Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

Abundance of Skeena River Chum Salmon during the Early Rise of Commercial Fishing

Michael H. H. Price [a] [b] , Nick Gayeski [c] & Jack A. Stanford [d]

[a] SkeenaWild Conservation Trust , 4505 Greig Avenue, Terrace , British Columbia , V8G 1M6 , Canada

[b] Mayfly Ecological Research , 2115 22nd Avenue, Smithers , British Columbia , V0J 2N6 , Canada

[c] Wild Fish Conservancy Northwest , Post Office Box 402, 15629 Main Street Northeast, Duvall , Washington , 98019 , USA

[d] Flathead Lake Biological Station , University of Montana , 32125 Bio Station Lane, Polson , Montana , 59860 , USA

To cite this article: Michael H. H. Price , Nick Gayeski & Jack A. Stanford (2013): Abundance of Skeena River Chum Salmon during the Early Rise of Commercial Fishing, Transactions of the American Fisheries Society, 142:4, 989-1004

To link to this article: http://dx.doi.org/10.1080/00028487.2013.790842

Transactions of the American Fisheries Society 142:989–1004, 2013

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2013.790842

ARTICLE

Abundance of Skeena River Chum Salmon during the Early Rise of Commercial Fishing

Michael H. H. Price*
SkeenaWild Conservation Trust, 4505 Greig Avenue, Terrace, British Columbia V8G 1M6, Canada; and Mayfly Ecological Research, 2115 22nd Avenue, Smithers, British Columbia V0J 2N6, Canada

Nick Gayeski
Wild Fish Conservancy Northwest, Post Office Box 402, 15629 Main Street Northeast, Duvall, Washington 98019, USA

Jack A. Stanford
Flathead Lake Biological Station, University of Montana, 32125 Bio Station Lane, Polson, Montana 59860, USA

Abstract
We used reported commercial catch data and historical information to estimate the abundance of Skeena River Chum Salmon *Oncorhynchus keta* during the early rise (1916–1919) in the commercial fishery to provide historical perspective for recovery plans. We applied a Bayesian analysis to address the uncertainties associated with the estimation process. Based on the historical catch of 204,000 in 1919 and an estimated harvest rate of 0.32–0.58, the estimated return of Skeena Chum Salmon ranged from 355,000 to 619,000, with the most probable single estimate being 431,000. The estimated return of Chum Salmon based on the 1916–1919 geometric mean catch of 154,000 ranged from 268,000 to 471,000, with the most probable single estimate being 325,000. Our posterior modal historical estimates are 8–11 times larger than the estimates for the contemporary period 1982–2010 and 39–52 times larger than those for the most recent period of 2007–2010. Intense harvest pressure is the single most probable factor explaining the sustained decline in Chum Salmon abundance, but other interactive factors, notably natural variations in survival, the loss of spawning and rearing habitat, and poor data quality, also are important considerations. Nonetheless, the Skeena catchment is largely pristine today, and our robust estimates of historical abundance should be of value to contemporary management and conservation agencies for the rebuilding of such severely diminished populations.

The rich ecological and cultural legacy of Canada's Pacific coast is shaped, if not defined, by wild Pacific salmon *Oncorhynchus* spp.; thus, these fish form a vital component of its future. Salmon contribute "identity" to coastal indigenous peoples (Campbell and Butler 2010; Hill et al. 2010), deliver essential nutrient subsidies to watersheds (Gende et al. 2002; Willson et al. 2004), and are important to coastal economies through nature-based tourism, harvesting, and processing (Schindler et al. 2010).

While many wild salmon stocks and species in British Columbia have been considerably diminished over the last century of intensive exploitation (see Slaney et al. 1996), a commercial mixed-stock fishery continues to harvest salmon. Recently, Sockeye Salmon *O. nerka* and Pink Salmon *O. gorbuscha* fisheries in British Columbia have acquired "sustainable" eco-certification labels from the Marine Stewardship Council (MSC; Tavel Certification 2010), and an application for Chum Salmon *O. keta* is in progress. This market-driven certification

*Corresponding author: pricem@skeenawild.org
Received July 23, 2012; accepted March 25, 2013

program provides financial incentive to fishers while promising adherence to international sustainability criteria. Although the MSC certification scheme is arguably failing to protect the ecological integrity of some marine systems (Jacquet et al. 2010), it is considered one important component of salmon conservation (Conn 2011). For example, the MSC certification of Skeena River Sockeye Salmon is conditional (in part) upon the creation and implementation of recovery plans for Skeena Chum Salmon (Tavel Certification 2010) that currently are at very low abundance and vulnerable to bycatch in the mixed-stock Sockeye Salmon and Pink Salmon fisheries (Walters et al. 2008).

To be effective, recovery planning for Skeena River Chum Salmon must address the rebuilding of life history characteristics and abundance; to be legitimate, it must endeavor to compare the current levels of abundance not only with the levels that immediately preceded recovery listing but also with historical estimates of abundance. Without such a historical perspective, recovery targets may considerably underestimate the potential abundance and diversity that is required to assure the persistence of these populations.

Estimates of the historical abundance of Skeena River Chum Salmon (and British Columbia salmon stocks in general) suffer from a "shifting baseline" syndrome of information (Price et al. 2008). All too often, run-reconstruction analyses and stock status evaluations are based on abundance data that date back only to the 1950s or even the 1980s (English et al. 2006; Spilsted and Pestal 2009; Cox-Rogers and Spilsted 2012; English 2012). However, Skeena salmon abundance was considerably reduced as early as the 1920s (Pritchard 1948; Ricker and Smith 1975), and roughly one-third of the original biodiversity is estimated to have disappeared before 1950 (Walters et al. 2008). Clearly, a historical perspective is needed, and herein we show how historical information for Skeena River Chum Salmon can be used to estimate past abundance. We use a Bayesian analysis framework to estimate Chum Salmon run sizes from company records of the canned pack and other products. Thus, our primary objective is to provide an evidence-based estimate of Chum Salmon abundance returning to the Skeena River during the early rise of the industrial commercial fishery. Our analysis provides a reasonable historical estimate to underpin recovery plans.

METHODS

Our source of historical harvest records for Skeena River Chum Salmon was the extensive commercial catch data compilation for British Columbia salmon of Argue and Shepard (2005, their Table 46). These data were based primarily on the canned-pack records of salmon canneries operating at the mouth of the Skeena River beginning in 1877 (Figure 1). The first commercial harvest records for Chum Salmon date from 1901, yet the catch remained negligible until 1914 compared with all other commercially caught Skeena salmonids (Argue and Shepard 2005). Annual Chum Salmon catch steadily increased from 1914 (64,000) to 1919 (204,000), then declined (with some variations) for several years, but peaked in 1926 (328,000). Before gasoline-powered vessels were introduced on the Skeena River in 1924, an oar and sail gill-net fishery prevailed (Milne 1955; Figure 2). The limited range of the row-boats confined the commercial fishery during this early period primarily to the Skeena River (Milne 1955; Wood 2008), which provides strong evidence that the vast majority of Chum Salmon caught were of Skeena origin.

We based our historical Chum Salmon abundance estimates on catch data from 1916 to 1919. This 4-year period, spanning approximately one generation (Ricker 1980; Salo 1991), represents the period when Skeena River Chum Salmon first experienced high rates of harvest but before the population showed clear signs of overharvesting. Thus, run size estimates based on the catch record for this period likely best represent the inherent capacity of the Skeena catchment to produce Chum Salmon during the period immediately prior to the continuous harvest of a large proportion of the run.

Despite the growing trend in catch during 1914–1919, Chum Salmon were incidentally caught during this period in Sockeye Salmon (the most profitable species) and Coho Salmon *O. kisutch* fisheries (Milne 1955; Lyons 1969). Sockeye Salmon were harvested annually between mid-June and the end of August, predominantly within the Skeena River (Milne 1955; Wood 2008). Some form of an "outside" fishery also existed, whereby a portion of fishing effort occurred within the Skeena estuary during the first 3 weeks of the Sockeye Salmon fishery (Ross 1967; Wicks 1975; Blyth 1991). The resulting catch abundance of the outside fishery was reportedly much smaller than the later "inside" fishery, when Sockeye Salmon concentrated within the Skeena River (Ross 1967; Wicks 1975; Figure 1). The Coho Salmon fishery occurred from the end of August to mid-September (Carrothers 1941; Milne 1955). Today, as we assume occurred in the past, the annual return of Skeena Chum Salmon peaks by the third week of August and the run continues into September (see Tyee Test Fishery 2012 for data).

Bayesian Estimation of Historical Run Sizes

We used the harvest rates on Skeena River Sockeye Salmon estimated by Ricker (1958, 1973) and substantiated by Wood (2008) to approximate the harvest rate on Chum Salmon during our period of evaluation (1916–1919). By considering the combined information about the harvest rate on Sockeye Salmon, the proportion of the Chum Salmon run coinciding with the Sockeye Salmon fishery, the post–Sockeye Salmon fishery for Coho Salmon, and the remaining proportion of the Chum Salmon run coinciding with the Coho Salmon fishery, we were able to place reasonable bounds on the total Chum Salmon harvest rate. This required that we estimate the following parameters: (1) *ChRS*, the proportion of the total Chum Salmon run that encountered (and was potentially subject to harvest during) the Sockeye Salmon fishery, (2) *SHCh*, the proportion of the annual harvest rate on Sockeye Salmon to which Chum Salmon in the overlapping proportion of the Chum Salmon run (*ChRS*) were vulnerable, (3) *SHR*, the total annual harvest rate on the Sockeye

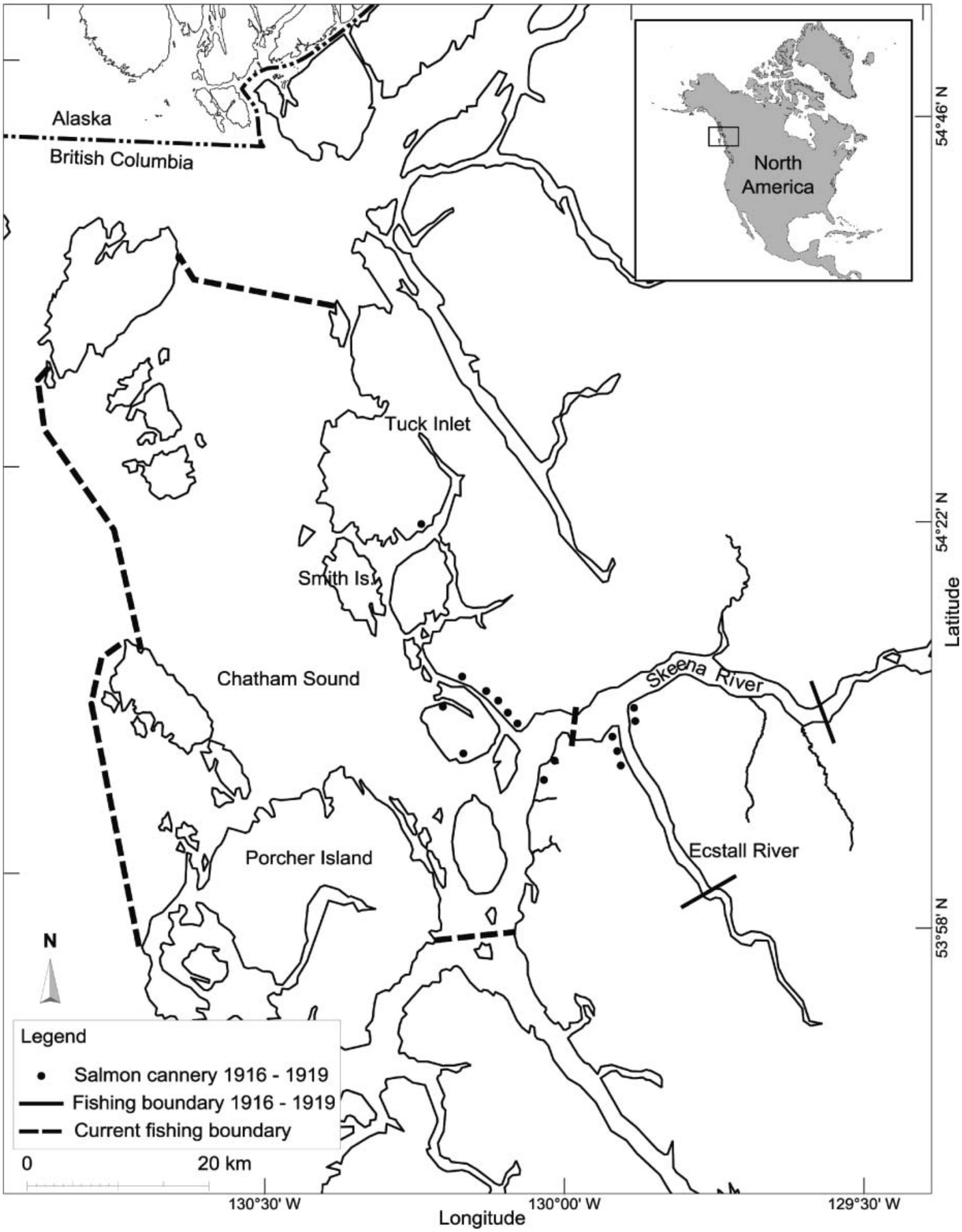

FIGURE 1. Study area, including the Skeena River and estuary; locations of the salmon canneries that operated during 1916–1919; and the historical and current commercial fishing boundaries.

FIGURE 2. Oar and sail gill-net vessels fishing the Skeena River in 1915 (source: Prince Rupert City and Regional Archives, Museum of Northern British Columbia, Wrathall Collection, JRW1421).

Salmon run, (4) *CoHCh*, the proportion of the total harvest rate on the post–Sockeye Salmon fishery for Coho Salmon to which the overlapping proportion of the Chum Salmon run ($1-ChRS$) was vulnerable, and (5) *CoHR*, the harvest rate on Coho Salmon during the post–Sockeye Salmon season Coho Salmon fishery. Hence, the harvest rate on Chum Salmon was estimated as

$$ChHR = (ChRS \cdot SHCh \cdot SHR) + [(1 - ChRS) \cdot CoHCh \cdot CoHR]. \quad (1)$$

We followed the general approach of Gayeski et al. (2011) to estimate the principal parameter of interest, the terminal Chum Salmon run size (N), from the total catch and estimates of the harvest rate applied to the total run. We employed a negative binomial likelihood based on the gamma–Poisson parameterization (see the appendix for justification) and treated the total commercial Chum Salmon catch (C) as a Poisson random variable in which the Poisson rate parameter (λ) is drawn from an underlying gamma distribution with a constant scale parameter (β) equal to the underlying average harvest rate (*ChHR*) and a shape parameter (α) equal to the total run from which the catch was obtained, that is, $C \sim$ Poisson(λ); Bin $\lambda \sim$ gamma(N, *ChHR*). Thus, we estimated the parameters of the negative binomial likelihood

$$P(C|\lambda,\ N,\ ChHR) = P(C|\lambda) \cdot P(\lambda|N,\ ChHR), \quad (2)$$

which is the joint probability of obtaining the catch C given a Poisson distribution with rate parameter λ and obtaining λ from a gamma distribution with parameters N and *ChHR*. In this parameterization, the expected value of the gamma is $\alpha \cdot \beta$ (in this case, $N \cdot ChHR$), which will also be the expected value of λ. Since the expected value of a Poisson-distributed random variable is also λ, the expected value of the Poisson-distributed catch C will also be equal to λ, which will be the mean of the negative binomial. But unlike the Poisson distribution, the variance of the negative binomial will be greater than the mean and equal to $\alpha \cdot \beta \cdot (1 + \beta)$. Thus, the variance of the catch will be: $N \cdot ChHR \cdot (1 + ChHR)$. In our situation, C (catch data) is a constant and λ, *ChHR*, and N are the parameters to be estimated.

There is little uncertainty in the estimation of λ, since the coefficient of variation (CV = SD/mean) for large values of λ (as is the case here) is very small (e.g., for $\lambda = 200{,}000$, the SD will be $\sqrt{200{,}000} = 447$, and CV = 447/200,000 = 0.00224). However, considerable uncertainty is involved in estimating N, *ChHR*, and each of the five independent parameters in equation (1) (*ChRS*, *SHCh*, *SHR*, *CoHR*, and *CoHCh*), from which the aggregate Chum Salmon harvest rate, *ChHR*, is derived. We address these uncertainties by employing a Bayesian approach, placing prior distributions on all unknown parameters and using a Metropolis-within-Gibbs Markov chain–Monte Carlo (MCMC) algorithm to sample the posterior distribution equation (3) corresponding to the negative binomial likelihood equation (2):

$$P(\lambda,\ N,\ ChHR|C) = P(\lambda|C) \cdot P(N,\ ChHR7|\lambda). \quad (3)$$

The Bayes estimate of the terminal run size was obtained using the Fortran shell program Metropolis-within-Gibbs (MTG) written by the late Daniel Goodman (Environmental Statistics

Group, Department of Biology, Montana State University, Bozeman). The MTG implements the Metropolis-within-Gibbs algorithm, sampling a joint distribution specified by a joint log proportional density function (which for the Bayes analysis is the joint posterior coded to a proportionality as the product of the joint prior and joint likelihood). The posterior distribution equation (3) was sampled for each of the two values of the total catch. For each estimate, 2,000,000 samples were retained using a thinning interval of 100 (i.e., every 100th sample was retained) to reduce the autocorrelation among parameter values (which results from the MCMC sampling of the posterior distribution) and to ensure thorough sampling of the entire posterior probability space. The priors and posteriors of the parameters selected for histogram display were binned into 100 equal-size bins on the *x*-axis to produce smooth histograms and to provide reasonably fine-scale resolution of the posterior probability densities. Histograms of the posterior distributions for the parameters contributing to the Chum Salmon harvest rate (i.e., *ChRS*, *SHCh*, *SHR*, 1−*ChRS*, *CoHCh*, and *CoHR*) were examined together with summary statistics for the MCMC samples to verify that the entire posterior parameter space had been properly sampled. The parameterizations of the prior distributions were based on available data regarding the conduct of the fisheries and associated gear type, the known and estimated run timings of each species, and the relative and absolute body sizes of Chum Salmon.

Justification of the Prior Distributions

The prior distributions and their parameters are listed in Table 1. To be conservative, we chose values that tended to give smaller estimates of the total Chum Salmon population size for the following priors:

*The Poisson rate parameter for the distribution of the Chum Salmon catch (*PLAM*).*—Given the assumption that the total catch of Chum Salmon is a Poisson random variable, we placed upper and lower limits on a uniform distribution of the rate parameter, *PLAM*, which spanned all possible values that could yield the numerical catch *C*. For values of *C* as large as those for the two time periods whose catch we evaluate, values of *PLAM* will lie well within plus or minus 10% of *C*, so we set the lower boundary at $0.9 \cdot C$ and the upper boundary at $1.1 \cdot C$. This guaranteed that all possible values of the posterior probabilities of *PLAM* would be found.

TABLE 1. Lower and upper limits of the uniform distributions for the prior parameters used in the Bayesian estimation of the terminal run size of Skeena River Chum Salmon. See Methods for an explanation of the parameters.

Parameter	Lower bound	Upper bound
PLAM (λ)	$0.9 \cdot C$	$1.1 \cdot C$
ChRS	0.67	0.75
SHCh	0.60	0.90
SHR	0.58	0.66
1 – *ChRS*	0.25	0.33
CoHR	0.45	0.60
CoHCh	0.60	0.90
N	Catch/max(*ChHR*)	Catch/min(*ChHR*)

*The proportion of the total Chum Salmon run that encountered the Sockeye Salmon fishery (*ChRS*).*—The commercial Skeena River Sockeye Salmon fishery historically closed by the end of August each year (Milne 1955). The majority of Chum Salmon are thought to return to the Skeena River before the end of August, but the exact proportion remains unknown. Data from the Tyee test fishery, which dates back to 1956, suggest that this proportion is somewhere between 67% and 75% of the entire annual return of Skeena Chum Salmon (Tyee Test Fishery 2012). As noted above, we reasonably assumed that this range also applies to the period of interest herein (1916–1919); thus, we placed a uniform distribution on the parameter between 0.67 and 0.75.

*The proportion of the annual Sockeye Salmon harvest rate to which Chum Salmon were vulnerable (*SHCh*).*—Although Chum Salmon were targeted by the Skeena River fishery to some extent, it is improbable that harvest rates were higher than those on Sockeye Salmon during the years of our evaluation because Chum Salmon had less market value (Milne 1955; Lyons 1969). Futhermore, Chum Salmon were substantially larger on average than Sockeye Salmon (i.e., 6.4 kg, compared with 2.9 kg; Argue and Shepard 2005), which made Chum Salmon less susceptible to capture in Sockeye Salmon-specific gill nets (i.e., 5.75-in [14.6-cm] mesh; Milne 1955) that retain fish within a narrow size range (Hamley 1975; Muir et al. 1994). Thus, the actual harvest rate on Chum Salmon likely was some fraction of the estimated Sockeye Salmon harvest rate, perhaps 50% to 60%, and certainly not more than 90%. Therefore, we placed a uniform distribution on *SHCh* bounded between 0.60 and 0.90.

*The total annual harvest rate on the Sockeye Salmon run (*SHR*).*—The harvest rate on Skeena River Sockeye Salmon during the period 1915–1919 has been estimated at 0.62 (Ricker 1958, 1973; Ricker and Smith 1975) and substantiated by Wood (2008). However, good as this estimate may be, it is likely that there is some degree of uncertainty surrounding it when it is applied to any single year; accordingly, we placed a uniform distribution on this parameter between the bounds 0.58 and 0.66.

*The proportion of the total Chum Salmon run that encountered (and were potentially subject to harvest during) the post–Sockeye Salmon season Coho Salmon fishery (1−*ChRS*).*—The sampling of this parameter was calculated deterministically by subtracting each value sampled from the prior of *ChRS* from 1. This is because we are estimating the proportion of the Chum Salmon run that remained after the Sockeye Salmon fishery but that were also vulnerable to the late-season Coho Salmon fishery (i.e., we assume that all Chum Salmon were either exposed to the Sockeye Salmon or Coho Salmon fishery).

*The proportion of the total harvest rate on the post–Sockeye Salmon season Coho Salmon run to which the overlapping proportion of the Chum Salmon run (1−*ChRS*) were vulnerable (*CoHCh*).*—Chum Salmon were substantially larger on average than Coho Salmon (i.e., 6.4 kg, compared with 4.4 kg; Argue and Shepard 2005) and may thus have been less likely than Coho Salmon to be caught in the late-season gill-net fishery. Additionally, Chum Salmon were unlikely to be caught in the hook-and-line fishery that targeted Coho Salmon during our period of interest. But to be conservative in our estimates, and given the paucity of information, we placed the same distribution and limits on the harvest rate on the late-season Chum Salmon run as we did for Chum Salmon subject to the Sockeye Salmon fishery. That is, we felt that Chum Salmon were as vulnerable to the Coho Salmon fishery as they were to the Sockeye Salmon fishery (i.e., 0.60 and 0.90).

*The harvest rate on the post–Sockeye Salmon season Coho Salmon fishery (*CoHR*).*—Harvest rates on Coho Salmon were not likely higher than the harvest rates on Sockeye Salmon because Sockeye Salmon had superior market value (Milne 1955); canneries and fishermen made the majority of their money on Sockeye Salmon (Ross 1967; Lyons 1969; Wicks 1975). And although some fishermen only participated in the Sockeye Salmon fishery (Knight and Koizumi 1976), others were involved in an additional hook-and-line fishery that targeted Coho Salmon (Blyth 1991). To conservatively account for the uncertainties in fishing effort, we placed a uniform distribution on the *CoHR* parameter between the bounds 0.45 and 0.60.

*The informative character of the prior distribution of the Chum Salmon harvest rate (*ChHR*).*—Despite our having to employ uniform priors for five independent parameters to obtain the prior distribution for the aggregate harvest rate on Skeena River Chum Salmon, the resulting prior had a unimodal bell shape centered around 0.45. This resulted from a common property of the multiplication of several uniform distributions and yielded a considerable reduction in the uncertainty surrounding this parameter. The critical information lies in the upper and lower limits of the contributing uniform priors, which we delimited as best we could given the available historical information. Thus, even with little or no information on the shape of the component parameters of this prior, the aggregation of multiple uniform priors yielded a prior that contained considerably more information than if we had placed a uniform prior directly on *ChHR*.

Sensitivity of the prior for the Chum Salmon harvest rate to the limits of the component parameter distributions.—We examined the sensitivity of the distribution of *ChHR* to the lower and upper limits of the parameter components to determine how influential each limit of each component was to the distribution of *ChHR*; our methods and results are presented in the appendix. Essentially, the prior on *ChHR* was moderately sensitive to increases of 0.1–0.2 in the upper limits of *SHR* and *CoHR* (Tables A.1–A.2 in the appendix), values for the Sockeye Salmon and Coho Salmon harvest rates that are well above any estimates made for these fisheries. The prior on *ChHR* was insensitive to changes of 0.1–0.2 to the lower or upper limits of *ChRS*, *SHCh*, and *CoHCh* (Tables A.3–A.5).

*The terminal Chum Salmon run size (*N*).*—The only information on historical Chum Salmon abundance is the company records of canned packs and other products, which were converted to catch in pieces by Argue and Shepard (2005). Accordingly, we simply bounded the prior distribution of *N* broadly between the minimum and maximum values possible, given the values of the prior distributions contributing to *ChHR*. Given the values of our priors, the minimum value of $ChHR = (0.67 \cdot 0.60 \cdot 0.58) + (0.33 \cdot 0.60 \cdot 0.45) = 0.32$. The maximum value of $ChHR = (0.75 \cdot 0.90 \cdot 0.66) + (0.25 \cdot 0.90 \cdot 0.60) = 0.58$. Given a value for *C*, the lower bound on $N = C/0.58$ and the upper bound on $N = C/0.32$. The posterior distribution of *N* then will be bounded by these limits; this permits the sampling of the posterior of *N* to examine only possible values of *N* and thereby increases the efficiency of the MCMC algorithm.

Choice of years on which to base the estimates of historical Chum Salmon abundance.—We calculated two estimates of Chum Salmon abundance during the period 1916–1919: (1) using the single large catch year of 1919 and (2) using a 4-year running geometric mean catch for the years 1916–1919. We chose to base our estimate on the large catch of 1919 (204,000) because the fishery at that time remained predominantly within the Skeena River (Milne 1955; Wood 2008), and the resulting estimate likely best reflects the potential of the river to produce Chum Salmon before the influence of intense fishing pressure and other human stressors. We chose to base our second estimate on the catch during the time period 1916–1919 (154,000) because this is when Chum Salmon began to be retained in considerable numbers and because this represents the average generation time of Skeena Chum Salmon at the onset of intense commercial fishing (Ricker 1980; Salo 1991).

Comparison of Historical and Contemporary Run Sizes

We used run-reconstruction estimates of Chum Salmon returning to the Skeena River during 1982–2010 (see English 2012) to compare our results of historical (1916–1919) run sizes with recent abundance. Because Chum Salmon in Canada are managed within the context of conservation units (CUs; WSP 2005), we apportioned our historical Chum Salmon abundance estimate into the CUs for the Skeena River; these include those for the Skeena estuary and the lower, middle, and upper Skeena River (Holtby and Ciruna 2007). We used Department of Fisheries and Ocean's management target escapement goals for each CU to approximate the historical proportion of Chum Salmon that returned to each CU. The assigned goals and proportions are as follows: Skeena estuary (2,775; 4%), Lower Skeena (43,975; 76%), and Middle Skeena (11,000; 19%; DeMarco 1991). Given the absence of target goal data for the Upper Skeena CU, which currently may consist of only a single small spawning population (Gottesfeld and Rabnett 2008), we assumed that this CU historically represented 1% of the combined Skeena Chum Salmon abundance.

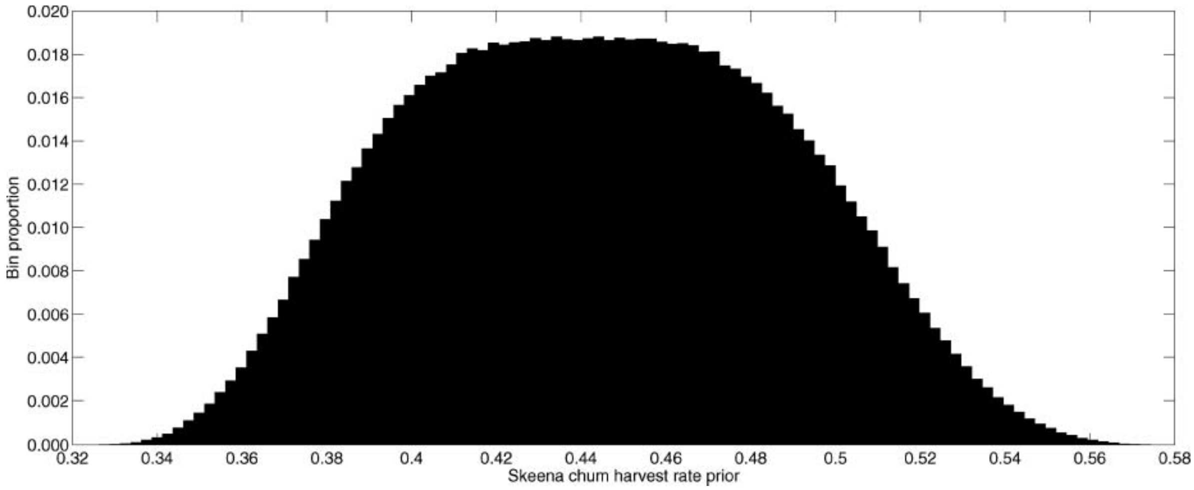

FIGURE 3. Histogram of the prior distribution of the aggregate harvest rate on Skeena River Chum Salmon for the period 1916–1919.

RESULTS

The prior distribution of the aggregate harvest rate on Chum Salmon during 1916–1919 ranged from 0.32 to 0.58, with the most probable value being 0.45 (Figure 3). Because the catch data fail to provide independent information on the harvest rate, the posterior distributions of *ChHR* are identical to the priors. Based on the historical catch of 204,000 in 1919, the estimated return of Chum Salmon to the Skeena River watershed ranged from a minimum of 355,000 to a maximum of 619,000, with a most probable (modal) single estimate of 431,000 (Table 2; Figure 4). There is a 95% probability that the terminal run exceeded 395,000 and a 5% probability that it was larger than 541,000. The estimated return of Chum Salmon based on the 1916–1919 geometric mean catch of 154,000 ranged from a minimum of 268,000 to a maximum of 471,000, with a most probable single estimate of 325,000 (Figure 5). There is a 95% probability that the run was greater than 297,000 and a 5% probability that it exceeded 408,000.

The average annual run size of Chum Salmon returning to the Skeena River estuary and watershed during the contemporary period 1982–2010 was 40,440. For the most recent 4-year period of 2007–2010, the average annual run size of Skeena-bound Chum Salmon was 8,271. The posterior modal historical estimates of the total run size of Chum Salmon returning to the Skeena during the periods 1916–1919 and 1919 are 8–11 times larger than those for 1982–2010 and 39–52 times larger than those for 2007–2010. Apportioning our historical modal Chum Salmon run size estimates for the period 1916–1919 and the peak year 1919 into separate Skeena CUs result in differences from the most recent contemporary period that range from 38- to 57-fold (Table 3).

DISCUSSION

Our objective was to provide a credible estimate of the historical return of Chum Salmon to the Skeena River watershed during the early development of the commercial fishery. We argue that our methodology and results in fact do provide such a credible estimate and that these results reveal a large discrepancy between the return of 94 years ago and those of today. There are at least four potential explanations for the discrepancy: differences in marine survival between the periods, loss of spawning and rearing habitat, overexploitation, and poor data quality.

Differences in Marine Survival

Marine climate variability at basinwide and regional scales has a well-known influence on Pacific salmon productivity (Mantua et al. 1997; Mueter et al. 2002). The ocean survival of Alaska and south-coast British Columbia salmon populations appears to exhibit a strong and consistent correlation with

TABLE 2. Commercial catch (*C*) of Skeena River Chum Salmon as estimated by Argue and Shepard (2005) and the posterior marginals of the estimated terminal run size (*N*).

		N				
Year	*C*	Mode	Median	Mean	SD	Central 90%
1919	204,000	431,000	456,000	462,000	45,400	395,000–541,000
1916–1919	154,000	325,000	344,000	348,000	34,600	297,000–408,000

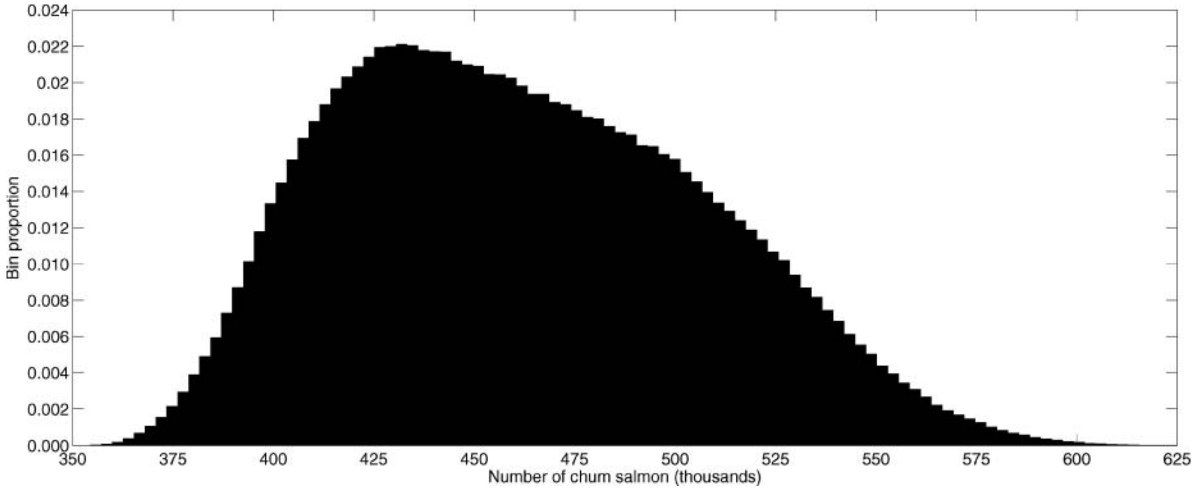

FIGURE 4. Histogram of the posterior distribution of the terminal Skeena River Chum Salmon run in 1919, based on the commercial catch of 204,000 reported by Argue and Shepard (2005).

indices of ocean productivity, such as the Pacific Decadal Oscillation (PDO; Mantua et al. 1997; Beamish et al. 2000). Similarly, consistent effects of regional sea surface temperatures (SSTs) on the survival of Pacific salmon have been observed (Mueter et al. 2002, 2005; Connors et al. 2012). For example, the relatively recent 20- to 30-year time period associated with warmer ocean temperatures on British Columbia's south coast are thought to have contributed to the fourfold decline in the marine survival of steelhead *O. mykiss* (Ward 2000). Furthermore, the large and consistent decreases in Sockeye Salmon productivity in many areas along the West Coast of North America since the late 1990s may be due to similar processes (Peterman and Dorner 2012). However, we believe that it is unlikely that the large difference in abundance between historical and contemporary periods that we have estimated for Skeena River Chum Salmon can be accounted for by differences in ocean productivity. There are three reasons for this. First, the salmon populations in northern British Columbia do not appear to respond to productivity indices such as the PDO as strongly as populations further south or north (Hare et al. 1999; Hill et al. 2009). Second, even if Skeena River Chum Salmon responded strongly to such indices, the ocean conditions in the decade leading up to the large run of 1919 (as indexed by the PDO) were not distinctly favorable or vastly different from those experienced in recent years (Hare et al. 1999; Biondi et al. 2001). Finally, coastal ocean conditions (as measured by PDO or SST, both of which are admittedly indirect and statistically noisy indices) explain a small proportion of the variability in salmon productivity (i.e., recruitments per spawner) relative to other factors (Mueter et al. 2005; Connors et al. 2012).

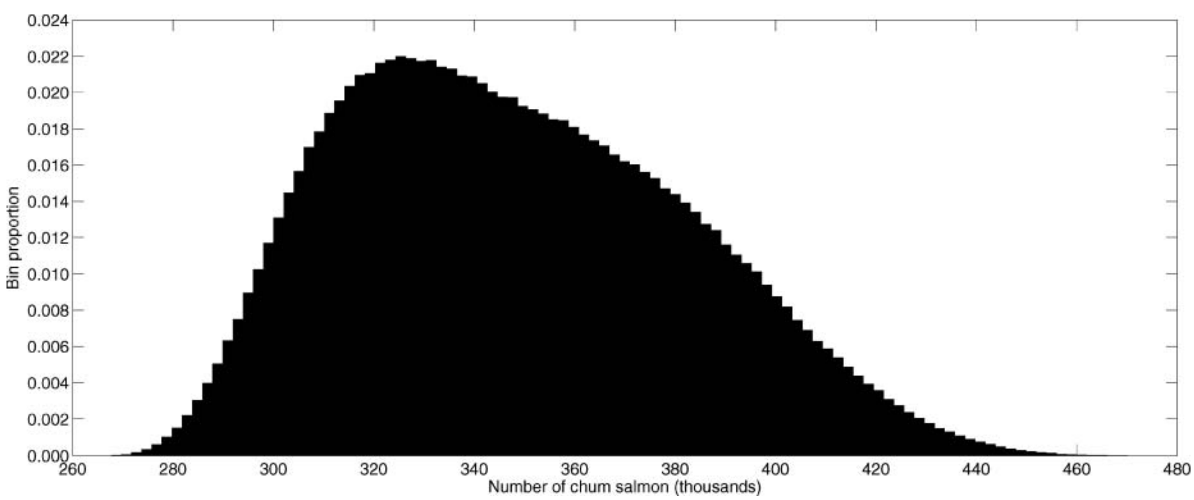

FIGURE 5. Histogram of the posterior distribution of the terminal Skeena River Chum Salmon run for the period 1916–1919 based on the geometric mean commercial catch of 154,000 reported by Argue and Shepard (2005).

TABLE 3. Comparison of historical (1916–1919) and contemporary (1982–2010) Skeena River Chum Salmon abundance by conservation unit (CU).

CU	1916–1919	1919	1982–2010	2007–2010
Skeena Estuary	13,012	17,080	800	308
Lower Skeena	247,228	324,520	34,372	6,531
Middle Skeena	61,807	81,130	5,268	1,432
Upper Skeena	3,253	4,270		

Salmon share a common resource pool in the North Pacific; as a result, large increases in salmon abundance can reduce survival rates (Peterman 1984; Ruggerone and Nielsen 2004; Helle et al. 2007). For example, the dramatic increase in the abundance of artificially produced (hatchery) salmon has likely increased competition in oceanic feeding grounds for wild salmon populations, leading to reduced productivity (Cooney and Brodeur 1998; Heard 1998; Zaporozhets and Zaporozhets 2004). Pink Salmon abundance in the North Pacific, which has more than doubled since the 1950s owing to hatchery supplementation (Ruggerone et al. 2010), is suspected to have had a strong negative influence on the productivity of numerous British Columbia Sockeye Salmon populations (Connors et al. 2012). Moreover, the large release of hatchery-produced Chum Salmon in Alaska since the late 1980s is considered a likely factor in the steep and recent decline of wild Chum Salmon north of Southeast Alaska (Ruggerone et al. 2010). The annual release of 2 billion Japanese hatchery-produced Chum Salmon could affect the growth of wild Chum Salmon from Alaska and British Columbia because these enhanced fish are broadly distributed throughout the North Pacific (Myers et al. 2004). Russia also releases 360 million hatchery Chum Salmon annually (Ruggerone et al. 2010), and combined with the annual release of Alaskan and Japanese hatchery Chum Salmon and Pink Salmon, could negatively affect the survival of wild Chum Salmon from the Skeena River.

Might competitive effects from the increased abundance of hatchery fish be the primary driver of the decline in the abundance of Skeena River Chum Salmon over the last century? Again, we believe not, for two reasons. First, although the annual release of billions of Japanese and Russian hatchery-produced Chum Salmon is thought to be inhibiting the recovery of wild Chum Salmon populations in Russia (Radchenko 1998; Kaeriyama et al. 2007), overharvest and perhaps freshwater habitat degradation in the southern area of the Russian Far East are considered the key factors in the overall decline of Russian wild Chum Salmon (Ruggerone et al. 2010). Second, Skeena Chum Salmon populations were already significantly reduced by the 1930s and remained low until at least 1950 (Argue and Shepard 2005), long before large-scale hatchery production commenced. We do believe, however, that the substantial increase in hatchery fish now utilizing the North Pacific may account for the large decline of Skeena Chum Salmon over the period 1982–2010.

Loss of Spawning and Rearing Habitat

The Skeena River is currently one of North America's most important salmon producers (Gottesfeld and Rabnett 2008). Chum Salmon spawn mostly in the coastal portion of the watershed and commonly utilize back channels and spring brooks in the lower Skeena River and adjacent tributaries. Emergent fry may hold for several weeks in floodplain spring brooks as presmolts (J. Stanford, unpublished data). While industrial development in the watershed remains in its infancy, some habitat degradation has occurred. With relevance to Chum Salmon, several back-channel habitats in the lower Skeena River have been altered or cut off by railroad and highway construction, and logging has been extensive (Gottesfeld and Rabnett 2008). Unfortunately, the extent of spawning habitat loss or degradation for Skeena Chum Salmon has not been quantified. But data deficiency aside, we believe that the difference between our historical abundance estimate and that for the contemporary period far exceeds even the most exaggerated estimate of decline due to spawning habitat loss. For example, habitat loss for the steelhead returning to Puget Sound (a region of high-density urban and industrial development) was recently estimated to be no more than 33% (Gayeski et al. 2011). Notably, this loss in habitat was deemed negligible in the context of a 25-fold reduction in steelhead abundance. The Skeena River, by comparison, is essentially in pristine condition. Although reductions in marine productivity owing to warmer sea temperatures or oceanic competition from hatchery fish likely far outweigh the effect of freshwater habitat loss, further work is needed to assess the current levels of spawning habitat abundance and to evaluate the current potential of these habitats to produce juveniles.

Overexploitation during the Rise of Industrial Fishing

Declines in marine productivity and available spawning habitat have undoubtedly contributed somewhat to the current low numbers of Chum Salmon returning to the Skeena River watershed. However, intense harvest pressure is the single most probable factor in the initial decline in Chum Salmon abundance. Severe overharvesting of most species of salmon is believed to have occurred during the rise of industrial fishing on the Skeena (Gottesfeld and Rabnett 2008), and an evaluation of the historical catch data lends support to this hypothesis. With regards to Chum Salmon, the peak catch years of 1919 and 1926 coincided with peaks in fishing effort. The number of canneries reached a maximum during the years 1917–1919 and 1926 (Ross 1967; Lyons 1969), and the number of gill-net licenses exceeded 1,000 for the first time in 1919 (Milne 1955), surpassing the previous maximum (in 1915) by approximately 200 licenses. Despite advances in fishing technology after 1924 (e.g., gasoline-powered vessels and mechanical net-drums, which substantially increased catch efficiency) and the perpetuation of intense fishing effort (annual gill-net licenses exceeded 1,100 until 1935; Milne 1955), the overall Chum Salmon catch has generally declined since 1926 (Argue and Shepard 2005). Thus, perhaps analogous to the situation with wild Chum Salmon in Russia south of the Amur River and Japan, fishing pressure is likely to have significantly reduced the abundance of Skeena River Chum Salmon and the other anthropogenic influences discussed above now inhibit their recovery.

An additional factor that may be inhibiting the recovery of Skeena River Chum Salmon (which is exacerbated by previous fishing-induced declines in spawner abundance) is the loss of marine-derived nutrient subsidies. Some evidence suggests that spawning salmon influence juvenile salmonid growth rates and the perpetuation of future generations through carcass deposition and nutrient cycling (Gende et al. 2002). Estuaries can receive a large proportion of postspawning salmon nutrients (Cak et al. 2008), which is of particular importance for Chum Salmon that rear as juveniles in estuaries. It is plausible that the fertility of the Skeena River and estuary has declined considerably owing to the more than 100 years of intense exploitation of most Skeena salmonids and the subsequent reduction in the nutrients provided by returning salmon. A nutrient shortage may keep population sizes far below their historical levels as a result of density-dependent mortality in juveniles (Larkin and Slaney 1997; Gresh et al. 2000) and thus impede the recovery of these populations (Achord et al. 2003).

Data Quality

One concern regarding the catch data used for our historical estimate is that a portion of the Chum Salmon caught during 1916–1919 may have originated in systems other than the Skeena River. It is generally understood that Chum Salmon were incidentally harvested in the more lucrative Sockeye Salmon fishery during the period of our evaluation (Milne 1955; Lyons 1969). Some fishing effort may have occurred beyond the river and within the Skeena estuary between mid-June and the first week of July (Ross 1967; Wicks 1975; Blyth 1991). Because Chum Salmon generally do not enter the Skeena River until after the second week of July (but may have historically returned earlier), it is plausible that a proportion of the Chum Salmon caught during the outside fishery originated elsewhere. Recent gill-net catch data (1970–2009) for DFO's statistical area 4 (a vast area that extends far beyond the mouth of the Skeena River) suggest that up to 12% of the Chum Salmon of unknown origin are caught before the second week of July (PSC 2011). The historical and contemporary run timings of Chum Salmon being equal, these data suggest that up to 12% of the total catch calculated by Argue and Shepard (2005) may not have originated in the Skeena. For the year 1919, this would amount to a maximum of 25,000 non-Skeena Chum Salmon. Importantly, this proportion was probably offset by Skeena-bound Chum Salmon caught in the Nass and Alaska fisheries that are not included in Argue and Shepard's (2005) catch reconstructions. Catch data from the southern Southeast Alaska management area show that a total of 4.1 million Chum Salmon were caught in 1919, with an average of 3.3 million Chum Salmon being caught annually during 1916–1919; more than 57 million Chum Salmon were caught during 1919 in the combined Alaska fisheries (Byerly et al. 1999). If only 0.05% of the Chum Salmon caught in the Alaska fisheries of 1919 were of Skeena origin, the number would exceed our estimated proportion of non-Skeena Chum Salmon. We believe this provides further evidence that our historical run size estimates are conservative and more likely to underestimate than to overestimate, the true historical run size of Skeena Chum Salmon.

Contemporary estimates of Chum Salmon abundance are based on poor data quality. Chum Salmon returning to the largest Chum Salmon spawning area in the Skeena River catchment, the Ecstall River, have not been enumerated since 2002; in fact, only 5 out of 59 known spawning areas have had spawner counts in the previous decade (see English 2012). Additionally, the contemporary run-reconstruction estimates that we examined are based on numerous assumptions related to limited catch, run timing, and escapement data, all of which have inherent uncertainties (English et al. 2012). Furthermore, a significant portion of the Chum Salmon run may spawn in the main-stem Skeena River, which very often is turbid and would make detection of spawners and redds difficult. Given these data uncertainties, and because hatchery-produced Chum Salmon constitute a portion of the aforementioned contemporary estimates, the number of wild Chum Salmon annually returning to the Skeena could be either lower or higher.

Relevance for Conservation

The principal value of our terminal run size estimate is that it provides an index of the historical capacity and potential of the Skeena River system to produce Chum Salmon. Based on our geometric mean run estimate of 325,000 during 1916–1919, of which 154,000 were harvested, the Skeena River had the capacity to support at least 171,000 Chum Salmon spawners annually. This historical escapement should be of value to contemporary management, particularly in the context of the order-of-magnitude-lower abundance of Chum Salmon returning to the Skeena River in the most recent period. Admittedly, we cannot say anything about how this decline relates to the natural variability in Chum Salmon abundance over time, which may have been immense, as has recently been shown for western Alaska Sockeye Salmon (Rogers et al. 2013).

Canada's modern conservation policy for Pacific salmon attempts to protect distinct populations (WSP 2005). Four CUs have been identified for Skeena River Chum Salmon (Holtby and Ciruna 2007), and our analysis suggests that currently these CUs are severely diminished compared with a century ago. Although two separate investigations have shown that Skeena Chum Salmon may represent a single large population (e.g., Beacham et al. 1987; Kondzela et al. 1994), other data suggest that at least two separate races exist in addition to the four CUs. For example, there appear to be an early run of Chum Salmon that spawns in downwelling areas of main river channels and a late run that spawns in upwelling groundwater of back channels (J. Stanford unpublished data), as has been described for Chum Salmon in Russia (Kuzishchin et al. 2010) and Alaska (Gilk et al. 2005). Given the disproportionately large harvest pressure on the early Chum Salmon run during the approximately 40-year Skeena Sockeye Salmon fishery leading up to 1916, this type of life history diversity for Skeena-bound Chum Salmon may be significantly less than it was 150 years ago. Indeed, as Gottesfeld and Rabnett (2008) suggest, "Chum are probably the Skeena watershed salmon species in greatest danger of significant loss of spawning stocks and genetic diversity."

Conservation initiatives and recovery plans for Skeena River Chum Salmon will require an evaluation of credible hypotheses about the decline in historical abundance that our estimates suggest. An assessment of this loss is necessary to identify appropriate abundance targets for recovery that will ensure the persistence of Skeena Chum Salmon. Competitive interactions with hatchery fish, loss of genetic diversity and spawning habitat, bycatch in mixed-stock fisheries, possible changes in the magnitude of marine productivity, and loss of marine-derived nutrient subsidies are all likely contributors to the historical decline in Skeena Chum Salmon. It is imperative that monitoring efforts for wild Chum Salmon returning to the Skeena watershed be vastly improved, as the continued erosion of monitoring effort handicaps fishery and conservation decisions (Price et al. 2008). Notably, "[t]he available data are not adequate to assess current [Chum Salmon] status." (Walters et al. 2008). While there is evidence that a portion of the Chum Salmon spawning groups have been lost and others are at very low abundance, some optimism is warranted. The Skeena watershed remains a relatively intact salmon-producing system, such that recovering substantially larger wild Chum Salmon populations is a foreseeable possibility—but only if conservation measures aimed at reducing the factors inhibiting their recovery are immediately initiated.

ACKNOWLEDGMENTS

We are grateful to the Pacific Salmon Foundation for providing accessible contemporary run-reconstruction data, the Gordon and Betty Moore Foundation for funding, A. Argue for thoughtful discussions on historical catch data, and G. Knox, B. Spilsted, and two anonymous reviewers for comments that greatly improved the manuscript.

REFERENCES

Achord, S., P. S. Levin, and R. W. Zabel. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? Ecology Letters 6:335–342.

Argue, A. W., and M. P. Shepard. 2005. Historical commercial catch statistics for Pacific salmon (*Oncorhynchus* spp.) in British Columbia, 1828 to 1950. Canadian Technical Report of Fisheries and Aquatic Sciences 2601.

Beacham, T. D., A. P. Gould, R. E. Withler, C. B. Murray, and L. W. Barner. 1987. Biochemical genetic survey and stock identification of Chum Salmon (*Oncorhynchus keta*) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44:1702–1713.

Beamish, R. J., D. J. Noakes, G. A. McFarlane, W. Pinnix, R. Sweeting, and J. King. 2000. Trends in Coho marine survival in relation to the regime concept. Fisheries Oceanography 9:114–119.

Biondi, F., A. Gershunov, and D. R. Cayan. 2001. North Pacific decadal climate variability since 1661. Journal of Climate 14:5–10.

Blyth, G. Y. 1991. Salmon canneries: British Columbia north coast. Oolichan Books, Fernie, British Columbia.

Byerly, M., B. Brooks, B. Simonson, H. Savikko, and H. J. Geiger. 1999. Alaska commercial salmon catches, 1878–1997. Alaska Department of Fish and Game, Regional Information Report 5J99-05, Juneau.

Cak, A. D., D. T. Chaloner, and G. A. Lamberti. 2008. Effects of spawning salmon on dissolved nutrients and epilithon in coupled stream–estuary systems of southeastern Alaska. Aquatic Sciences 70:169–178.

Campbell, S. K., and V. L. Butler. 2010. Archaeological evidence for resilience of Pacific Northwest salmon populations and the socioecological system over the last ∼7,500 years. Ecology and Society [online serial] 15(1):article 17.

Carrothers, W. A. 1941. The British Columbia fisheries. University of Toronto Press, Toronto.

Conn, C. 2011. Conservation biology through the lens of a career in salmon conservation. Conservation Biology 25:1075–1079.

Connors, B. M., D. C. Braun, R. M. Peterman, A. B. Cooper, J. D. Reynolds, L. M. Dill, G. T. Ruggerone, and M. Krkošek. 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. Conservation Letters 5:304–312.

Cooney, R. T., and R. D. Brodeur. 1998. Carrying capacity and North Pacific salmon production: stock-enhancement implications. Bulletin of Marine Science 62:443–464.

Cox-Rogers, S., and B. Spilsted. 2012. Update assessment of Sockeye Salmon production from Babine Lake, British Columbia. Canadian Technical Report of Fisheries and Aquatic Sciences 2956.

DeMarco, R. 1991. Fish habitat inventory and information program: stream summary catalogue, subdistricts 4A-4D. Canadian Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia.

English, K. K. 2012. Datasets: extended time-series of catch and escapement estimates for Skeena Sockeye, Pink, Chum and Coho salmon stocks. Pacific Salmon Foundation, Skeena Salmon Program, Vancouver. Available: http://skeenasalmonprogram.ca/library/lib_263/. (May 2013).

English, K. K., T. Mochizuki, and D. Robichaud. 2012. Review of north and central coast salmon indicator streams and estimating escapement, catch, and run size for each salmon conservation unit. Pacific Salmon Foundation, Skeena Salmon Program, Vancouver. Available: skeenasalmonprogram.ca/libraryfiles/lib_1.pdf. (February 2013).

English, K. K., D. Peacock, and B. Spilsted. 2006. North and central coast core stock assessment program for salmon. Report to the Pacific Salmon Foundation and Fisheries and Oceans, Canada, LGL Limited Environmental Research Associates, Sidney, British Columbia.

Gayeski, N., B. McMillan, and P. Trotter. 2011. Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data. Canadian Journal of Fisheries and Aquatic Sciences 68:498–510.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917–928.

Gilk, S. E., W. D. Templin, D. B. Molyneaux, T. Hamazaki, and J. A. Pawluk. 2005. Characteristics of fall Chum Salmon *Onchorhynchus keta* in the

Kuskokwim River drainage. Alaska Department of Fish and Game, Fishery Data Series 05-56, Anchorage.

Gottesfeld, A. S., and K. A. Rabnett. 2008. Skeena River fish and their habitat. Ecotrust Publications, Portland, Oregon.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25(1):15–21.

Hamley, J. M. 1975. Review of gillnet selectivity. Journal of the Fisheries Research Board of Canada 32:1943–1969.

Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries 24(1):6–14.

Heard, W. R. 1998. Do hatchery salmon affect the North Pacific Ocean ecosystem? Pages 405–411 *in* D. W. Welch, editor. Assessment and status of Pacific salmonid stocks. North Pacific Anadromous Fish Commission, Bulletin 1, Vancouver. Available: www.npafc.org/new/pub_bulletin4.html. (February 2013).

Helle, J. H., E. C. Martinson, D. M. Eggers, and O. Gritsenko. 2007. Influence of salmon abundance and ocean conditions on body size of Pacific salmon. Pages 289–298 *in* Status of Pacific salmon and their role in North Pacific marine ecosystems. North Pacific Anadromous Fish Commission, Bulletin 4, Vancouver. Available: www.npafc.org/new/pub_bulletin4.html. (February 2013).

Hill, A. C., T. S. Bansak, B. K. Ellis, and J. A. Stanford. 2010. Merits and limits of ecosystem protection for conserving wild salmon in a northern coastal British Columbia river. Ecology and Society [online serial] 15(2):article 20.

Hill, A. C., J. A. Stanford, and P. R. Leavitt. 2009. Recent sedimentary legacy of Sockeye Salmon (*Oncorhynchus nerka*) and climate change in an ultraoligotrophic, glacially turbid British Columbia nursery lake. Canadian Journal of Fisheries and Aquatic Sciences 66:1141–1152.

Holtby, L. B., and K. A. Ciruna. 2007. Conservation units for Pacific salmon under the wild salmon policy. Canadian Science Advisory Secretariat Research Document 2007/070.

Jacquet, J., D. Pauly, D. Ainley, S. Holt, P. Dayton, and J. Jackson. 2010. Seafood stewardship in crisis. Nature 467:28–29.

Kaeriyama, M., A. Yatsu, M. Noto, and S. Saitoh. 2007. Spatial and temporal changes in the growth patterns and survival of Hokkaido Chum Salmon populations in 1970–2001. Pages 251–256 *in* Status of Pacific salmon and their role in North Pacific marine ecosystems. North Pacific Anadromous Fish Commission, Bulletin 4, Vancouver. Available: http://www.npafc.org/new/pub_bulletin4.html. (February 2013).

Knight, R., and M. Koizumi. 1976. A man of our times: the life-history of a Japanese-Canadian fisherman. New Star Books, Vancouver.

Kondzela, C. M., C. M. Guthrie, S. L. Hawkins, C. D. Russell, J. H. Helle, and A. J. Gharrett. 1994. Genetic relationships among Chum Salmon populations in southeast Alaska and northern British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 51(Supplement 1):50–64.

Kuzishchin, K. V., M. A. Gruzdeva, K. A. Savvaitova, D. S. Pavlov, and J. A. Stanford. 2010. Seasonal races of Chum Salmon *Oncorhynchus keta* and their interrelations in Kamchatka rivers. Journal of Ichthyology 50(2):159–173.

Larkin, G. A., and P. A. Slaney. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. Fisheries 22(11):16–24.

Lyons, C. 1969. Salmon: our heritage. Mitchell Press, Vancouver.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

Milne, D. J. 1955. The Skeena River salmon fishery, with special reference to Sockeye Salmon. Journal of the Fisheries Research Board of Canada 12:451–485.

Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 59:456–463.

Mueter, F. J., B. J. Pyper, and R. M. Peterman. 2005. Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. Transactions of the American Fisheries Society 134:105–119.

Muir, J., R. Staska, and J. Blick. 1994. Catch efficiency comparisons of four commercial gillnet mesh sizes in the taking of Sockeye and Chum salmon in districts 111 and 115, southeast Alaska. Alaska Department of Fish and Game, Regional Information Report IJ94-13, Juneau.

Myers, K. W., R. V. Walker, N. D. Davis, and J. L. Armstrong. 2004. Diet overlap and potential feeding competition between Yukon River Chum Salmon and hatchery salmon in the Gulf of Alaska in summer. Final Report to the Yukon River Drainage Fisheries Association, Fisheries Research Institute, University of Washington, Seattle. Available: digital.lib.washington.edu/researchworks/handle/1773/4541. (February 2013).

Peterman, R. M. 1984. Density-dependent growth in early ocean life of Sockeye Salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 41:1825–1829.

Peterman, R. M., and B. Dorner. 2012. A widespread decrease in productivity of Sockeye Salmon (*Oncorhynchus nerka*) populations in western North America. Canadian Journal of Fisheries and Aquatic Sciences 69:1255–1260.

Price, M. H. H., C. T. Darimont, N. F. Temple, and S. M. MacDuffee. 2008. Ghost runs: management and status assessment of Pacific salmon (*Oncorhynchus* spp.) returning to British Columbia's central and north coasts. Canadian Journal of Fisheries and Aquatic Sciences 65:2712–2718.

Pritchard, A. L. 1948. Skeena River salmon investigations, interim report 1944–1948. Fisheries Research Board of Canada, Pacific Biological Station, Nanaimo, British Columbia.

PSC (Pacific Salmon Commission). 2011. U.S./Canada northern boundary area 2010 salmon fisheries management report and 2011 preliminary expectations. PSC, Report TCNB 11-1, Vancouver. Available: www.psc.org/pubs/TCNB11-1.pdf. (February 2013).

Radchenko, V. I. 1998. Historical trends of fisheries and stock condition of Pacific salmon in Russia. Pages 28–37 *in* D. W. Welch, editor. Assessment and status of Pacific salmonid stocks. North Pacific Anadromous Fish Commission, Bulletin 1, Vancouver. Available: www.npafc.org/new/pub_bulletin1.html. (July 2012).

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 119.

Ricker, W. E. 1973. Two mechanisms that make it impossible to maintain peak-period yields from stocks of Pacific salmon and other fishes. Journal of the Fisheries Research Board of Canada 30:1275–1286.

Ricker, W. E. 1980. Changes in the age and size of Chum Salmon (*Oncorhynchus keta*). Canadian Technical Report of Fisheries and Aquatic Sciences 930.

Ricker, W. E., and H. D. Smith. 1975. A revised interpretation of the history of the Skeena River Sockeye Salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 32:1369–1381.

Rogers, L. A., D. E. Schindler, P. J. Lisi, G. W. Holtgrieve, P. R. Leavitt, L. Bunting, B. P. Finney, D. T. Selbie, G. Chen, I. Gregory-Eaves, M. J. Lisac, and P. B. Walsh. 2013. Centennial-scale fluctuations and regional complexity characterize Pacific salmon population dynamics over the past five centuries. Proceedings of the National Academy of Sciences of the USA 110:1750–1755.

Ross, W. M. 1967. Salmon cannery distribution on the Nass and Skeena rivers of British Columbia, 1877–1926. Bachelor's thesis. University of British Columbia, Vancouver.

Ruggerone, G. T., and J. L. Nielsen. 2004. Evidence for competitive dominance of Pink Salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. Reviews in Fish Biology and Fisheries 14:371–390.

Ruggerone, G. T., R. M. Peterman, B. Dorner, and K. W. Myers. 2010. Magnitude and trends in abundance of hatchery and wild Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 2:306–328.

Salo, E. O. 1991. Life history of Chum Salmon (*Oncorhynchus keta*). Pages 233–309 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.

Slaney, T. L., K. D. Hyatt, T. G. Northcote, and R. J. Fielden. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21(10):20–35.

Spilsted, B., and G. Pestal. 2009. Certification unit profile: north coast and central coast Chum Salmon. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2879.

Tavel Certification. 2010. The British Columbia commercial Sockeye Salmon fisheries: public certification report, volume 1. Canadian Pacific Sustainability Fisheries Society, Vancouver. Available: www.msc.org/track-a-fishery/fisheries-in-the-program/certified/pacific / british-columbia-sockeye-salmon. (February 2013).

Tyee Test Fishery. 2012. Salmon test fishing—Pacific region: daily salmon indices. Fisheries and Oceans Canada, Pacific Region, Skeena Tyee Test Fishery, Vancouver. Available: www-ops2.pac.dfo-mpo.gc.ca/xnet/content/salmon/testfish/sockeye/tyee_gillnet.htm. (February 2013).

Walters, C. J., J. A. Lichatowich, R. M. Peterman, and J. D. Reynolds. 2008. Report of the Skeena independent science review panel. Report to the Canadian Department of Fisheries and Oceans and the British Columbia Ministry of the Environment, Skeena Watershed Initiative, Vancouver.

Ward, B. R. 2000. Declivity in steelhead (*Oncorhynchus mykiss*) recruitment at the Keogh River over the past decade. Canadian Journal of Fisheries and Aquatic Sciences 57:298–306.

Wicks, W. 1975. The early gillnet fishermen. Pages 76–79 *in* A. Downs, editor. Pioneer days in British Columbia, volume 2. Heritage House, Surrey, British Columbia.

Willson, M. F., S. M. Gende, and P. A. Bisson. 2004. Anadromous fishes as ecological links between ocean, fresh water, and land. Pages 284–300 *in* G. A. Polis, M. E. Power, and G. R. Huxel, editors. Food webs at the landscape level. University of Chicago Press, Chicago.

Wood, C. C. 2008. Managing biodiversity of Pacific salmon: lessons from the Skeena River Sockeye Salmon fishery in British Columbia. Pages 349–364 *in* J. L. Nielsen, J. J. Dodson, K. Friedland, T. R. Hamon, J. Musick, and E. Verspoor, editors. Reconciling fisheries with conservation: proceedings of the fourth world fisheries congress, volume 1. American Fisheries Society, Symposium 49, Bethesda, Maryland.

WSP (Wild Salmon Policy). 2005. Canada's policy for conservation of wild Pacific salmon. WSP, Fisheries and Oceans Canada, Vancouver. Available: www.pac.dfo-mpo.gc.ca/fm-gp/species-especes/salmon-saumon/wsp-pss/docs/wsp-pss-eng.pdf. (February 2013).

Zaporozhets, O. M., and G. V. Zaporozhets. 2004. Interaction between hatchery and wild Pacific salmon in the Far East of Russia: a review. Reviews in Fish Biology and Fisheries 14:305–319.

APPENDIX: JUSTIFICATION OF THE USE OF THE GAMMA–POISSON DISTRIBUTION

The catch of migratory salmon in a gauntlet-type fishery, whereby a more or less stationary fishing fleet captures fish as they attempt to proceed upstream (such as the historical lower Skeena River commercial fishery), is not well represented as a series of independent Bernoulli trials at the fine spatiotemporal scale of an individual boat or a single fishing period for the fleet. Each salmon is not independently susceptible to the fishing gear, nor is it reasonable to think that each fish in the run has the same probability of being captured by the gear. In actuality, migrating salmon tend to be aggregated and their spatial and temporal distributions are clumped. Additionally, local conditions such as river discharge or flow, tidal stage, weather, water temperature, water clarity, moon phase, and time of day result in varying capture efficiencies for the fishing gear.

The clumped distribution that characterizes catches at fine scales likely approximates a gamma–Poisson process, which will generate a negative binomial distribution of the catches from any particular size run of fish subject to the fishing gear during any period of interest. For each such period (such as a single hour's fishing by the fleet), the catch can be thought of as a Poisson random variable in which the rate parameter (λ) of the corresponding Poisson distribution (which is equal to the expected catch) is itself a random variable drawn from an underlying gamma distribution with the shape parameter α equal to the total run susceptible to the gear during the fishing period, and the scale parameter β equal to the underlying average harvest rate, over all similar fishing periods. In this parameterization, the expected value of λ will equal $\alpha \cdot \beta$ with variance $\alpha \cdot \beta \cdot (1 + \beta)$.

The aggregate catch over a season will include numerous (often hundreds) of such individual catches. For a given type of gear in a given fishing area during each discrete fishing period i (such as 1 h), the expected catch (λ_i) will depend only on the total run of fish susceptible to the gear during each period (α_i), assuming a constant season-average harvest rate (β). The additive property of independent gamma random variables with a common scale parameter β insures that for $\lambda_1 \sim$ gamma(α_1, β) and $\lambda_2 \sim$ gamma(α_2, β) the distribution of $\lambda_1 + \lambda_2 \sim$ gamma($\alpha_1 + \alpha_2$, β; Gelman et al. 1995: 479). Consequently, under these conditions—and conditions that reasonably approximate them—the value of the Poisson rate parameter for the entire season (λ) will be distributed as gamma[$\Sigma(\alpha_i)$, β], where $\Sigma(\alpha_i)$ is the sum of all of the individual runs of fish susceptible to the gear during each discrete period of fishing i. The Poisson distribution possesses this same additive property (Gelman et al. 1995: 482), so that the seasonal catch $C \sim$ Poisson{gamma[$\Sigma(\alpha_i)$, β]} will have the same distribution as Poisson[$\Sigma(\lambda_i)$].

In other words, the distribution of the total catch will be the same whether it is estimated from the sum of the expected catches based on estimates of the individual run sizes (if the data with which to make those estimates were available) or from estimates of the total run size over the entire season. This ensures that the inverse problem of obtaining a Bayesian estimation of the run size from the total catch plus estimates of the average seasonal harvest rate using the gamma–Poisson likelihood will derive the same advantage of additivity of the parameters of the likelihoods applicable to the fine-scale harvest. This phenomenon is a manifestation of the law of large numbers. Essentially, the same conditions hold when the individual catches, C_i, are obtained from varying harvest rates, β_i, provided that the β_i are drawn from an underlying probability distribution with mean equal to β when the number of individual catches is large (as was the case with Skeena River Chum Salmon during our period of interest).

Thus, at the scale of the aggregate seasonal catch (for which the estimation of historical run size takes place), the law of large numbers will result in the total catch's being represented with reasonable accuracy from the dual process of sampling the average seasonal harvest from a gamma distribution with a shape parameter equal to the total run and a scale parameter equal to the average harvest rate, and then sampling the actual catch as a Poisson random variable with a rate parameter equal to the average harvest. The only caveat is that the period of time (e.g., weeks) over which the run is harvested must be long relative to the length of time of individual fishing events (e.g., hours) where the extra-binomial variation is concentrated, which was the case here.

At very large sample sizes, the distribution of the catch from an estimate of total run size and average harvest rate derived from a gamma–Poisson process will be well approximated by a simple binomial with the parameters total run size and average harvest rate. Consequently, the inverse problem of obtaining a Bayesian estimation of the run size from the total catch and an estimate of the average harvest rate using the binomial likelihood will also closely approximate the posterior distribution of the run size estimated using the gamma–Poisson distribution. Extensive simulations (not shown) confirm these general conclusions.

In summary, the uncertainty in our historical abundance estimate, which is due primarily to uncertainties surrounding the aggregate harvest rate at the time of the fishery, will be robustly represented by employing either the gamma–Poisson likelihood or the binomial likelihood. The gamma–Poisson will more often achieve a marginal improvement in precision at a very small additional computational cost (due to having to estimate the additional [Poisson rate] parameter), which is why we chose it for our analyses.

SENSITIVITY OF THE PRIOR ON THE CHUM SALMON HARVEST RATE TO THE LIMITS OF THE COMPONENT UNIFORM PRIOR DISTRIBUTIONS

To evaluate the sensitivity of *ChHR* to the lower and upper limits of the uniform distributions of the component prior distributions from which *ChHR* was derived, we created 21 samples (each consisting of 1,000,000 random values) of *ChHR* generated by randomly sampling the uniform distributions of the five underlying component uniform distributions and calculating *ChHR* using equation (1):

$$ChHR = (ChRS \cdot SHCh \cdot SHR) + [(1 - ChRS) \cdot CoHCh \cdot CoHR]. \tag{1}$$

The 21 samples included the default parameterizations of the five component distributions. Each of the remaining 20 samples was created by changing the lower or upper limits of one of the component distributions as shown in Tables A.1–A.5. The quintile values (the minimum; 20th, 40th, 60th, and 80th percentiles; and maximum) of the cumulative distribution of each sample of 1,000,000 were calculated for comparison with the quintiles of the default parameterization. This is a limited sensitivity analysis, in which the upper or lower limit of a single component was changed while keeping all other limits at their default values. As noted in the text, the results of the evaluation of the individual limits show that the interactions among the component parameters under multiple changes to the upper and lower limits would be unlikely to have a large impact on the range and shape of the distribution of *ChHR*.

The caption of each table lists the lower and upper limits of the default parameterization of the uniform distribution of the component parameter being analyzed. The first row of each table shows the quintile values of *ChHR* under the default parameterization of all five component distributions. The next four rows show the quintile values of *ChHR* when the lower or upper limit of the uniform distribution of the component parameter is changed from the default value to the value indicated in the first column. For example, the third row of Table A.1 shows the change in *ChHR* when the lower limit on the uniform distribution of the Sockeye Salmon harvest rate is set to 0.50 instead of the default 0.58, and the default upper limit of 0.66 is retained together with the default lower and upper limits of the remaining four independent parameters.

Table A.1 shows results of reducing the lower limit on *SHR* from the default value of 0.58 to 0.50 and 0.40 (14% and 31%, respectively), and increasing the upper limit from the default 0.66 to 0.75 and 0.85 (14% and 29%, respectively). The reduced limits have a negligible impact on the maximum value

TABLE A.1. Results of the sensitivity analysis from changes made to the lower and upper limits of the total annual harvest rate on the Sockeye Salmon run (*SHR*) from the default uniform distribution (0.58, 0.66).

SHR parameter	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
Default	0.325	0.403	0.431	0.457	0.485	0.574
			Low			
0.4	0.253	0.348	0.379	0.408	0.445	0.574
0.5	0.295	0.381	0.409	0.434	0.464	0.574
			High			
0.75	0.330	0.422	0.452	0.481	0.514	0.635
0.85	0.328	0.439	0.475	0.508	0.551	0.699

TABLE A.2. Results of the sensitivity analysis from changes made to the lower and upper limits of the total annual harvest rate on the Coho Salmon run (*CoHR*) from the default uniform distribution (0.45, 0.60).

CoHR parameter	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
Default	0.325	0.403	0.431	0.457	0.485	0.574
			Low			
0.25	0.288	0.379	0.409	0.435	0.465	0.574
0.35	0.309	0.392	0.420	0.446	0.475	0.572
			High			
0.75	0.327	0.417	0.447	0.473	0.503	0.616
0.90	0.328	0.430	0.462	0.490	0.523	0.653

TABLE A.3. Results of the sensitivity analysis from changes made to the lower and upper limits of the proportion of the total Chum Salmon run that encountered the Sockeye Salmon fishery (*ChRS*) from the default uniform distribution (0.67, 0.75).

ChRS parameter	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
Default	0.325	0.403	0.431	0.457	0.485	0.574
			Low			
0.50	0.315	0.400	0.425	0.449	0.476	0.572
0.60	0.323	0.402	0.429	0.454	0.481	0.573
			High			
0.85	0.329	0.405	0.433	0.461	0.491	0.581
0.95	0.328	0.405	0.436	0.465	0.497	0.587

TABLE A.4. Results of the sensitivity analysis from changes made to the lower and upper limits of the proportion of the annual Sockeye Salmon harvest rate to which Chum Salmon were vulnerable (*SHCh*) from the default uniform distribution (0.60, 0.90).

SHCh parameter	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
Default	0.325	0.403	0.431	0.457	0.485	0.574
			Low			
0.40	0.247	0.334	0.378	0.422	0.466	0.572
0.50	0.287	0.369	0.404	0.440	0.475	0.574
			High			
0.70	0.325	0.380	0.394	0.406	0.420	0.484
0.80	0.326	0.393	0.413	0.431	0.451	0.527

TABLE A.5. Results of the sensitivity analysis from changes made to the lower and upper limits of the proportion of the total harvest rate on the post–Sockeye Salmon season Coho Salmon run to which the overlapping proportion of the Chum Salmon run were vulnerable (*CoHCh*) from the default uniform distribution (0.60, 0.90).

CoHCh parameter	Minimum	20th percentile	40th percentile	60th percentile	80th percentile	Maximum
Default	0.325	0.403	0.431	0.457	0.485	0.574
			Low			
0.40	0.296	0.386	0.415	0.442	0.471	0.575
0.50	0.315	0.395	0.423	0.450	0.478	0.576
			High			
0.70	0.327	0.389	0.415	0.442	0.469	0.546
0.80	0.327	0.396	0.423	0.449	0.476	0.560

of the posterior of *ChHR*, and the reduction to 0.40 produces a negligible increase in the range of the central 20% of the distribution (from [0.431, 0.457] to [0.379, 0.408]). The range of the entire distribution is increased from [0.325, 0.574] to [0.253, 0.574] for the 31% reduction in the lower limit. Any such reduction in the lower limit on *SHR* would, of course, increase the upper limit of the posterior distribution of the terminal run.

Increasing the upper limit of the uniform distribution on *SHR* from the default value of 0.66 (the maximum harvest rate estimated by Ricker 1975, which was substantiated by Wood 2008) for Skeena River Sockeye Salmon throughout the period of record) to 0.75 and 0.85 (14% and 29%, respectively) has a negligible effect on the minimum value of *ChHR* but a noticeable and biologically significant effect on the maximum value. For example, increasing the upper limit to 0.75 increases the maximum value of *ChHR* to 0.635 and increasing it to 0.85 increases the maximum value to 0.70, which would produce a reduction in the lower tail of the posterior distribution of the Chum Salmon terminal run size, lowering the minimum run size from 268,000 to 220,000 for the 1916–1919 geometric mean catch of 154,000 and from 355,000 to 291,000 for the 1919 catch of 204,000. The effect of either increase on the central 20% of the distribution of *ChHR* is much less dramatic. For example, increasing the upper limit to 0.85 increases the central 20th percentile range from [0.431, 0.457] to [0.475, 0.508].

The results of similar changes in the lower and upper limits of the component prior for the Coho Salmon harvest rate (*CoHR*) are similar but smaller than those for *SHR* (Table A.2). Increasing the upper limit from the default of 0.60 to 0.75 increases the maximum value of *ChHR* from 0.574 to 0.616, which has only a small impact on the central 20% of the distribution, increasing the range from [0.431, 0.457] to [0.447, 0.473]. This would produce a small reduction in the posterior of the terminal run size. Increasing the upper limit on *CoHR* to 0.90 increases the maximum of *ChHR* to 0.653 and the central 20% to [0.462, 0.490]. This would produce a further modest reduction in the posterior of the run size.

The changes to *ChHR* resulting from alterations of similar magnitudes to the limits of the remaining three independent component priors are noticeably smaller (Tables A.3–A.5). Because the upper limits of both *SHCh* and *CoHCh* (the proportions of the total harvest rates on Sockeye Salmon and Coho Salmon to which Chum Salmon were vulnerable) in the default parameterization were very large (i.e., 0.90), only reductions of 0.10 and 0.20 in the upper limit were evaluated and these only contribute to lowering the *ChHR* upper limit. Overall, the changes in the upper and lower limits shown in Tables A.3–A.5 produced negligible changes in the magnitude and range of the central 20% of the distribution of *ChHR*. Notably, increasing the upper limit on the proportion of the Chum Salmon run encountering the Sockeye Salmon fishery from the default of 0.75 to 0.95 (Table A.3) increases the maximum value of *ChHR* to 0.587 from 0.574 and produces an even smaller increase in the location and magnitude of the central 20%, to [0.436, 0.465] from [0.431, 0.457]. All of the other alterations of the lower limits, of course, serve to further reduce the values of *ChHR* across the entire distribution, which would result in increases of the posterior distribution of the terminal Chum Salmon run size.

APPENDIX REFERENCES

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin 1995. Bayesian data analysis. Chapman and Hall/CRC, Boca Raton, Florida.

Ricker, W. E., and H. D. Smith. 1975. A revised interpretation of the history of the Skeena River Sockeye Salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 32:1369–1381.

Wood, C. C. 2008. Managing biodiversity of Pacific salmon: lessons from the Skeena River Sockeye Salmon fishery in British Columbia. Pages 349–364 *in* J. L. Nielsen, J. J. Dodson, K. Friedland, T. R. Hamon, J. Musick, and E. Verspoor, editors. Reconciling fisheries with conservation: proceedings of the fourth world fisheries congress, volume 1. American Fisheries Society, Symposium 49, Bethesda, Maryland.