ± 0.6^{2,3}**	**5.9–8.8**	**19.3 ± 0.8^{1,2}**	**18.2–21.0**	**70.0 ± 0.8**	**68.6–71.8**
Pink (*O. gorbuscha*)	Skeena River	11	5.6 ± 1.5	3.6–9.4	17.8 ± 0.5	17.1–18.5	72.7 ± 2.2	68.5–75.2
	Puget Sound	10	3.9 ± 0.9	2.8–5.8	17.8 ± 0.7	16.8–19.3	73.8 ± 1.6	71.0–76.1
	All pink	**21**	**4.8 ± 1.5^{3,4}**	**2.8–9.4**	**17.8 ± 0.6^{3}**	**16.8–19.3**	**73.2 ± 2.0**	**68.5–76.1**
Chum (*O. keta*)	Kimsquit	10	2.9 ± 0.6	2.0–4.2	18.8 ± 1.1	17.1–21.0	74.2 ± 1.5	72.3–76.7
	Puget Sound	11	3.2 ± 1.1	1.5–5.1	18.7 ± 0.9	17.7–20.9	74.2 ± 1.9	71.2–77.6
	All chum	**21**	**3.1 ± 0.9^{4}**	**1.5–5.1**	**18.8 ± 1.0^{2}**	**17.1–21.0**	**74.2 ± 1.7**	**71.2–77.6**

diate lipid values were observed for the Puget Sound blackmouth (10.0%); these were not significantly different from values for the Sacramento population but were significantly higher than values for the Columbia River fall run (6.3%) and Puget Sound mature fish (6.1%). No other significant differences in lipid values of Chinook salmon were observed.

The protein values were significantly higher for Puget Sound Chinook salmon (mature: 20.8%) than for other populations, followed by the Fraser River, Sacramento River, and Columbia River fall runs, ranging from 19.9 to 19.6% (Table 3; ANOVA, F = 64.196, df = 6,63, $p < 0.001$; Holm-Sidak test). All these values were significantly higher than those for the Skeena River (18.6%) and Columbia River spring run fish (18.4%). Most notably, the immature Puget Sound blackmouth had significantly lower average protein values (16.8%) than the other mature Chinook populations.

Energy content

Species comparisons

The average energy density (kcal kg^{-1}) of mature salmon varied among species (Kruskal-Wallis, H = 95.42, df = 4, $p < 0.001$). Sockeye and Chinook salmon had similarly high energy densities (averages = 1794 and 1724 kcal kg^{-1}; Fig. 2; Dunn's test), these were significantly higher than values for coho salmon (average = 1389 kcal kg^{-1}), followed by those of pink and chum salmon, with similarly low energy densities (averages = 1143 and 1026 kcal kg^{-1}). Energy density was highly correlated (positively) with lipid content (Fig. 3a; r^2 = 0.99; F = 9907, df = 1,140, $p < 0.001$), regardless of species, and was predicted by the equation:

$$\text{kcal kg}^{-1} = 91.8\,(\%\text{Lipids}) + 749.9 \quad (5)$$

The total energy value (kcal fish^{-1}) of mature Pacific salmon species was highly correlated with fish mass and lipid content, accounting for 89 and 10.6% of the observed variation (linear regression on ln[kcal], with ln[mass] and arcsine square-root-transformed percent lipids as independent variables [r^2 = 0.89; F = 40633, df = 1,139, $p < 0.001$]). The total energy value of Pacific salmon is predicted by the equation:

$$\ln(\text{kcal fish}^{-1}) = 1.023\,[\ln(\text{mass})] + 0.057\,[\text{arcsin square root}\,(\%\text{Lipids})] + 6.33 \quad (6)$$

For all 5 Pacific salmon species, larger fish had more total energy; however, species with higher energy densities had higher kilocalorie levels for a given

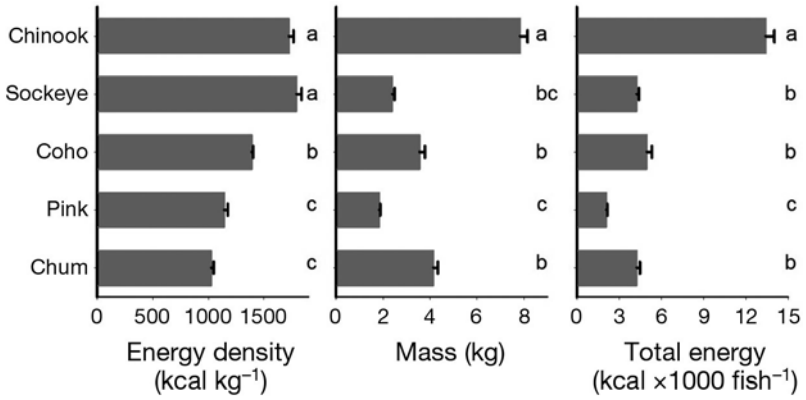


Fig. 2. *Oncorhynchus* spp. Average (±SE) energy density, mass, and total energy of whole-body samples of mature Pacific salmon. Significant differences in energy density, fish mass, and total energy (in kcal) among mature Pacific salmon population-complexes are noted by different letters (a to c). See Table 2 for individual species names

mass (Fig. 3b; $r^2 = 0.96$ for the full model; for ln[mass], $F = 1527.4$, df = 1,138, $p < 0.0001$; for species groups, $F = 127.1$, df = 2,138, $p < 0.0001$). Overall, the total energy value for the 5 species of Pacific salmon is predicted from 3 equations:

$$\ln(\text{kcal fish}^{-1})\ \text{Chinook and Sockeye} = 0.94\,[\ln(\text{mass})] + 7.56 \quad (7)$$

$$\ln(\text{kcal fish}^{-1})\ \text{Coho} = 0.94\,[\ln(\text{mass})] + 7.31 \quad (8)$$

$$\ln(\text{kcal fish}^{-1})\ \text{Pink and Chum} = 0.94\,[\ln(\text{mass})] + 7.04 \quad (9)$$

Sockeye and Chinook salmon, the most lipid-rich species, had significantly higher total energy for a given mass; pink and chum salmon were the least lipid-rich species and had significantly lower total energy for a given mass (Fig. 3b). Coho salmon showed intermediate energy density, significantly different from all other species (Fig. 3b).

Although the average lipid content and energy density of sockeye and Chinook salmon were similar, Chinook salmon were larger bodied (Fig. 2; Kruskal-Wallis, $H = 118.51$, df = 4, $p < 0.001$; Dunn's test) and consequently had significantly more total energy than any other salmon species (average = 13 409 kcal fish^{-1}; Fig. 2; $H = 117.37$, df = 4, $p < 0.001$; Dunn's test). The high energy density of sockeye was offset by its smaller size. Coho and chum salmon were heavier than sockeye salmon, but not significantly so, and the 3 species did not differ significantly in total energy (averages = 4982, 4265, and 4264 kcal fish^{-1}, respectively; Fig. 2; Dunn's test). The greater mass of chum salmon was offset by their lower energy density, and coho salmon were heavier but lower in energy density than sockeye salmon. The total energy of pink salmon (average = 2101 kcal fish^{-1}) was significantly lower than that of any other species; this was a result of its lower mean mass and energy density.

Chinook salmon population-complex comparisons

The energy density and total energy value varied considerably among Chinook population-complexes, due to variation in lipid content and body size. Significantly higher average energy densities (kcal kg^{-1}) were

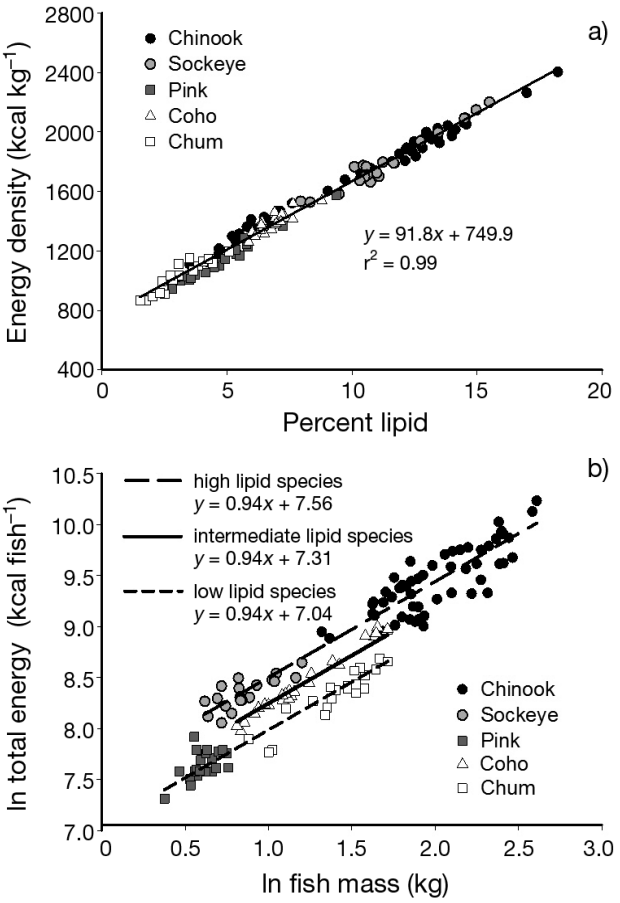


Fig. 3. *Oncorhynchus* spp. Relationship between (a) lipid content and energy density and (b) fish mass and total energy of 5 species of Pacific salmon. Only mature fish are included. Predicted total energy regression lines are adjusted for species-specific differences associated with lipids. See Table 2 for individual species names

measured for fattier spring run Columbia River fish and summer/fall run fish returning to the Skeena, Fraser, and Sacramento River (population means ranging from 1863 to 2064) than leaner fall run fish residing in or returning to Puget Sound rivers or the Columbia River (population means ranging from 1353 to 1570; Fig. 4; ANOVA, $F = 29.17$, df = 6, 63, $p < 0.001$; Holm-Sidak test). The immature Puget Sound blackmouth had intermediate average energy density values (Fig. 4).

Overall, energy density (kcal kg^{-1}) was highly correlated with lipid content, for all populations ($r^2 = 0.97$; $F = 1997$, df = 1, 68, $p < 0.0001$), and could be predicted by the following equation:

$$\text{kcal kg}^{-1} = 85.6\,(\%\text{Lipids}) + 807.7 \quad (10)$$

Total energy (kcal $fish^{-1}$) varied significantly among Chinook salmon populations (Kruskal-Wallis, $H = 49.38$, df = 6, $p < 0.001$). The immature blackmouth, weighing less than any other Chinook salmon except the Columbia River spring run fish (Fig. 4; Kruskal-Wallis on mean composite weights, $H = 49.74$, df = 6, $p < 0.001$) and having an intermediate energy density, had the lowest mean total energy value (3076 kcal $fish^{-1}$). However, it was not significantly lower than that of mature fish from Puget Sound or the Columbia River spring run populations (8941 and 10 559 kcal $fish^{-1}$, respectively; Dunn's test). Among mature fish, Puget Sound Chinook salmon had a lower mean total energy value than those determined for the other populations, except the Columbia River spring run (Kruskal-Wallis, $H = 27.16$, df = 5, $p < 0.001$; Dunn's test). The Columbia River spring and fall run fish did not differ significantly in total energy (10 253 vs. 13 868 kcal $fish^{-1}$, respectively) because the higher energy density of the spring fish was offset by the larger size of the fall run fish.

Fish mass and lipid content predicted total energy among Chinook salmon populations, accounting for 85 and 13% of the observed variation, respectively ($r^2 = 0.98$; $F = 1536$, df = 2, 67, $p < 0.001$).

$$\text{kcal fish}^{-1} = 1717.4\,(\text{fish mass}) + 594.4\,(\%\text{Lipids}) + 6237.7 \quad (11)$$

The total energy of Chinook salmon increased with fish mass across all populations; however, the effect of lipid content depended on the population-complex; populations with higher lipid levels (and higher energy densities) had more total energy (in kcal) for a given mass (linear regression on kcal $fish^{-1}$, with fish mass as a continuous independent variable and population as a categorical independent variable; $r^2 = 0.96$; $F = 1658$, df = 1, 66, $p < 0.0001$ for fish mass and $F = 101.1$, df = 6, 66, $p < 0.0001$ for population group). Chinook salmon from the Skeena, Fraser, Sacramento, Puget Sound blackmouth, and Columbia River spring populations had significantly higher kilocalories for a given mass than the Puget Sound and Columbia River fall populations (Fig. 5b; Holm-Sidak test). The Puget Sound fish had significantly more kilocalories for a given mass than the Columbia River fall fish, but there was little overlap in the range of fish sizes between populations. Overall, when we account for the lipid differences among populations, the total energy value of Chinook salmon for all population-complexes is predicted from 3 equations:

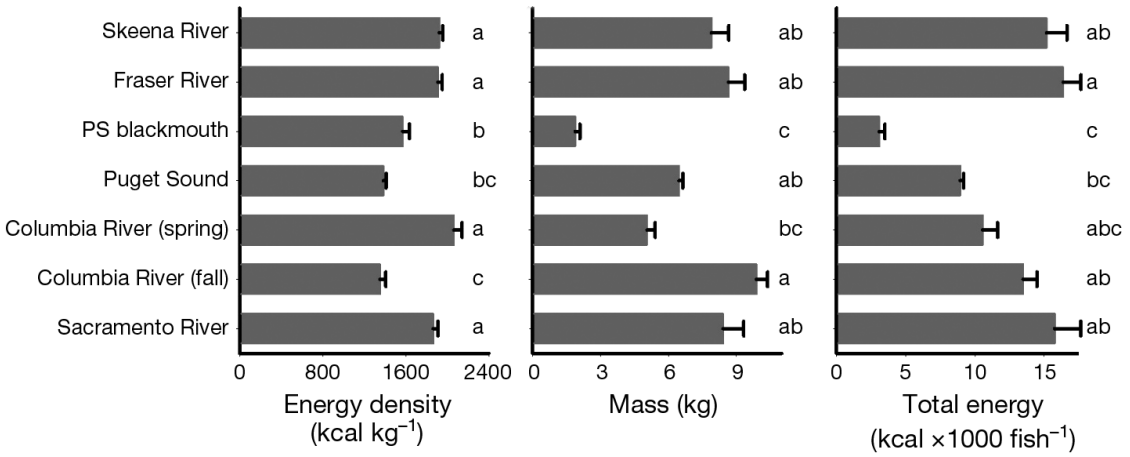


Fig. 4. *Oncorhynchus tshawytscha*. Average (±SE) energy density, mass, and total energy of whole-body samples of Chinook salmon from 7 population-complexes: Skeena River, Fraser River, Puget Sound mature (Puget Sound) and immature residents (Puget Sound blackmouth), Columbia River spring, Columbia River fall, and Sacramento River. Significant differences in energy density, fish mass, and total energy (in kcal) among Chinook salmon population-complexes are noted by different letters (a to c)

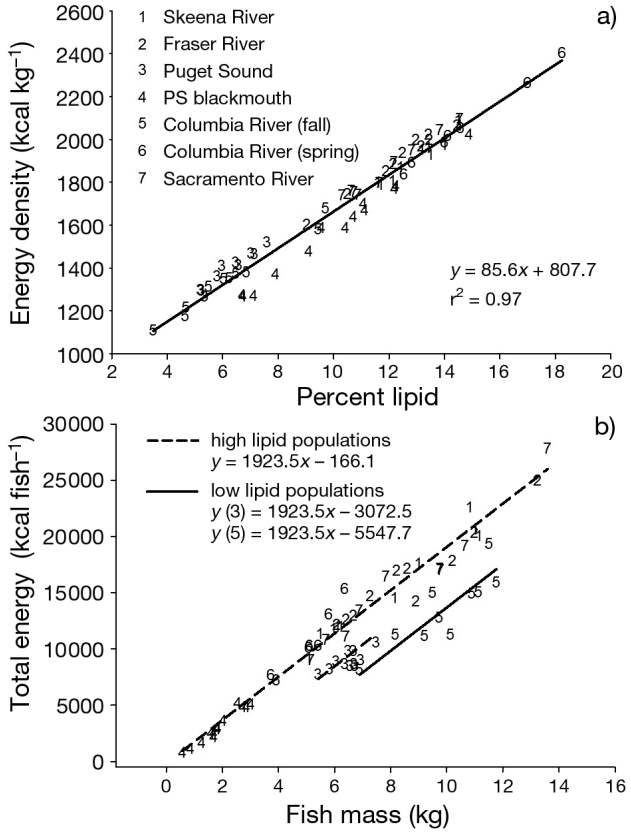


Fig. 5. *Oncorhynchus tshawytscha*. Relationship between (a) lipid and energy density and (b) fish mass and total energy for Chinook salmon caught in terminal and in-river fisheries. Predicted regression lines are based on linear regression models as described in 'Materials and methods: Statistical analyses'. Numbers along the regression lines refer to populations in the key. Due to the nature of the data, some of the digits used to represent the data points for the individual fish populations overlap

$$\text{kcal fish}^{-1}\,(\text{P1, P2, P4, P6, P7}) = 1923.5\,(\text{fish mass}) - 166.1 \quad (12)$$

$$\text{kcal fish}^{-1}\,(\text{P3}) = 1923.5\,(\text{fish mass}) - 3072.5 \quad (13)$$

$$\text{kcal fish}^{-1}\,(\text{P5}) = 1923.5\,(\text{fish mass}) - 5547.7 \quad (14)$$

where P1 is Skeena, P2 is Fraser, P3 is Puget Sound, P4 is Puget Sound blackmouth, P5 is Columbia fall, P6 is Columbia spring, and P7 is Sacramento.

Predictive kcal–fish length relationship for Chinook salmon populations

Lipid content and fish mass can be used to estimate the total energetic value of Chinook salmon to NRKW and SRKW, but individual fish mass and lipid content data are typically not available for specific salmon populations. To facilitate application of the information in this study to the management of Chinook salmon, a simple predictive relationship between length and total energy content was developed. Fish length predicted total energy value (kcal fish^{-1}) among populations of Chinook salmon, accounting for 91% of the variation (based on ln[kcal] and ln[fish length]; $r^2 = 0.91$; $F = 732.98$, df = 1, 68, $p < 0.001$).

$$\text{kcal fish}^{-1} = 0.000011\,(\text{fish length})^{3.122} \quad (15)$$

The relationship between total kilocalories and fish length (Fig. 6) was robust, as evidenced by its consistency when any population was removed from the regression analysis (Table 4). For example, removing the Puget Sound blackmouth (which included many fish that were smaller and younger than fish consumed from May to September in the Salish Sea by NRKW and SRKW) from the analysis shifted the slope of the best-fit regression line slightly but not significantly, and fish length still accounted for most of the observed variation. Excluding the 2 smallest-bodied populations, Puget Sound mature (in-river) and immature (blackmouth), from the regression analyses changed the overall slope of the kcal to fish length relationship significantly (Table 4).

To better characterize the effect of population-specific energy density on the total energy value of Chinook salmon of various lengths, we also modeled energy using the 90th and 10th percentile lipid content values measured for all samples (14.5 and 5.5%, respectively: outer dashed lines in Fig. 6). These lipid values better reflect the high and low energy densities of Chinook salmon populations that occur in terminal marine waters where NRKW and SRKW feed. Using this approach, a fish of typical size (800 mm) with a 14.5% lipid content would have a total energy value of 15766 kcal, whereas the same-sized fish with a 5.5% lipid content would have a total energy value of 9602 kcal, approximately 40% lower.

DISCUSSION

The energy density of salmon was highly correlated with lipid content, but the total energy value was determined primarily by fish size, measured as mass. After accounting for size and lipid differences, salmon species and populations did not vary appreciably in total energy value. Previous studies have documented the importance of fish size and lipid content in determining the energy content of salmon (Gilhousen 1980, Brett 1995, Hendry & Berg 1999), but ours is the first comprehensive assessment of

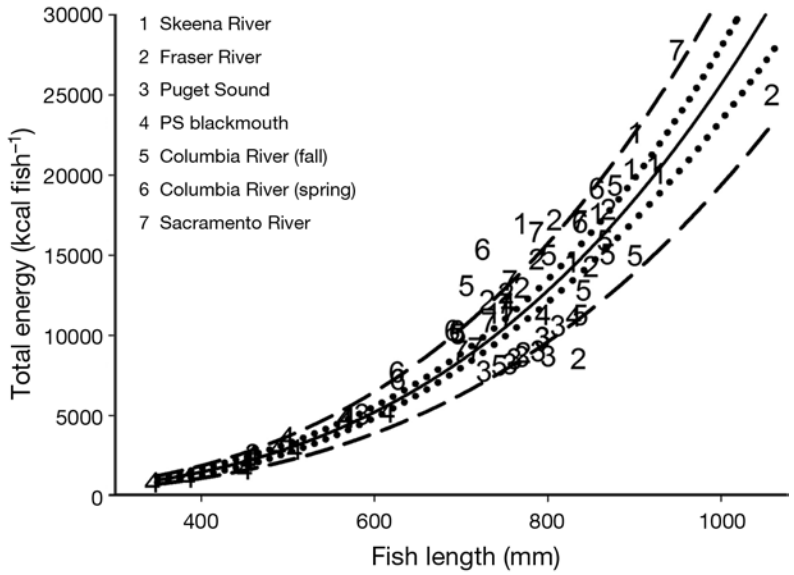


Fig. 6. *Oncorhynchus tshawytscha*. Relationship between total energy (kcal fish^{-1}) and fish size (fork length) for Chinook salmon based on 7 population complexes sampled in terminal marine or in-river fisheries. The solid line is the best-fit trend line based on fish length [$y = 0.000011 \times (\text{fish length}^{3.122})$]. The inner dotted lines depict the predicted 95% confidence intervals around the trend line. The outer dashed lines depict the hypothesized energy values using the 90th and 10th percentile lipid content measured for all samples, 14.47 and 5.47, respectively. Mature fish were sampled at all sites, except for the Puget Sound blackmouth population-complex, which represented immature fish residing in Puget Sound. Numbers along the regression lines refer to populations in the key. Due to the nature of the data, some of the digits used to represent the data points for the individual fish populations overlap

energy content of 5 species of Pacific salmon and multiple populations of Chinook salmon from the standpoint of salmon as prey to apex predators.

Salmon kilocalorie levels are derived mostly from lipids and proteins, because carbohydrates constitute <0.5% of the somatic tissue of salmonids (Jonsson et al. 1991, 1997). Variation in energy density among salmon species and populations is almost entirely determined by the degree to which they store lipids, because the protein content, structurally important in muscle development and swimming performance, varies little among mature fish (Brett 1995, Hendry & Berg 1999). Accordingly, the energy density among salmon species and among Chinook salmon populations was highly correlated with lipid content (Figs. 3a & 5a, respectively). As salmon mature and migrate upriver, they first burn fat to provide energy for migration and egg development, conserving protein for the subsequent development of secondary sexual characteristics (Hendry & Berg 1999).

Table 4. *Oncorhynchus tshawytscha*. Results of linear regression analyses for the measured total energy of Chinook salmon (kcal fish^{-1}) associated with fish length (fork length, mm) using ln-transformed values [ln kcal = (slope coefficient × ln MCL) + intercept coefficient], where MCL is mean composite fish length). The 'full model' regression is the best fit for all 7 Chinook salmon population-complexes sampled (Skeena River, Fraser River, Columbia River fall run, Columbia River spring run, Puget Sound, Puget Sound blackmouth, and Sacramento River). Other models excluded 1 or more of the populations as noted, and the slope that is significantly different ($p < 0.001$) from the full model is noted by **. N: number of fish sampled

Model	N	r^2	Factor	Estimated coefficient	SE	*t*-value
Full model	70	0.91	Intercept	−11.413	0.765	−14.92
			Slope	3.122	0.116	26.91
Excluded Puget Sound blackmouth	57	0.56	Intercept	−7.216	1.974	−3.66
			Slope	2.494	0.295	8.44
Excluded Sacramento River	61	0.91	Intercept	−11.061	0.800	−13.83
			Slope	3.065	0.122	25.21
Excluded Columbia River (fall run)	60	0.92	Intercept	−11.805	0.803	−14.70
			Slope	3.184	0.122	26.06
Excluded Columbia River (spring run)	63	0.93	Intercept	−11.648	0.725	−16.06
			Slope	3.153	0.110	28.69
Excluded Fraser River	60	0.92	Intercept	−11.351	0.805	−14.11
			Slope	3.109	0.122	25.40
Excluded Puget Sound	59	0.95	Intercept	−12.032	0.630	−19.08
			Slope	3.224	0.096	33.65
Excluded Skeena River	60	0.91	Intercept	−11.256	0.842	−13.37
			Slope	3.096	0.128	24.19
Excluded Puget Sound & Puget Sound blackmouth	46	0.73	Intercept	−6.631	1.461	−4.54
			Slope**	2.419	0.219	11.07

Lipid content in mature salmon populations at river entry is an adaptation for the duration of time spent in freshwater prior to spawning and the arduousness of their upriver migration (Gilhousen 1980, Brett 1995, Quinn 2005), and is correlated with migration length and elevation (Quinn 2005). Two divergent life-history patterns in river migration and maturation have been described for Pacific salmon, resulting in 2 separate behaviors and associated energy content for coastal and interior populations, described by Gilhousen (1980) and reviewed by Brett (1995). Coastal populations, including most pink, chum, coho, and many Chinook salmon, enter freshwater in an advanced state of maturity and spawn in the lower reaches of rivers soon after leaving the sea. These populations store less of their total energy as fat while feeding at sea and have lower lipid levels at river entry. In contrast, interior populations of Chinook salmon are typically in a less advanced state of maturity and have higher fat content when they leave the ocean, and spend more time in freshwater prior to spawning. Sockeye salmon deviate from this dichotomy between low-energy populations near the coast and high-energy interior populations. Some sockeye salmon populations have high energy content when they leave the ocean because they have lengthy migrations but other populations have high energy content despite short migrations because they leave the ocean early in the year and fast for long periods of time prior to spawning (Hodgson & Quinn 2002). Overall, the lipid content in coastal populations of salmon is generally 2 to 5% of the somatic tissues (9% for downstream sockeye salmon), whereas in upriver, interior spawning populations these values range from 12 to 15% (Brett 1995).

Consistent with the above-mentioned patterns, we observed high lipid values in sockeye, intermediate values in coho, and lower levels in pink and chum salmon (Table 3). Lipid content in Chinook was similar to that in sockeye salmon (Table 3) but varied widely among population-complexes. The lower lipid contents of the Chinook salmon from Puget Sound and Columbia River fall run fish sampled for this study (mostly lower river stocks) are likely due to the short distances they migrate upstream to spawn. Some of the variation in lipid content among Chinook salmon populations may also be associated with their advancing maturation state, as lipid content declines dramatically as fish move into freshwater and become sexually mature (Shearer et al. 1994, Ewald et al. 1998, Hendry & Berg 1999). For example, the difference in lipid content between immature (9.9%) and mature in-river-caught fish (6.1%) from Puget Sound suggests that the mature fish had started to metabolize their fat reserves for reproduction when sampled. However, all of the in-river-caught fish obtained for this study were silver in color and lacked the sexual dimorphism more evident in mature fish (e.g. hooked snouts). Moreover, mature Chinook salmon caught in the marine waters of Puget Sound had only slightly higher average lipid values (7.6%; O'Neill unpubl. data) than the in-river fish sampled here. Fish caught in offshore waters, prior to initiating their home migration, would likely have higher lipid content and kilocalorie levels than those observed in this study, but the lower lipid levels in downstream versus upstream migrants would have been observed regardless.

Body size also varied systematically among species (Chinook > chum > coho > sockeye > pink), consistent with information in prior reviews (Quinn 2005). The average fork lengths of fish collected for this study were — Chinook: 800 mm; chum: 698 mm; coho: 631 mm; sockeye: 579 mm; and pink: 538 mm. This is similar to the central tendency in length reported by Quinn (2005) for salmon species along the west coast of North America — Chinook: 871 mm; chum: 683 mm; coho: 643 mm; sockeye: 553 mm; and pink: 413 mm. Although Chinook are larger than other salmon species, we observed considerable variation in body size among populations, as has been documented elsewhere (Healey 1991, Roni & Quinn 1995, Myers et al. 1998).

As prey to killer whales, fish with more mass have more total energy, although, for a given mass, total energy increased with lipid content (Figs. 3b & 5b). Chinook salmon had the highest observed total energy value, and pink salmon had the lowest (Fig. 2). Overall, large fish size off-set energy density in determining their total energy value (Figs. 2 & 4). Assuming that the fish we sampled were representative of the sizes and lipid content of fish available for consumption, killer whales would need to consume approximately 2.7 coho, 3.1 chum, 3.1 sockeye, or 6.4 pink salmon to obtain the equivalent total energy value of 1 Chinook salmon.

Interestingly, the rank of total energy values of salmon as prey to killer whales is the opposite of the rank of their abundance in coastal waters of British Columbia. Chinook salmon are the least abundant (Henderson & Graham 1998) but offer the highest energy value. Pink salmon are the most abundant (in odd years; Henderson & Graham 1998) but provide the lowest energy values. Sockeye salmon are generally more abundant than chum, and chum are simi-

larly abundant to coho salmon in British Columbia (Henderson & Graham 1998): all 3 of these species provide similar energy values that lie between those of Chinook and pink salmon. Given the frequency of Chinook salmon in the diet of killer whales, and their lower abundance compared to the other Pacific salmon species, resident whales seem to consume salmon in proportion to the energy payoff per fish rather than the salmon species' density.

Our results support the hypothesis by Ford & Ellis (2006) that the large size and high lipid content of Chinook salmon relative to other species, in combination with their year-round availability in the coastal waters where killer whales feed, explains why they are more prevalent in the diet than other salmon species. Resident killer whales selectively feeding on individual Chinook salmon may maximize their prey profitability, a common foraging strategy in many animals (Stephens & Krebs 1986, Scheel 1993, Bowen et al. 2002), by consuming prey with the greatest energy value relative to the effort needed to catch it. As demonstrated in this study, prey size and energy density directly affect the total energy value of salmon as prey, with Chinook salmon being the most valuable. However, the profitability of Chinook salmon as prey is also affected by the relative effort needed to capture the various species of salmon. The catchability of Chinook relative to smaller salmon species is unknown; however, several lines of evidence suggest that such differences are not important to the overall profitability of the various salmon species. Resident killer whales may expend more energy pursing Chinook salmon than smaller salmon species because fish swimming speed scales with length, approximately 1 body length s^{-1} (Quinn 1988). However, mass increases as the cube of length, so longer fish like Chinook salmon will provide considerably more total energy as prey than smaller fish, likely offsetting the cost of capturing faster fish. Moreover, although Chinook salmon should be able to swim faster than the other species of salmon because of their size, they actually migrate more slowly through coastal waters than other schooling salmon species, although at greater depths (Candy & Quinn 1999). Even at these greater depths, individual Chinook salmon migrating through coastal waters would be detectable by killer whales via echolocation at ranges of 100 m or more (Au et al. 2004).

Chinook and coho salmon populations vary in marine distributions, but they generally have more coastal marine distributions (as opposed to the open ocean) than other salmon species (Quinn 2005). Consequently, Chinook (and coho) salmon are available year-round as prey to resident killer whales in coastal waters, although in the winter months, only immature fish are available. During the summer months, the smallest maturing Chinook salmon provide more total energy as prey than any of the other Pacific salmon species except the largest coho salmon. Killer whales shift to less profitable chum salmon in the fall, but only after the abundance of maturing Chinook in nearshore waters has declined (Ford et al. 2010b, Hanson et al. 2010).

Differences in the energy content among Chinook populations were also observed, associated with size and lipid content (Fig. 4). Mature Puget Sound Chinook salmon were smaller and leaner than other populations and generally provided less total energy. Assuming that the Chinook salmon we sampled were representative of the sizes and lipid content of fish available for consumption, killer whales would have to eat 1.8 and 1.5 times more Puget Sound fish to get the same total energy value obtainable by feeding on Chinook salmon from fall runs of Fraser River or Columbia River, respectively, possibly explaining the predominance of the Fraser River fish in their diet while feeding in the Salish Sea (Hanson et al. 2010).

Reducing uncertainty in the caloric estimates of Chinook salmon populations that are available to resident killer whales is necessary to better inform conservation and management of whales. Although Chinook salmon were sampled from 5 coastal regions spanning the documented feeding range of resident killer whales, they represent a small fraction of the Chinook salmon populations available as prey, and body size varies considerably among populations and among years within populations. We produced a simple relationship between fish body length and total energy value for use where population-specific energy content information is not available (Fig. 6). Fish length accounted for most (91%) of the variation in kilocalories among Chinook salmon samples, and was robust, as evidenced by its consistency when any population was removed from the regression analysis (Table 4). This relationship was consistent with that of Yukon River Chinook salmon (Margraf et al. 2005). We also estimated length to kcal relationships for high- and low-fat Chinook salmon populations (based on 90th percentile values) that occur in terminal marine waters where resident killer whales feed. These high- and low-lipid values approximate energy densities for Chinook salmon with typical upstream and downstream migration patterns, respectively (Brett 1995). Consequently, the samples provided should be adequate to estimate the total energy for other popu-

lations of interest, given their size distribution, distance, and elevation of the spawning grounds (see Figs. 4 to 6 in Quinn 2005) and information on the duration of holding in freshwater prior to spawning.

Implications for conservation of killer whales and Chinook salmon

Conservation and recovery plans have been developed for both resident killer whales (NMFS 2008a, Fisheries and Oceans Canada 2008) and Chinook salmon (NMFS 2007–2011). However, achieving conservation objectives for recovery of killer whales may conflict with the recovery objectives of Chinook salmon (Williams et al. 2011). Compared to killer whales, a wider array of management options are available to directly enhance and recover Chinook salmon because of differences in their life history. Salmon are short-lived, anadromous, impacted by habitat degradation, and the target of valuable fisheries, whereas killer whales are long-lived, unaffected by factors in freshwater habitats that are so important to salmon, and are already protected from hunting. Placing restrictions on salmon fisheries to enhance prey availability to killer whales is one option currently being evaluated by the US NMFS and Fisheries and Oceans Canada (Hilborn et al. 2012).

Improved estimates of the prey base are needed to better model the effects of possible fishery closures and other management options that affect prey availability, enhancing the integration of killer whale conservation with salmon management. The predictive relationships between fish size and caloric content for populations with a range of lipid levels presented in this paper can be used to improve estimates of the total energy value of salmon to killer whales, a gap identified by Williams et al. (2011). These estimates, in turn, will help refine estimates of the numbers of Chinook salmon (including populations not specifically sampled in our study; Ford et al. 2010b, Hanson et al. 2010) needed to support killer whales. Indeed, several recently published studies have used unpublished data from our study to estimate the number of Chinook salmon needed to meet the caloric demands of resident killer whales. Noreen (2011) and Williams et al. (2011) used the average energy value of Fraser River Chinook salmon (16 386 kcal fish^{-1}) that was measured in this study to estimate the number of Chinook salmon necessary to meet the energetic demands of SRKWs, assuming they consumed only Chinook salmon. Williams et al. (2011) also estimated the number of fish necessary to meet the energetic requirements SRKWs based on simplistic 'calorie-rich' and 'lean' Chinook salmon prey options. More recently, the Fisheries and Oceans Canada and NMFS have used the predictive relationship between fish length and caloric content for Chinook salmon presented in this study to estimate the number of Chinook salmon needed to meet the annual caloric demands of NRKW and SRKW (Ford et al. 2010b, p. 43; NMFS 2011, p. 83) throughout their feeding range.

As new information about the year-round diet of resident killer whales is revealed (summarized in Hilborn et al. 2012), including the importance of specific Chinook salmon populations and other salmon species, the predictive models between salmon size (fish length and mass) and the total energy value of a fish can be used to refine the estimates of the prey base of resident killer whales. Of particular interest, as Chinook salmon become scarce, it is important to know whether whales continue to pursue them, devoting more effort to foraging, or shift to more abundant but less energetically valuable salmon species, or other prey. Whales have been known to travel 50 km d^{-1} and may follow Chinook salmon long distances rather than shifting to other species. Alternatively, the ability of resident killer whales to switch prey may be constrained by their culturally inherited foraging strategies (Ford et al. 2010a). Over the long-term, the growth of resident killer whale populations may increase natural mortality of Chinook salmon. The fundamental life-history differences between salmon and killer whales will make integration of recovery plans especially challenging.

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