Estimating the Future Decline of Wild Coho Salmon Populations Resulting from Early Spawner Die-Offs in Urbanizing Watersheds of the Pacific Northwest, USA

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Original Research

ABSTRACT

Since the late 1990s, monitoring efforts evaluating the effectiveness of urban stream restoration projects in the greater metropolitan area of Seattle, Washington, USA, have detected high rates of premature mortality among adult coho salmon (*Oncorhynchus kisutch*) in restored spawning habitats. Affected animals display a consistent suite of symptoms (e.g., disorientation, lethargy, loss of equilibrium, gaping, fin splaying) that ultimately progresses to death on a timescale of a few hours. Annual rates of prespawn mortality observed over multiple years, across several drainages, have ranged from approximately 20% to 90% of the total fall run within a given watershed. Current weight-of-evidence suggests that coho prespawn mortality is caused by toxic urban stormwater runoff. To evaluate the potential consequences of current and future urbanization on wild coho salmon, we constructed life-history models to estimate the impacts of prespawn mortality on coho populations and metapopulations. At the low (20%) and high (90%) ends of the range of observed mortality, model results indicated the mean time to extinction of localized coho populations in 115 and 8 y, respectively. The presence of productive source populations (i.e., unaffected by prespawn mortality) within a metapopulation reduced local extinction risk. However, as more populations within a metapopulation become affected by spawner die-offs prior to spawning, the source population's productivity declined. These simple models demonstrate the potential for rapid losses from coho populations in urbanizing watersheds. Because the models do not account for possible impacts of toxic runoff to other coho life stages, they likely underestimate the cumulative impacts of nonpoint source pollution on wild populations. Integr Environ Assess Manag © 2011 SETAC

Keywords: Nonpoint source pollution Stormwater runoff Urbanization Population model Coho salmon

INTRODUCTION

The decline of Pacific salmon (*Oncorhynchus spp.*) in the Pacific Northwest has been attributed to many factors. These include the physical, biological, and chemical degradation of freshwater and estuarine habitats as well as fishing pressure, hatchery production, and hydropower operations (National Research Council 1996; Good et al. 2007). To reverse salmon declines due to loss or deterioration of freshwater habitat, many lowland urban streams have been the focus of active restoration efforts (Katz et al. 2007). These projects have generally included postproject monitoring to assess the effectiveness of the restoration effort in terms of habitat use by salmon spawners and their progeny. Beginning in the late 1990s, spawner surveys in streams within the greater Seattle, Washington, USA, metropolitan area discovered that adult coho salmon (*O. kisutch*) returning to spawn in small urban catchments were behaving abnormally. Affected animals were found gaping and swimming in circles at the surface of these creeks. The symptoms typically progressed to a loss of equilibrium and death within a few hours. In most cases, egg retention in dead females was nearly 100% (City of

Seattle 2007; McCarthy et al. 2008; Wild Fish Conservancy 2008).

This phenomenon has been referred to as coho prespawn mortality (PSM) (McCarthy et al. 2008; Wild Fish Conservancy 2008) and has now been documented in several lowland urban streams around Puget Sound, Washington. The discovery that returning coho salmon were dying in restored urban streams prompted the National Oceanic and Atmospheric Administration (NOAA Fisheries), the US Fish and Wildlife Service (USFWS), the City of Seattle (Seattle Public Utilities), the Wild Fish Conservancy, and others to expand and coordinate fall spawner surveys. In addition, a forensic investigation was initiated by NOAA Fisheries to determine possible causes of PSM (McCarthy et al. 2008; Wild Fish Conservancy 2008). Conventional water quality parameters (i.e., temperature, dissolved O_2, ammonia, pH) are favorable for salmon survival (City of Seattle 2007), and PSM-affected animals show no consistent signs of pathogen infection or disease (N.L. Scholz, personal observation). Therefore, the urban coho mortality phenomenon is dissimilar from other documented circumstances of adult salmon dying prematurely at the spawner life stage because of disease, predation, altered flows, inaccessible spawning habitat, and other nonchemical stressors (St-Hilaire et al. 2002; Kocan et al. 2004; Keefer et al. 2010).

All of the streams where coho prespawn mortality has been observed receive urban stormwater runoff in the fall when coho return to spawn. The severity of the fish kills correlates

with both fall patterns of rainfall (McCarthy et al. 2008) as well as with the amount of impervious surface within the drainage (B.E. Feist, personal communication). The weight of evidence to date therefore suggests that coho are dying from exposure to chemical pollutants in nonpoint source urban runoff. Urban stormwater contains a very diverse mix of contaminants (Eriksson et al. 2007), including metals (Tiefenthaler et al. 2008), polycyclic aromatic hydrocarbons (Stein et al. 2006), pesticides (Hoffman et al. 2000), and other chemicals. The precise agent, whether alone or as a component of a chemical mixture, that causes coho PSM has not yet been identified and is the focus of ongoing investigation.

The Pacific Northwest is currently undergoing substantial human population growth and development. By 2025, 1.4 million persons are expected to join the 4 million persons currently residing in the Puget Sound region (Puget Sound Action Team 2007). Similar growth patterns are projected for the Willamette Basin in Oregon, USA (Baker et al. 2004) and the lower Columbia River region. Much of the projected urban and residential growth will occur in watersheds that currently support both productive and at-risk wild coho populations. Streams in these systems serve as sentinels for anthropogenic impacts (Williamson et al. 2008). Coho populations belonging to the lower Columbia River evolutionarily significant unit (distinct population segment) were recently listed as threatened under the US Endangered Species Act (ESA). Puget Sound coho have declined from historical levels and are presently designated as a ''species of concern'' in the context of the ESA (for current designations, see http://www.nwr.noaa.gov/ESA-Salmon-Listings/Salmon-Populations/Coho/Index.cfm). The ongoing and future conversion of forested and agricultural lands for residential and commercial uses is likely to increase the loading of nonpoint source pollutants to lakes, rivers, and streams that have historically supported viable coho populations. This, in turn, is likely to expand the geographical range over which adult coho are affected by PSM.

In the present study, we used a modeling approach to forecast the potential impacts of increasing PSM on wild coho stocks. Our aim was to assess extinction risks for isolated populations and evaluate how these risks might be modified by straying between different populations within a larger metapopulation. This approach allowed us to relate effects on coho within an urbanizing catchment to the dynamics of a metapopulation across a larger watershed. The models were parameterized with empirical life history data for coho, and basic assumptions were used to produce modeled populations that were initially stable and viable. To simulate the effects of changes in land use and the intermittent nature of stormwater runoff, the severity of PSM was held steady, varied, or gradually increased over a timespan of a few decades. The results provide insights into how coho salmon populations may respond to complex and rapidly changing human land use activities throughout urbanizing areas of the Pacific Northwest.

METHODS

Projection matrices integrating age-specific survival and reproductive demographic rates were selected as the modeling environment for investigating effects of PSM on solitary coho populations and metapopulations. A metapopulation is a group of populations connected by migration or dispersal (a ''population of populations'') (Hanski and Gyllenburg 1993). Salmon dispersal takes the form of adults straying to spawn in habitats other than their stream of origin. This produces a series of genetic linkages between individual populations within a watershed or collection of watersheds. Projection matrix methods followed Caswell (2001) and were used to 1) calculate the transition matrix, 2) determine the intrinsic population growth rate (λ) and stable age distribution, and 3) conduct a sensitivity analysis. These analyses were performed for control (baseline; no PSM) and constant PSM scenarios outlined below using MATLAB (The Math Works, version 6.5). Model projections were run by year for 200 y and incorporate various levels of prespawn mortality. RAMAS® Metapop (Applied Biomathematics, version 5.0) was used for conducting the projections.

The modeled coho population assumes a 3-y lifespan for individual fish. Spawning occurs in late fall and early winter with fry emergence occurring from March to May. Fry rear for 14 to 18 months in freshwater before they smolt and then migrate to the ocean. They spend 16 to 20 months in the ocean before returning to freshwater streams to spawn. For the purpose of the model, vital rates for survival and reproduction were drawn from field data collected for wild coho populations as summarized by Knudsen et al. (2002). Adult upstream migration survival was 0.97 ($\pm$0.01). The average fecundity of each female was 4510 eggs with a standard deviation (SD) of 500. The male to female ratio was 1:1. Survival from spawning to emergence was 0.335 ($\pm$0.07). Survival from emergence to smolt was 0.0296 ($\pm$0.0029) and marine survival was 0.0505 ($\pm$0.01). All parameters followed a normal distribution (Knudsen et al. 2002).

The availability of food and freshwater rearing habitat are both known to influence the 1st-year survival rate in density-dependent salmon populations (DeAngelis et al. 1980; Bradford et al. 1997; Kareiva et al. 2000). Therefore, the models were constructed using 1st-year survival (S1) as the density-dependent factor. We assumed a ceiling density dependence that did not provide compensatory growth rates for low abundances. This was based on age 1 (1st-year) abundance with a carrying capacity of 2 900 000 individuals and a low SD of 2900 for each population. This produced an equilibrium spawning abundance of approximately 3300 age 3 adults. This value falls within the range of documented abundances for small catchments in the Puget Sound region (Weitkamp et al. 1995). Natural variability was incorporated by randomly selecting each vital rate value in the projection matrix for each year from a normal distribution within the reported means and SD (Knudson et al. 2002). Straying of individuals in and out of the modeled solitary populations was assumed to be equal, with zero net effect on population abundance and population fitness. Modeled initial conditions were calculated from the stable age distribution of the control transition matrix scaled to produce approximately 3300 age 3 adults annually. This resulted in a distribution of 2 199 120 1st year, 64 900 2nd year, and 3300 3rd year individuals. The transition elements and SD for the control coho model are provided in Table 1.

The direct impacts of PSM were incorporated in the model as a reduction in the percentage of female adults successfully spawning. It was assumed that mean survival rates for embryos, fry, and smolts were unaffected. Model outputs included adult abundance and time to local extinction (abundance <1 individual). The modeled scenarios simulated

Table 1. Matrix transition elements (SD) for S1, S2, and R3 for control conditions[a]

Transition element	Control matrix values	Sensitivity values	Sensitivity changes from PSM
S1	0.0296 (0.0029)	0.143	–
S2	0.0505 (0.01)	18.67	–
R3	732.8 (51.25)	0.0001	+

PSM = prespawn mortality; R3 = reproduction by 3rd-year adults; SD = standard deviation; S1 = 1st-year survival; S2 = 2nd-year survival.
[a]Sensitivity analysis on models incorporating PSM showed decreased sensitivity of λ to changes in survival (S1 and S2) and increased sensitivity to changes in reproduction (R3).

solitary coho populations impacted by PSM with different degrees of severity. Populations in the constant PSM scenarios experienced a steady rate of spawner die-off over the entire 50-y model projection at the PSM rates shown in Table 2. Another set of scenarios explored the consequences of gradually increasing the level of PSM to simulate a gradual urbanization of a watershed. This was modeled in 2 ways: 1) a relatively rapid increase in PSM (from 0% to 75% PSM over 20 y) and 2) a slower and less severe impact (from 0% to 25% PSM over 30 y). In both cases, changes in adult abundance and time to local extinction were predicted. The impact on population growth rate for each PSM scenario was calculated as the percent of the control intrinsic population growth rate. In addition, 200-y projections were run to determine mean time to extinction, minimum time to extinction, and SD. All

projection scenarios were repeated 1000 times to incorporate the variation reported in the literature.

To assess the relative impacts of prespawn mortality on populations connected by straying (dispersal), we constructed a metapopulation model in RAMAS Metapop consisting of 5 linked populations. The model simulated individual populations within a watershed (Figure 1), with each connected to the others by a low and consistent rate of spawner straying. We assumed that 5% of the age 3 individuals in each population would stray in equal numbers to the other 4 populations within the metapopulation, resulting in 1.25% of spawners in a given population moving to each of the other 4 populations. Mortality rates for straying spawners matched the PSM rate for the destination population. The straying rates and their distribution across populations reflect documented straying observed for coho in coastal watersheds of the Pacific Northwest (Quinn 1993; VanderHaegen and Doty 1995). Demographic rates, carrying capacities, and initial conditions for all 5 populations were assumed to be equal and were incorporated into the individual population matrix model as described above. The populations in the metapopulation are defined based on their spawning stream location and carrying capacity. Therefore, changes to survival or reproduction, such as PSM, resulting from conditions in a particular stream habitat become intrinsic to the population demographics.

The metapopulation modeling approach was used to forecast the impacts of increasing urbanization (i.e., increasing PSM) on coho salmon in large watersheds and to estimate changes in the abundance of the linked individual populations as well as the larger metapopulation over time. Constant PSM

Table 2. Isolated populations affected by constant or gradually increasing levels of PSM[a]

PSM (%)	Percent of 1000 model runs extinct within 50 y	Average years to extinction (SD)	Minimum years to extinction	Change in λ (%)
0	0	NO	NO	0
10	0	>200	135	−3.4
20	0	135 (30)	65	−7.2
25	1	94 (21)	50	−9.1
30	6	70 (13)	41	−11.2
40	74	44 (7)	26	−15.6
50	100	30 (5)	17	−20.6
60	100	22 (3)	15	−26.3
70	100	16 (2)	10	−33.0
75	100	14 (2)	8	−37.0
80	100	12 (2)	7	−41.5
90	100	8 (2)	5	−53.6
0–25 over 30 y	0	115 (21)	68	NA
0–75 over 20 y	100	30 (2)	24	NA

NO = no extinction deserved; NA = not applicable because the population growth rate ranges over the projection; PSM = prespawn mortality; SD = standard deviation.
[a]The values reflect the incorporation of natural variability in survival rates and fecundity as well as density dependence during 1st-year survival.
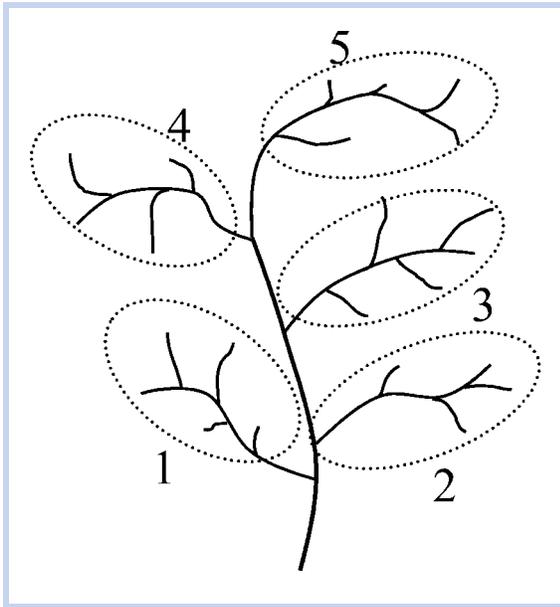
Figure 1. Ovals in the cartoon represent locations of populations in a watershed based on their spawning grounds. Straying between the populations links them into a metapopulation.

levels of 25%, 50%, 75%, and 100% were applied to 1, 2, 3, and 4 of the 5 populations to simulate the gradual and recurrent prespawn die-offs across a watershed that supported an initially viable coho metapopulation. The importance of stray rate for model outcomes was evaluated by comparing results from stray rates of 3%, 5%, and 10%, levels that have been observed for wild coho (Quinn 1993). An additional set of model scenarios investigated how the proportion of the metapopulation impacted by PSM may influence both the population and metapopulation abundance over time. These scenarios also let us assess whether the distribution of the affected proportion across populations affected the responses. The proportion was calculated as the relative equilibrium abundance for each population at its carrying capacity. The metapopulation models discussed above have populations with equal carrying capacities and a population ratio of 1:1:1:1:1. The impacts of PSM to 20%, 40%, 60%, and 80% of the metapopulation were represented as effects on 1, 2, 3, and 4 of the 5 populations, respectively. To determine whether the responses to PSM were influenced by the distribution of the population carrying capacities in the metapopulation, we changed the carrying capacities of the 5 populations to a ratio of 4:2:2:1:1. The total metapopulation abundance at equilibrium was maintained. This allowed us to investigate whether impacts on 40% of the metapopulation consisting of 1 population produced the same results as when 40% was made up of 2 or 3 populations. Simulations for 25% and 75% PSM were run for all possible population combinations to simulate impacts on 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, and 90% of the metapopulation. All of the metapopulation models were run for 50 y and repeated 500 times to integrate natural variability as described above. The output was the adult abundance for each population at year 50. Further analysis was conducted with other carrying capacity ratios with similar results to the 2 sets presented here (data not shown).

RESULTS

The modeled dynamics for solitary coho populations in the absence of PSM (control) produced an intrinsic population growth rate (λ) of 1.03. This resulted in a slow increase in population abundance until the carrying capacity defined by the model (approximately 3300 spawners) was reached. Control projections incorporating natural variability resulted in a range of abundances around an equilibrium with no populations going extinct (Table 2).

When realistic rates of PSM were incorporated into the model, the population growth rate declined in a nonlinear manner. This is indicated as a reduced population growth rate (as the percent of control) in Table 2. Sensitivity analysis showed that PSM reduced the extent to which changes in 1st- and 2nd-year survival contribute to changes in λ. PSM increased the relative importance of reproductive output to changes in λ (Table 1). The demographic rates of this coho salmon model made the population particularly sensitive to impacts on adult reproduction (the stage affected by PSM). Prespawn mortality also altered the age distribution of the population by increasing the proportion of 2nd- and 3rd-year individuals (results not shown).

Solitary and initially viable populations influenced continuously by PSM at a rate of 20% went locally extinct within 135 y. At higher PSM rates of 60%, 70%, 80%, and 90%, initially viable populations declined rapidly (Figure 2A shows output for 60% and 80%) with mean times to extinction of 22, 16, 12, and 8 y, respectively (Figure 2B and Table 2).

To simulate the population-scale impacts of PSM in response to varying rates of urbanization within a watershed, rates of PSM were gradually increased over time. A scenario that simulated rapid urbanization incorporated an increase in PSM from 0% to 75% over 20 y. A second scenario represented a more moderate rate of urban development with a less severe impact (0%–25% PSM) over a longer time interval (30 y; Figure 3). With all initial conditions equal, coho populations predictably persisted longer when the rate of PSM increased more slowly. When PSM rates were increased to 75% over 20 y, the model output predicted the extinction of a solitary coho population in 30 y. This was extended to 115 y for a population experiencing a lower rate of PSM (25%) over 30 y (Table 2).

Connecting 5 individual coho model populations through straying created a metapopulation and afforded individual populations some degree of protection from localized extinction when at least 1 unaffected population served as a source of straying emigrants to the other populations. Whereas constant rates of PSM drove solitary coho populations to extinction, the larger metapopulation and the populations within it declined but did not go extinct when only 1 to 3 of the 5 component populations were impacted by PSM at these same rates. Transient, localized extinctions of the affected component populations were observed when 4 of 5 populations experienced $\geq 20\%$ PSM. When the rate of PSM across 4 populations was 25% and the 5th experienced 10% PSM, approximately half (52%) of the model outputs resulted in metapopulation-wide extinctions. As expected, gradually increasing the number of populations experiencing a given level of PSM produced a decreasing equilibrium adult abundance in both the affected and unaffected populations (Figure 4 and Table 3). These results show that individuals straying from source populations to PSM-affected populations within a metapopulation can prevent the extinction of
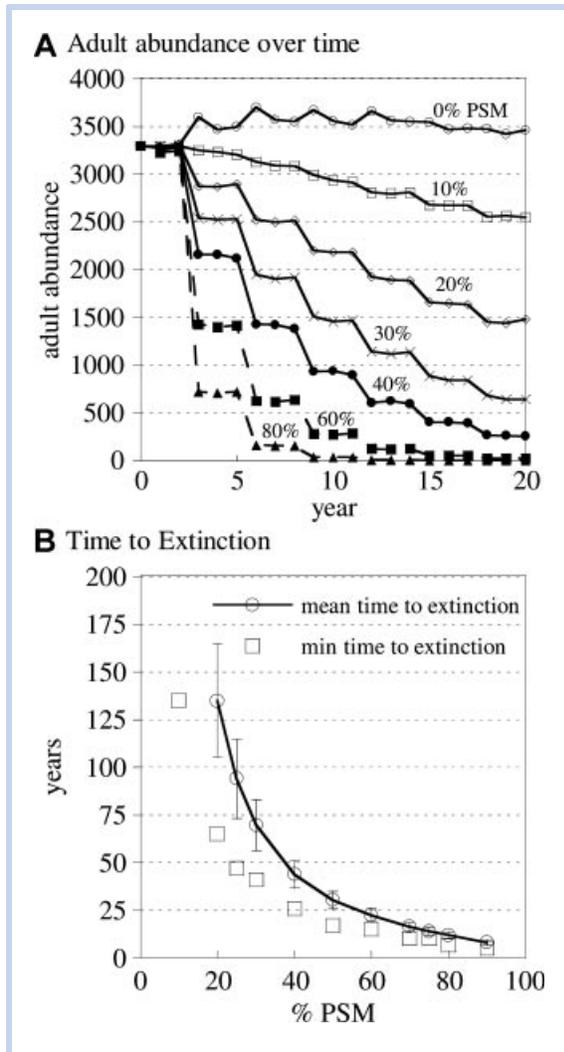
Figure 2. (A) Mean coho adult abundance for solitary populations experiencing density dependence, natural variability in survival and fecundity, and constant rates of prespawn mortality (PSM). (B) Estimated mean time to localized extinction for isolated coho populations experiencing various levels of PSM using density-dependent models with no straying. Mean time to extinction (○), standard deviation, and minimum time to extinction (−) for 1000 repetitions.

the latter (as predicted by the model for solitary populations). For example, a solitary population experiencing 75% PSM can be expected to decline to extinction in an average of 14 y. However, if the same affected population is connected to a source population by straying, the model predicted a significant decline (to <6% of control) but no extinction over the 50-y run of the model using a 5% stray rate (Table 3).

When individual populations within the metapopulation became sink populations, with more adult spawners straying in than out, a net (indirect) effect was a reduction in the abundance of the remaining source populations. The unaffected population (Population 5) declined due to a net loss of strays as other populations were increasingly impacted by PSM (Figure 4). In this example, the decrease in source population abundance (model Population 5) over time due to 75% PSM in 1, 2, 3, and 4 of the other populations resulted in equilibrium abundance reductions to 94%, 87%, 80%, and 71% of control abundances, respectively (Figure 4 and Table 3). At the scale of the entire metapopulation, even
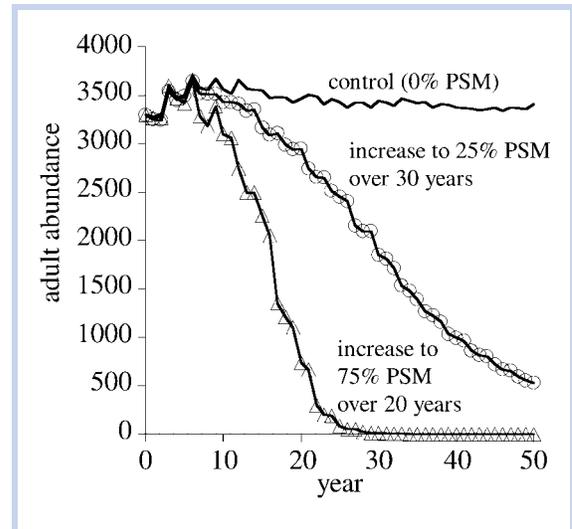

Figure 3. Adult abundance for isolated coho populations exposed to gradually increasing levels of prespawn mortality (PSM). Slow increases to 25% PSM over 30 y (○) and a rapid change to 75% PSM over 20 y (Δ).

low rates of PSM affecting a subset of populations produced large reductions in equilibrium abundance due to these source-sink dynamics (Table 3).

The proportion of the metapopulation experiencing PSM (i.e., the number of sinks) was a stronger driver for loss of potential productivity than the relative rate of PSM. For example, a single population experiencing 50% PSM reduced the overall metapopulation abundance by 23%, whereas 2 populations experiencing PSM at half the rate (25%) reduced the metapopulation abundance by 38% (Table 3). Similarly, the proportion of the metapopulation experiencing PSM was a more important determinant of the final metapopulation abundance than the rate of PSM (Figure 5). This was shown by changing the relative proportions of the carrying capacity and initial abundances of the 5 populations from a ratio of 1:1:1:1:1 to a ratio of 4:2:2:1:1. The modeled rates of PSM
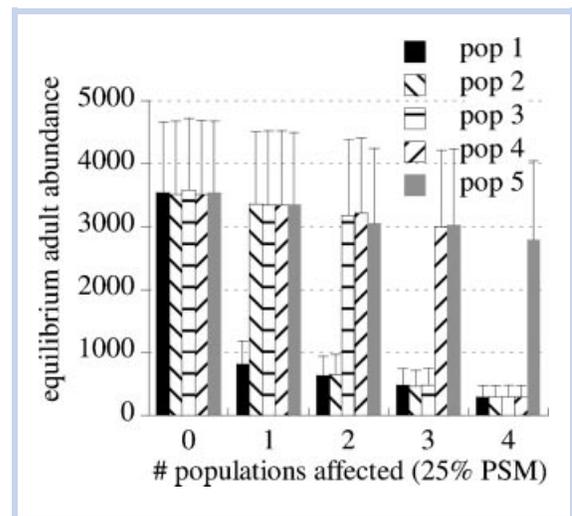

Figure 4. Equilibrium adult abundance of each population (pop) within the metapopulation after constant 25% prespawn mortality (PSM) affecting 0 to 4 populations for 50 y. Coho metapopulation models incorporate variable annual survival and fecundity, 1st-year density dependence, and 5% straying within the metapopulation.

Table 3. Impacts of PSM showing direct and indirect effects on each of the 5 populations and the whole metapopulation as the percentage of the control abundances (SD)[a]

Scenario	Control abundance (%)		
	Impacted populations	Unimpacted populations	Metapopulation
1 population affected (20% of metapopulation)			
25% PSM	23 (10)	94 (34)	82 (15)
50% PSM	9 (3)	94 (34)	78 (14)
75% PSM	6 (2)	94 (32)	76 (14)
Range 0%–25% PSM	52 (28)	98 (33)	89 (16)
Range 25%–75% PSM	11 (3)	93 (33)	78 (14)
Range 50%–100% PSM	6 (2)	93 (34)	76 (14)
2 populations affected (40% of metapopulation)			
25% PSM	18 (8)	89 (34)	62 (13)
50% PSM	7 (3)	88 (34)	56 (13)
75% PSM	4 (2)	87 (35)	55 (13)
Range 0%–25% PSM	48 (27)	93 (33)	76 (15)
Range 25%–75% PSM	8 (3)	89 (35)	57 (13)
Range 50%–100% PSM	4 (2)	87 (34)	54 (13)
3 populations affected (60% of metapopulation)			
25% PSM	13 (7)	85 (34)	42 (12)
50% PSM	4 (2)	80 (35)	35 (11)
75% PSM	3 (1)	80 (35)	34 (11)
Range 0%–25% PSM	44 (27)	92 (33)	64 (14)
Range 25%–75% PSM	5 (2)	80 (36)	35 (12)
Range 50%–100% PSM	3 (1)	80 (35)	34 (12)
4 populations affected (80% of metapopulation)			
25% PSM	8 (5)	79 (37)	23 (9)
50% PSM	2 (1)	71 (37)	17 (8)
75% PSM	1 (1)	71 (37)	15 (8)
Range 0%–25% PSM	39 (25)	88 (34)	49 (14)
Range 25%–75% PSM	2 (1)	73 (37)	16 (10)
Range 50%–100% PSM	1 (1)	59 (39)	16 (9)

PSM = prespawn mortality; SD = standard deviation.
[a]Each scenario was run for 50 y and repeated 1000 times. The percentage of initial metapopulation carrying capacity that is impacted is indicated at the top of each section.

were then adjusted to 25% and 75%. This relatively large difference in PSM rate produced only slight differences in the relationship between the proportion impacted and metapopulation abundance. The SD about the mean metapopulation abundances for the 25% and 75% PSM overlapped (suggesting no significant difference) and the linear regressions for abundances at the 2 rates of PSM had similar slopes

(−97.167 and −104.37 for 25% and 75%, respectively) (Figure 5).

The influence of stray rates on the responsiveness of a coho metapopulation to PSM was investigated by varying straying between populations (3%, 5%, and 10%) while holding PSM constant at 75%. At lower rates of straying, PSM-affected populations were more isolated and therefore more likely to
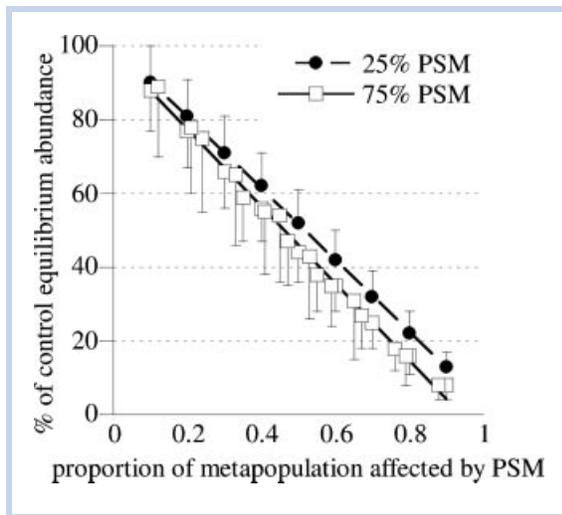
Figure 5. The influence of the level of prespawn mortality (PSM; 25% and 75%) relative to the proportion of the metapopulation that was affected by PSM. The percent of control metapopulation equilibrium abundance after 50 y experiencing 25% (●) or 75% (□) PSM. The *x* axis shows the proportion of the metapopulation carrying capacity that is exposed to PSM.

experience localized extinction when 3 or more linked populations were affected. A higher stray rate provided more emigrants from source populations and maintained PSM-affected populations at higher abundances (Figure 6). However, the larger migrant exchange connecting the populations came at a cost in terms of reducing the total metapopulation abundance.

DISCUSSION

The coho prespawn mortality models developed for this study predicted rapid declines in adult abundances for isolated populations affected by PSM. Importantly, local population extinctions were predicted across the range of PSM rates that have been recently documented in Puget Sound urban streams (20%–90%) (McCarthy et al. 2008; Wild Fish Conservancy 2008; City of Seattle 2007). Interannual variation in spawner die-offs may slightly delay predicted population declines and extinction. Nevertheless, models simulating slow, gradual increases in PSM predicted significant declines in the abundance of solitary wild coho populations. Overall, our analysis shows that PSM could pose an extinction risk for local coho populations on a timescale of a few years to a few decades.

Under natural conditions, up to 10% of adult coho may stray to nearby populations each spawning season. When straying was integrated into the metapopulation models, PSM-affected populations within the larger metapopulation were less likely to go extinct. As expected, migrant strays from unaffected populations provided directly impacted populations a degree of protection from extinction. Accordingly, rates of PSM that drove isolated populations extinct had less impact on populations linked by straying. However, by creating sink populations that drain nearby source populations, PSM has the potential to reduce local abundance of coho in habitats of a watershed that are unaffected by development or polluted runoff (Figures 4 to 6). We therefore expect straying to have 2 important consequences for wild coho metapopulations affected by PSM. First,
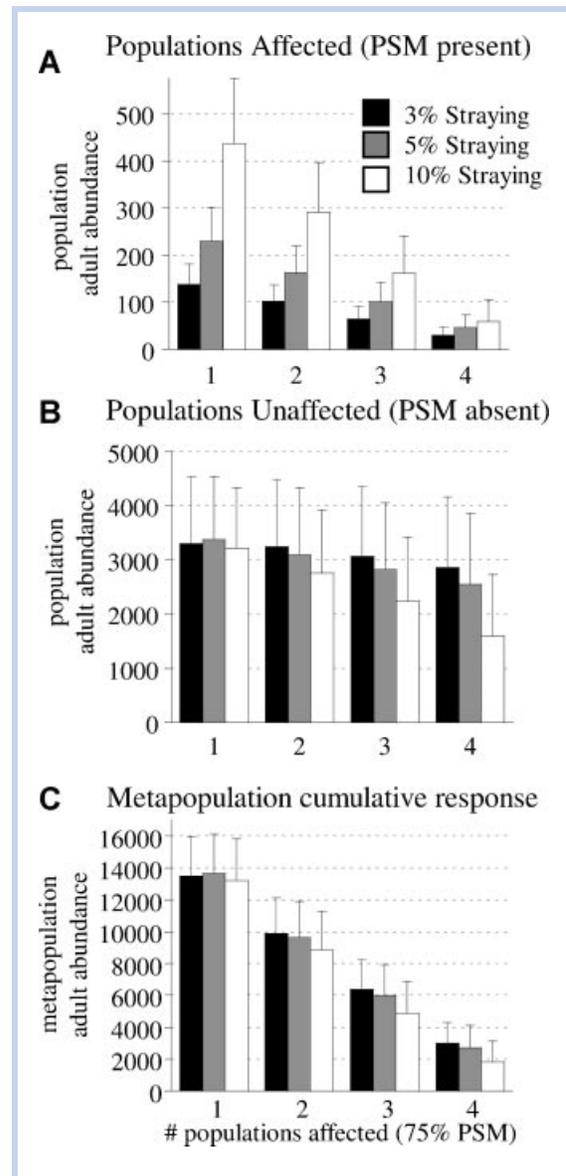

Figure 6. Adult abundances (mean and standard deviation [SD]) for (**A**) populations experiencing 75% prespawn mortality (PSM), (**B**) unimpacted populations, and (**C**) metapopulation for 1 to 4 populations affected by PSM that exhibit 3%, 5%, and 10% straying rates. One impacted and 1 unimpacted population is depicted for each scenario because the remaining populations have similar means to their respective counterparts. SD subtracted from the mean was not shown for image clarity.

straying will provide a buffer against local extinction in urbanizing stream catchments. Second, the source–sink dynamics of the metapopulation will draw down coho spawner abundances in geographic areas where freshwater habitat conditions are favorable.

The number and relative size of PSM-affected populations within a metapopulation was a more important determinant of declining metapopulation abundance than the rate of PSM. For example, a relatively large shift in PSM rate (25% to 75%; Table 3 and Figure 5) produced only a slight reduction in the overall number of spawners in the metapopulation. The relative size of individual populations within a metapopulation is determined by local carrying capacity (i.e., availability of spawning and rearing habitat). Therefore, PSM impacts on

Puget Sound coho will be more significant if the occurrence of PSM is distributed across multiple linked populations, or if the affected populations occupy habitats that would otherwise be highly productive for the metapopulation. Although our current understanding of adult spawner mortality is drawn from streams where die-off rates are high (up to 90%), this finding points to the ongoing, incremental, and distributed development of Puget Sound lowland areas (Alberti et al. 2007) as a potentially important driver for future coho metapopulation declines.

The relative impacts of adult spawner die-offs on source and sink populations were strongly influenced by different rates of straying. With increased straying, the supplementary spawners from source populations effectively masked the local impacts of polluted terrestrial runoff. By delaying local extinctions, straying has the potential to make it more difficult to accurately assess the location-specific impacts of PSM at a population scale. For example, it may be difficult during the course of conventional census activities within an urbanizing watershed to detect the initial impacts of PSM on local coho abundance. Conversely, the indirect drains of PSM on source populations may increase their vulnerability to emerging stressors that are unrelated to urban growth and development. These include, for example, future climate change and freshwater quantity for river systems in the Pacific Northwest (Mote et al. 2005; Battin et al. 2007; Williamson et al. 2008).

Our model results suggest that the Seattle-area urban streams that have been surveyed for spawners over the last decade are all sinks. Self-sustaining wild coho runs have largely disappeared from the streams where coho PSM has been documented to date. PSM-affected wild coho have been observed in urban streams (McCarthy et al. 2008; Wild Fish Conservancy 2008). However, most of the adults that return to spawn in these drainages are products of artificial propagation (as identified by coded wire tags and the absence of adipose fins). Regional hatchery operations have therefore served as ''source'' populations for these restored urban streams. Daily spawner surveys for PSM in streams that traverse current urban growth boundaries have not been conducted. Therefore, at present, we do not have an accurate understanding of the source-sink dynamics for wild Puget Sound coho that are likely to be increasingly impacted by PSM over the timescales considered in this study. More work in this area is needed.

Given our finding that even moderate rates of spawner mortality (approximately 40%) can lead to rapid declines in the local abundance of adults in only a few years, it may be difficult to restore coho to Pacific Northwest streams where urban runoff and associated PSM are likely to occur. This has several implications for future stream restoration projects, particularly in the vicinity of regional urban growth boundaries. First, an increase in natural coho production should not necessarily be an expected outcome for projects in highly urbanized watersheds, particularly if these projects do not specifically address water quality and nonpoint source runoff. Second, reconnecting urban stream segments (e.g., via culvert removal) can have the unintended consequence of drawing coho spawners into contact with urban runoff (Jackson and Pringle 2010). If PSM ensues, this would have the net effect of transforming the restored habitat into a sink habitat for coho (an attractive nuisance habitat; Simenstad et al. 2005). Third, consideration should be given to PSM before new

restoration projects are implemented in urbanizing areas. This might include, for example, preproject surveys for local spawner mortality. Baseline information on PSM will help ensure the physical objectives of stream habitat restoration (Bernhardt and Palmer 2007; Katz et al. 2007) are not undermined by degraded water quality.

Incorporating population source-sink dynamics into management decisions could also help identify appropriate areas in a watershed that should be protected from urban sprawl. The protected habitats could support source populations that could then maintain PSM-affected populations whereas remediation efforts may be established for those runs. Protected upstream habitat areas within urbanizing watersheds may still see losses at the metapopulation level because PSM-affected populations will drive the unaffected populations and metapopulation downward, especially as the impacted proportion of the metapopulation increases. Protecting habitat that supports large proportions of the metapopulation's spawners will be more effective than protecting headwaters alone.

In the larger picture of cumulative toxic stormwater impacts on wild coho populations, our modeled predictions only incorporate losses at the spawner stage, and do not aggregate impacts across the entire coho salmon life cycle. As noted earlier, coho spend more than 1 y rearing in freshwater environments, including small streams that are receiving waters for urban runoff containing metals, pesticides, petroleum hydrocarbons, plasticizers, and other nonpoint source pollutants. Low-level exposures to these contaminants can adversely affect juvenile salmon physiology and behavior (Sandahl et al. 2005, 2007), and they also pose potentially important but poorly understood threats to stream food webs that support coho growth and survival (Macneale et al. 2010). Given this potential for toxic-driven losses at other life stages, our model outputs here are likely underestimates of the overall population-scale effects of toxic runoff in urban and urbanizing watersheds. Future modeling efforts should therefore be expanded to capture potential toxicity to coho embryos, alevins, parr, and smolts.

CONCLUSIONS

In conclusion, our current results show that degraded stormwater quality has the potential to drive local coho populations to extinction on a timeline of a few years to a few decades based on the observed, real-world range of spawner mortalities in Puget Sound urban streams. Moreover, focal coho spawner losses in developed catchments can constrain population abundances in undeveloped regions of river basins through source–sink metapopulation dynamics. Spawner mortality rates are closely associated with land cover attributes within catchments (impervious area, road density, and so forth; B.E. Feist, personal communication). It will therefore be possible in future studies to estimate water quality driven declines in coho abundances for specific population segments that spawn along discrete gradients of urbanization in western North America (e.g., the threatened Lower Columbia River ESU). This, in turn, will inform current efforts to conserve and recover ESUs in large river basins where human population growth and development represent persistent, ecosystem-scale forcing pressures on freshwater habitat quality.

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