

HABITAT SATURATION DRIVES THRESHOLDS IN STREAM SUBSIDIES

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Abstract. Understanding how abundance regulates the effects of organisms on their ecosystems remains a critical goal of ecology, especially for understanding inter-ecosystem transfers of energy and nutrients. Here we examined how territoriality and nest-digging by anadromous salmon mediate trophic subsidies to stream fishes. Salmon eggs become available for consumption primarily by the digging of salmon that superimpose their nests on previous nests. An individual-based model of spawning salmon predicted that territoriality and habitat saturation produce a nonlinear effect of salmon density on numbers of available eggs to resident predators. Field studies in Alaskan streams found that higher densities of salmon produce disproportionately more eggs in stream drift and in diets of resident fishes (Arctic grayling and rainbow trout). Bioenergetics model simulations indicated that these subsidies produce substantially enhanced growth rates of trout. These results demonstrate that small changes in salmon abundance can drive large changes in subsidies to stream food webs. Thus, the ecological consequences of population declines of keystone species, such as salmon, will be exacerbated when behavior generates nonlinear impacts.

Key words: density dependence; ecosystem-based management; eggs; fisheries; food web; foraging; functional extinction; grayling; marine-derived nutrients; salmon; superimposition; trout.

INTRODUCTION

A few dominant species often control communities through a combination of high population densities and large per capita impacts (Paine 1966, 1992, Power et al. 1996). However, in some cases, behavioral changes in organisms across population densities can lead to nonlinearities in interaction strength; per capita impacts may decrease at low populations (Abrams 2001, Soulé et al. 2005). Understanding these nonlinear dependencies is critical for strongly interacting species (e.g., keystone), as small changes in abundance can cause widespread ecological change (Soulé et al. 2005). Given the prevalence of population declines of numerous organisms (e.g., Thomas et al. 2004), there is concern that nonlinearities may lead to functional extinction prior to species extinction (Soulé et al. 2005). For example, territoriality by flying foxes drives nonlinear relationships between their abundance and role as seed dispersers; they only disperse seeds large distances when fruit trees are saturated with other flying foxes (McConkey and Drake 2006).

Anadromous, semelparous Pacific salmon (*Oncorhynchus* spp.) have been termed a keystone species in Pacific coastal ecosystems (Willson and Halupka 1995). After achieving >99% of their mass while growing large in the ocean (Quinn 2005), salmon return to spawn and die in coastal freshwaters, subsidizing (sensu Polis et al. 1997)

these food webs (Schindler et al. 2003). For example, nutrients from salmon bodies can stimulate primary production (e.g., Johnston et al. 2004). In addition, salmon tissues (eggs and carcasses) are consumed by a variety of organisms (Willson and Halupka 1995). Salmon eggs, also derived from oceanic productivity, are an especially important food subsidy for stream fishes (e.g., Bilby et al. 1998, Scheuerell et al. 2007), being rich in nutrients and energy (Gende et al. 2004). However, it is unknown how variation in salmon abundance translates into variation in trophic subsidies and subsequent consumption by stream fishes.

Salmon behavior may regulate the availability of their eggs to stream-dwelling fishes, driving nonlinear relationships between spawner density and egg subsidies. Female salmon dig nests in streams, rivers, and lake beaches where they bury their eggs, protecting them from most predators (Quinn 2005). A small proportion of eggs are unsuccessfully buried, spilling out of the nest during spawning (Briggs 1953). Suitable spawning habitat can be a limiting resource (Semenchenko 1988), producing substantial competition for spawning space. Females that superimpose their nests on top of previous nests dig up previously buried eggs, driving negative density dependence in progeny survival (Semenchenko 1988, Fukushima et al. 1998, Essington et al. 2000). However, superimposition is regulated by territorial defense by females (e.g., van den Bergh and Gross 1989). Superimposition can be more frequent at higher spawner densities; salmon are more likely to dig nests on top of previous nests when few suitable spawning sites are available (McNeil 1967, Fukushima et al. 1998, Essington et al. 2000).

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We investigated the relationship between adult salmon abundance and egg subsidies to resident fishes in streams. Specifically, we investigated whether high salmon densities produce disproportionately greater subsidies to aquatic food webs. We used an individual-based model of salmon spawning and comparative field studies of egg subsidies to demonstrate that salmon-spawning behavior generates nonlinear relationships between salmon density and egg subsidies. Our results demonstrate that small changes in salmon populations can have large impacts on stream fishes, suggesting conflicts between commercial fisheries for salmon and recreational fisheries for stream fishes.

METHODS

This study was based on streams in the Wood River system of southwestern Alaska. Over the last 50 years, an average of 1.1 million sockeye salmon (*O. nerka*) have spawned in the streams, rivers, and beaches of this system every year after an additional 1.7 million sockeye are caught in fisheries (Baker et al. 2006). Arctic grayling (*Thymallus arcticus*) and rainbow trout (*Oncorhynchus mykiss*) are the common stream fishes. For example, in Hidden Lake Creek, these two species comprise >95% of the resident fish biomass (D. E. Schindler, unpublished data).

Model

In the most general sense, the salmon-spawning system is simply a case of a finite number of sites available for use; once sites are filled, individuals are forced to use occupied sites. If salmon completely avoid displacing previous occupants until necessary, we would predict a threshold relationship between salmon-spawning density and egg subsidies, with high per capita egg subsidies only occurring past a density threshold where all sites are filled. Two main factors could smooth this relationship. Female salmon are not always able to successfully defend their nest, leading to occasional superimposition before all sites are filled. In addition, if new individuals enter the stream after early spawning individuals have died, reuse (superimposition) may occur regardless of territoriality. Thus, as the ratio of female lifespan to run duration decreases, superimposition will occur at lower densities.

We used a simple individual-based model (IBM) of salmon spawning to explore the relationship between salmon density and egg subsidies. This model simulates the seasonal progression of female salmon spawning, incorporating nest choice, egg-laying, territoriality, and the resultant density of dislodged eggs. The model incorporates two sources of dislodged eggs. First, egg spillage is the low level of eggs that are unsuccessfully buried during the normal spawning process. Second, egg superimposition occurs when a female spawns on top of a previous nest, dislodging the prior spawners' eggs. Both of these mechanisms can render eggs available for consumption by resident fishes. The model estimates daily production of eggs that become available to

consumers due to spillage or superimposition from a given area and day (eggs per square meter per day) of the spawning run, given different durations and densities of spawning (Appendix A). We ran three scenarios to investigate how salmon-spawning behavior influenced egg subsidies (Appendix B). Specifically, we ran a scenario (1) based on our best estimates of parameters from the literature (intermediate), (2) where female salmon avoided conflict and spawning timing was extremely contracted (extreme territoriality), and (3) where salmon did not avoid conflict and with an extended spawning timing (no territoriality). These latter two model scenarios represent the extremes in the degree of superimposition avoidance and extremes in the resultant relationships between salmon density and egg subsidies. This model output was converted to observed egg drift density and compared to field observations of egg drift density (Appendix A).

Field estimates of egg drift

We used natural gradients in sockeye salmon density among 10 streams and up to two years (16 stream-year combinations) to examine the relationship between salmon density and egg subsidies. Seasonal dynamics of egg subsidies were estimated by sampling eggs transported in stream drift before, during, and after salmon spawning. For 10 of these stream-years, we sampled egg drift between three and 10 dates per season (mean = 5.7 times) in these streams. In addition, egg drift was sampled once in six streams at the peak of salmon abundance. During each sampling event, 2–8 (mean = 3.9) drift net sets were collected. Drift nets (0.09 m²; mesh size, 0.5 mm) were placed in streams in runs for up to 20 minutes. We measured stream depth and water velocity at each site. At the end of each drift set, eggs were enumerated. We estimated drift densities of eggs (eggs per cubic meter) within each stream at a given time by dividing the number of eggs by the estimated volume of water filtered through the net during a drift set. Filtered water volume was calculated by multiplying the duration of each drift set by stream flow rate and net opening area, thus assuming 100% net efficiency. We compared observed egg production (converted from egg drift; see Appendix A) vs. salmon density during peak salmon density across all stream-years using AIC_c (Akaike Information Criterion for small sample sizes; Burnham and Anderson 1998) model fitting of three competing models: linear, power, and threshold (broken regression). We excluded data from one stream where salmon had not yet initiated spawning.

Resident fish

To investigate the impact of different densities of salmon on resident fish prey consumption, we collected diet samples from fishes during six years that varied in salmon density. Diets of rainbow trout and Arctic grayling were periodically taken from Hidden Lake Creek from June to August (before and during salmon

spawning) from years 2000 to 2005 (rainbow trout, $n = 228$; grayling, $n = 257$). Fish included in these analyses were at least 134 mm for grayling and 74 mm for rainbow trout, capable of eating eggs. Fish were captured using a stick seine and anesthetized with a 50 ppm solution of MS-222 (tricaine methane sulfonate). Each fish was measured and weighed before sampling their diets via gastric lavage. Diets were either counted in the field or were preserved in 95% ethanol for later prey identification, length measurement, and enumeration. Prey from diets were classified as: benthic invertebrates, terrestrial invertebrates, fishes, and salmon eggs. We estimated the ration size (milligrams of dry prey per gram of fish) of all prey items within each diet. We calculated prey mass by measuring prey and using taxon-specific length–mass regression equations. Using the diet data collected during middle to late August and salmon spawner counts from years 2000 to 2005, we estimated prey and egg consumption by resident fishes as a function of salmon density (rainbow trout, $n = 106$; grayling, $n = 131$). We investigated the relationship between sockeye salmon density and consumption of eggs by comparing competing models: a linear model, a threshold broken regression model, and a power function. We compared the performance of these models using AIC_c .

We used bioenergetics simulations to estimate rainbow trout growth responses to increasing salmon densities (Hanson et al. 1997). Growth was estimated for a 100-g fish, from 1 July to 30 Aug. Temperature data were from I-button temperature logging devices from Hidden Lake Creek. We focused on rainbow trout, as the bioenergetics parameters are well described (Rand et al. 1993). Ration size and composition of diets collected before salmon were present, averaged across all years, were used as the pre-salmon diet. During salmon spawning, non-egg ration and composition was estimated from pre-salmon diets. In addition, egg consumption changed as a function of salmon density by using the observed positive and nonlinear relationship (Fig. 1c) between salmon density and egg consumption (see Appendix C for more details).

RESULTS

Nest-digging produced a strongly nonlinear relationship between salmon density and egg subsidies, regardless of model scenarios (Fig. 1a). The scenario with more extreme territoriality and contracted spawning run duration produced a threshold relationship between salmon density and egg subsidies. In contrast, the scenario with little territoriality and extended spawning duration produced a less drastic transition across salmon densities. The positive relationship between salmon density and egg subsidies is driven by larger per capita egg contribution at higher salmon densities from superimposition. All model scenarios resulted in egg subsidies increasing nonlinearly as spawning habitat became saturated with salmon. Within a stream, egg drift densities increased as spawning progressed within a

season, and eventually decreased as spawning subsided and salmon died (Appendix D). The model captured 66% of the observed variation of seasonal dynamics of egg production, across all streams (Appendix E).

Field observations of egg drift densities (converted to egg production) across a gradient in salmon density (0.06–0.58 live salmon/m²) also revealed a nonlinear relationship between salmon density and egg subsidies. There was a positive and nonlinear relationship between egg production and live salmon density (Fig. 1b; power function: $r^2 = 0.85$). According to AIC_c , a power function fit substantially better than a linear or a threshold model (Appendix F).

Variation in salmon density in Hidden Lake Creek among years translated into substantial variation in foraging rates of resident fishes. Specifically, grayling and trout fed at substantially higher rates during years with higher salmon densities, driven primarily by increased consumption of salmon eggs (Fig. 1c, d). Over the six years of this study, we observed large variability in salmon density (0.14–0.88 salmon/m²), associated with large changes in consumption of eggs (trout, 0.66–4.25 mg eggs/g fish; grayling, 0.00–2.05 mg eggs/g fish). Eggs dominated diets; thus salmon density variation drove large changes in intake of these resident fishes. For example, a sixfold increase in salmon densities between 2002 and 2004 led to a 12-fold increase in total ration size (milligrams dry prey per gram of fish) for grayling (Fig. 1c, d). For both trout and grayling, the relationship between salmon density and egg consumption was described best by a nonlinear threshold (broken regression) relationship, with an increase in consumption rate occurring above ~ 0.4 salmon/m² (Appendix G).

This nonlinearity is likely driven predominantly by the nonlinear relationship between salmon density and egg subsidies (Fig. 1a, b). For rainbow trout, a small proportion of the nonlinearity appears to be driven by prey switching to eggs at higher salmon densities. During years with higher sockeye densities, rainbow trout switched away from non-egg prey. Thus, there was a significant negative relationship between salmon density and consumption of non-egg prey ($r^2 = 0.65$, $P = 0.05$). In contrast, grayling continued to feed on non-egg prey during years of peak salmon abundance; indeed feeding rate on non-egg prey was not related to salmon density ($r^2 = 0.06$, $P = 0.64$). These observations that grayling and rainbow trout eat the most eggs at highest salmon densities, coupled with the fact that these fishes are virtually the only egg predators in these streams, demonstrate that the observed nonlinearity in egg drift (Fig. 1b) is not driven by higher removal (predation) rates of eggs from the drift at lower salmon densities, but is indeed controlled by habitat saturation and superimposition.

Due to substantial increases in prey quantity and prey quality, increased salmon density translated into increased rainbow trout growth, according to bioenergetics simulations (Fig. 1e). Specifically, over two months

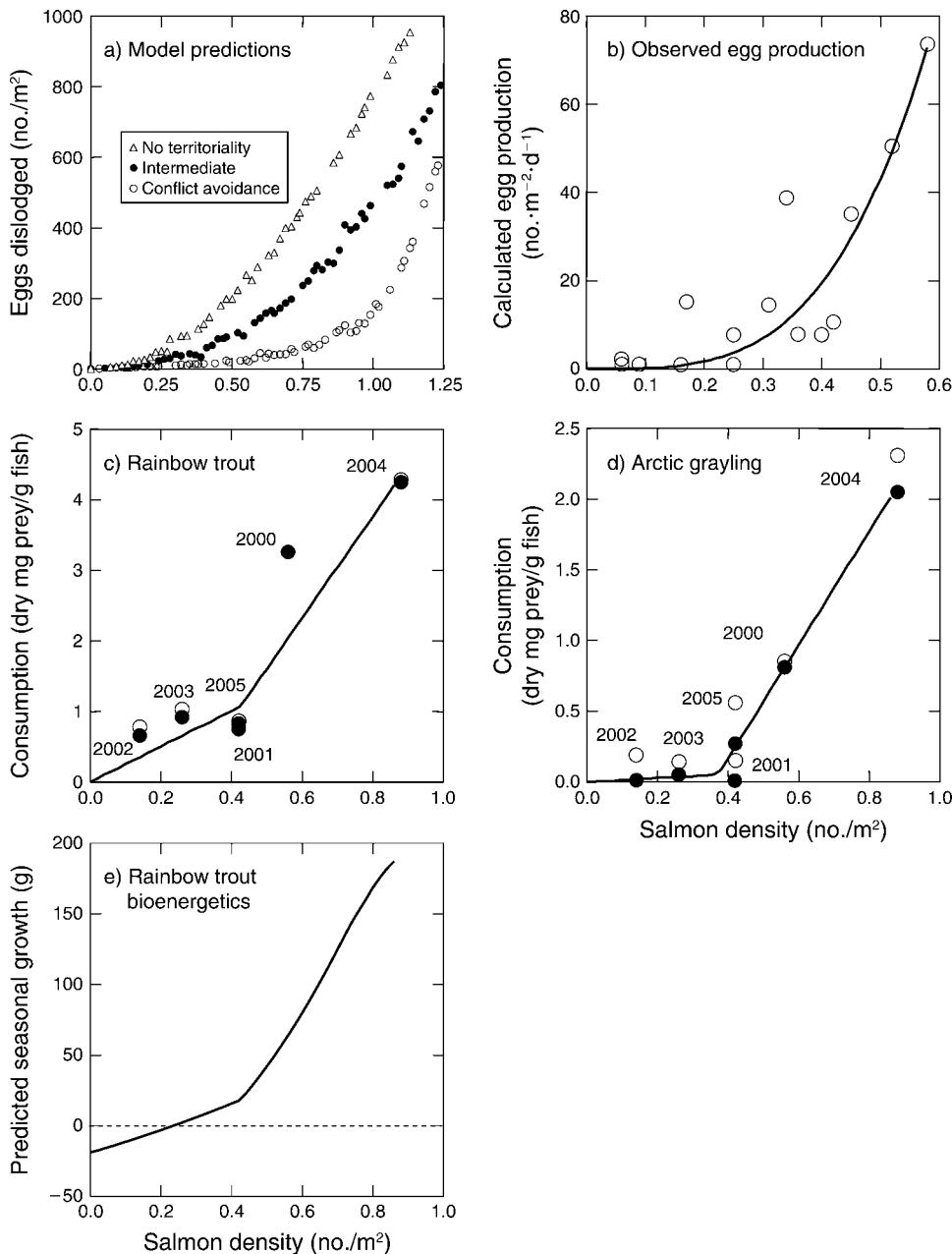


FIG. 1. Relationships between salmon density and egg subsidies. (a) Egg production as a function of salmon density based on the individual-based model (IBM) of salmon spawning. Three model scenarios represent different levels of territoriality (Appendix A). Shown are means of 20 model runs per salmon density, and the seasonal totals of egg production (measured as eggs dislodged). (b) Observed egg production in streams. Shown is the calculated egg production (EP_{raw}), after transforming egg drift (Appendix A), as a function of live salmon density (salmon/ m^2). Live salmon densities were quantified in the 200-m reach upstream of drift sampling location. Each point represents a different stream-year and is the average of a set of drift samples taken from a stream during peak salmon spawning. The line represents the best fit of a power function, which produced a substantially better fit than a linear model (Appendix F). (c, d) Consumption of eggs (solid circles) and all prey (open circles) of rainbow trout and Arctic grayling, respectively. Diet samples were taken during mid- to late August, the period when salmon are spawning and eggs are available. Shown is average ration size, normalized by fish body size, across six years of sampling that spanned a large gradient in salmon density. The x-axis represents observed total sockeye density (live and dead sockeye/ m^2) of that year. Sample years are beside points. The solid line represents best-fit threshold broken regression model (Appendix G). (e) Predicted growth of a 100-g rainbow trout over two summer months, based on bioenergetics simulations (Appendix C). Note the different axis scales between panels.

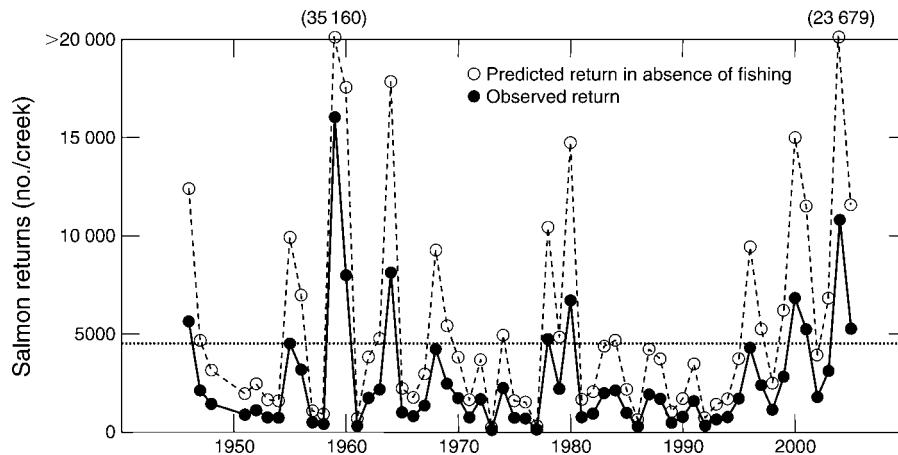


FIG. 2. Sockeye salmon returns to Hidden Lake Creek, Alaska, from 1946 to 2005. Counts are from annual spawner counts during the peak of spawning performed by personnel from the Alaska Salmon Program at the University of Washington. Shown are observed returns (black line and solid symbols), and predicted return in the absence of fishing, estimated by multiplying the observed return by the average harvest rate over this period (dashed line and open symbols). The dotted horizontal line represents the threshold where egg consumption increased, as estimated from the best-fit broken regression model (see Fig. 1c, d).

during the summer, which represents much of the constrained growing season, rainbow trout actually lost mass over the season in simulations with no or low salmon densities, similar to previous findings (Scheuerell et al. 2007). However, it should be noted that this negative growth only represents the summer period; simulations that included the winter period indicated that trout would exhibit slight positive growth over the entire year in the absence of salmon (*data not shown*). In contrast, at higher salmon densities, rainbow trout increased substantial mass over the summer. For example, trout are expected to increase by 50% in mass (50 g of growth) with 0.53 salmon/m² and increase by 100% (100 g of growth) with 0.65 salmon/m².

DISCUSSION

Our results demonstrate that habitat saturation and territorial behavior of spawning salmon regulate density-dependent egg subsidies to stream fishes. Both model predictions and field observations revealed that superimposition, caused by high densities of salmon spawning in finite stream areas, produced an accelerating relationship between salmon density and egg subsidies. Because of this nonlinearity, variation in salmon density magnified observed variation in egg production (Fig. 1b). The increased subsidies associated with high salmon densities translated into increased consumption by resident fishes during years with high salmon densities. Indeed, resident fishes showed a nonlinear relationship between salmon density and egg consumption (Fig. 1c, d). Based on bioenergetics modeling, these egg subsidies led to substantial differences in trout growth rates across salmon densities (Fig. 1e). We hypothesize that grayling do not feed on eggs at low salmon densities because rainbow trout monopolize the few eggs available (Fig. 1c, d). While previous work has noted the importance of

salmon eggs to stream fishes (e.g., Bilby et al. 1998, Meka et al. 2003, Wipfli et al. 2003, Lang et al. 2006, Scheuerell et al. 2007), this is the first investigation of the nonlinear relationship between salmon density and egg subsidies. In addition to drift-feeding fishes, in other systems a diverse set of consumers also feed on unburied salmon eggs, including benthic invertebrates and birds (Willson and Halupka 1995), and would benefit from this subsidy.

Our model predicted subsidies to drastically increase between 0.5 and 1.0 salmon/m² (Fig. 1a). This inflection occurred at higher densities than that observed for relationships between salmon density and both egg drift (~0.4 salmon/m²; Fig. 1b) and egg consumption (0.4 salmon/m²; Fig. 1c, d). This difference is likely because the IBM assumed that all the area in a stream is suitable spawning habitat when, in reality, only a subset of the stream area is suitable for spawning.

Potential conflicts between commercial and recreation fisheries

Our analyses suggest potential conflicts between commercial salmon fisheries and recreational fisheries for resident stream fishes, exacerbated by the nonlinear relationship between salmon density and egg subsidies. There is increasing concern that inland fisheries directly overexploit many fish populations (Allan et al. 2005). Marine fisheries on anadromous species can indirectly impact inland fishes that depend on those migratory species for food. Recreational fisheries for resident fishes, predominantly rainbow trout, are a growing and important part of Alaskan economies. Anglers often pay >\$1000 (US\$) per day to fish at some of the fishing lodges that target the rainbow trout and grayling, species that are subsidized by marine-derived nutrients and energy in the form of salmon eggs. However, returning sockeye salmon are heavily harvested by a

gill-net fishery. In Bristol Bay, commercial fisheries for sockeye salmon are valuable; in 2005 the sockeye catch was worth $>91 \times 10^6$ US\$ (Alaska Department of Fish and Game, unpublished data). Over the last 50 years, the commercial fishery has harvested an average of 56% of the returning sockeye salmon to the Wood River systems (Baker et al. 2006). For example, over the last 58 years in Hidden Lake Creek, annual spawner surveys have only observed 10 years where salmon densities exceeded the threshold allowing for high egg consumption (Fig. 2). However, if harvest had not occurred, we estimate that there would have been 23 years when salmon densities would have exceeded the threshold. Salmon populations are often managed to avoid spawner densities characterized by high levels of superimposition (e.g., Semenchenko 1988). From a commercial salmon fishery managers' perspective, high levels of superimposition represent missed opportunity for harvest. Our study has shown that superimposition drives egg subsidies to resident fishes such as rainbow trout and grayling. To date, we know of no efforts to investigate the integrated economic trade-offs between commercial salmon and recreational trout fisheries. This study illustrates the potential importance of identifying thresholds in management (Groffman et al. 2006).

Many populations of Pacific salmon have declined, with ecological consequences that are poorly understood (Ruckelshaus et al. 2002). Our results indicate that flows of marine-derived nutrients and energy (here in the form of salmon eggs) to the upper trophic levels of stream food webs have been reduced even more than would be inferred from the numerical decrease in salmon abundance. Salmon-derived subsidies to resident freshwater fishes represent a concrete example of how functional extinction can precede population extinction (sensu Soulé et al. 2005). The ecological consequences of population declines will be exacerbated when behavior mediates nonlinear impacts.

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APPENDIX A

A description of the individual-based model (IBM) and parameter fitting to egg drift data (*Ecological Archives* E089-019-A1).

APPENDIX B

A description and justification of the parameters used for the IBM of salmon spawning (*Ecological Archives* E089-019-A2).

APPENDIX C

A description and table of the details of the bioenergetics modeling (*Ecological Archives* E089-019-A3).

APPENDIX D

A figure showing observed and predicted seasonal egg production in streams (*Ecological Archives* E089-019-A4).

APPENDIX E

Estimated parameters comparing model predictions of egg drift and observed egg drift (*Ecological Archives* E089-019-A5).

APPENDIX F

Model fits (by AIC_c) and parameter values for competing models that described the relationship between salmon density and observed egg drift (*Ecological Archives* E089-019-A6).

APPENDIX G

Model fits for competing models that described the relationship between salmon density and egg consumption by grayling and rainbow trout in Hidden Lake Creek, Alaska, 2000–2005 (*Ecological Archives* E089-019-A7).