

Can nutrient additions facilitate recovery of Pacific salmon?

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Abstract: Multiple restoration actions have been implemented in response to declining salmon populations. Among these is the addition of salmon carcasses or artificial nutrients to mimic marine-derived nutrients historically provided by large spawning runs of salmon. A key assumption in this approach is that increased nutrients will catalyze salmon population growth. Although effects on aquatic ecosystems have been observed during treatments, it is unclear whether permanent population increases for salmon will occur. To test this assumption and address associated uncertainties, we linked a food web model with a salmon life cycle model to examine whether carcass additions in a river reach would improve conditions for salmon in the long term. Model results confirmed immediate increases in the biomass of periphyton, macroinvertebrates, and fish during carcass additions. In turn, juvenile salmon grew larger and experienced improved freshwater and smolt survival, which translated to a greater number of adults returning to spawn. However, once additions ceased, salmon abundance returned to pretreatment levels, which, based on our model, is owing to a combination of instream and out-of-basin factors. Overall, results of this work suggest that benefits during carcass and nutrient additions may not translate into persistent productivity of salmon unless additions are sustained indefinitely or other limiting factors are addressed.

Résumé : De nombreuses mesures de restauration ont été déployées pour contrer les déclin des populations de saumons. Parmi ces mesures figure l'ajout de carcasses de saumon et de nutriments artificiels pour imiter les nutriments de source marine que fournissaient auparavant les grandes migrations de frai de saumons. Une hypothèse centrale de cette approche est qu'une augmentation des nutriments disponibles catalysera la croissance des populations de saumons. Bien que des effets sur les écosystèmes aquatiques aient été observés durant des traitements, il n'est pas établi avec certitude que des augmentations permanentes des populations de saumons en découlent. Afin de valider cette hypothèse et d'explorer les sources d'incertitude associées, nous avons relié un modèle de réseau trophique à un modèle de cycle biologique des saumons pour vérifier si l'ajout de carcasses dans un tronçon de rivière entraînerait une amélioration à long terme des conditions auxquelles sont exposés les saumons. Les résultats du modèle confirment des augmentations immédiates de la biomasse de péryphyton, de macroinvertébrés et de poissons durant l'ajout de carcasses dont découle une augmentation de la taille des saumons juvéniles et de meilleurs taux de survie des saumons en eau douce, ainsi que des saumoneaux, ce qui se traduit par le retour d'un plus grand nombre de saumons adultes pour frayer. Cependant, une fois que les ajouts cessent, l'abondance des saumons retourne à ce qu'elle était avant les traitements, ce qui, selon notre modèle, est dû à une combinaison de facteurs internes au cours d'eau et externes au bassin. Globalement, les résultats de ces travaux donnent à penser que les bénéfices produits durant l'ajout de carcasses et de nutriments pourraient ne pas se traduire par une productivité durable des saumons, à moins que ces ajouts se poursuivent indéfiniment ou que d'autres mesures soient prises pour atténuer l'effet d'autres facteurs limitants. [Traduit par la Rédaction]

Introduction

Salmon accumulate ~99% of their adult body mass during their ocean residency (Gresh et al. 2000). Upon returning to natal streams to spawn, they contribute these marine-derived nutrients to local food webs in the form of inorganic nutrients, salmon eggs, and their own carcasses. These contributions can increase aquatic productivity via multiple pathways, especially when salmon spawn in nutrient-limited watersheds. For example, the marine-derived nutrients delivered by adult salmon can increase background nutrient levels (e.g., Chaloner et al. 2002, 2004), primary production (e.g., Levi et al. 2013; Benjamin et al. 2016), invertebrate abundance and biomass (e.g., Wipfli et al. 1998; Lessard et al. 2009), and fish growth and biomass (e.g., Bilby et al. 1996; Rinella et al. 2012). Because of apparent increases in aquatic productivity, it is often hypothesized that marine-derived nutrients can enhance the capacity for fresh waters to support juvenile salmon, thereby providing a positive feedback that helps sustain salmon populations

in environments that are otherwise considered nutrient-limited (Stockner 2003).

Declines in returning salmon adults of some populations (Nehlsen et al. 1991; Gustafson et al. 2007) have led to concerns that aquatic ecosystems are becoming less productive owing to subsequent declines in marine-derived nutrients (Stockner 2003). Moreover, with fewer adults returning to spawn, salmon smolts may export more nutrients from a watershed than delivered by their progenitors (Moore et al. 2011; Kohler et al. 2013). This has led to concerns about stream productivity, specifically that the benefits provided by marine-derived nutrients have been diminished, further limiting the potential for these imperiled populations to grow and recover (Stockner 2003).

In response, salmon recovery projects often consider supplementing streams with nutrients, such as salmon carcasses or analog materials, to replace lost nutrients and to enhance salmon population growth (Stockner 2003; Kohler et al. 2012). The hypoth-

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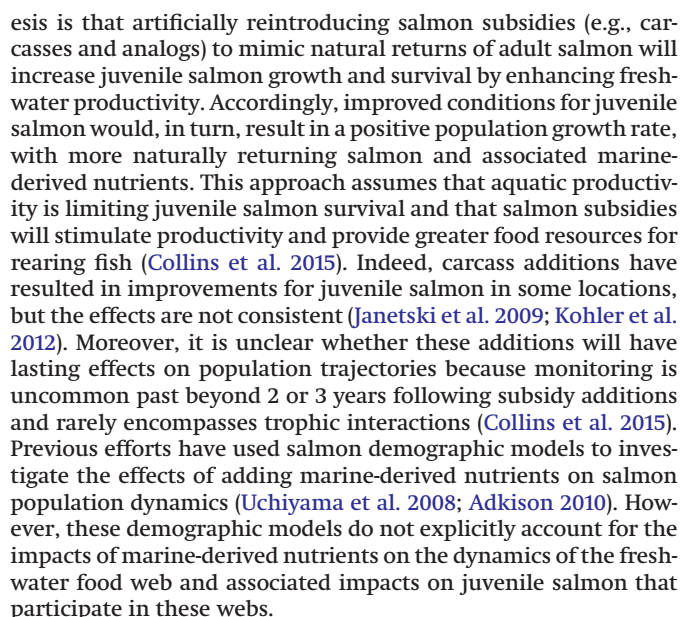
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additions to restore salmon populations. The model simulates the responses and interactions of multiple trophic levels that are directly and indirectly influenced by spawning salmon and their carcasses. Moreover, the model tracks the life cycle of salmon to explore population responses to carcass additions, which is difficult to evaluate with empirical studies. We used the model to ask three questions: (i) Do carcass additions translate into increased salmon populations? (ii) If so, what food web pathways influence the response? (iii) Do changes in salmon populations persist once carcass additions stop? We approached these simulations as a thought experiment aimed at developing more scientifically robust hypotheses about the population-level response to nutrient supplementation that have yet to be empirically evaluated.

We linked a salmon life cycle model with an aquatic food web model to explore potential consequences of using carcasses as a mitigation tool to recover salmon populations (Fig. 1). The model mechanistically links the availability of food resources that fuel fish growth to the abundance of adult spawning salmon and their carcasses. Within the model, adult salmon and (or) carcasses can increase aquatic productivity and associated food available to juvenile salmon via numerous direct and indirect pathways. When food resources are abundant, modeled juvenile salmon can grow

Table 1. Stages within the Chinook salmon life cycle, duration of each stage, mortality value or equation, and literature sources.

Stage	Duration (days)	Start of stage (calendar day)	Mortality	Source
Egg	226	1 September	0.4	Honea et al. 2009
Juvenile (predation)	365	15 April	$L_t^{-5.0}$	Keeley and Grant 2001
Juvenile (starvation)*			$\frac{L_t^{-5.0} + 60^{-5.0}}{K_t^{-7.5}}$	Railsback et al. 2009
Juvenile (length-based)†			$K_t^{-7.5} + 0.45^{-7.5}$	Railsback et al. 2009
Smolt	30	15 April	$0.01 \times e^{-0.03L_t}$	Zabel and Achord 2004
Ocean resident	730	15 May	$-0.0008W^2 - 0.047W + 1.013$	Honea et al. 2009
Adult migration	47	15 May	0.94	Honea et al. 2009
Adult at spawning ground	62	1 July	0.1	Honea et al. 2009

*Starvation mortality based upon condition factor (K) at time t .

†Length (L ; mm) based mortality at time t , estimated with $L = (W \times 100\,000)^{0.33}$, where W is weight (g).

faster and larger and, thus, experience lower rates of mortality. When food is limiting, fishes grow slower and experience higher mortality. We coded the model with parameters that reflect the environmental conditions, physiology, and life history of Chinook salmon (*Oncorhynchus tshawytscha*) that spawn and rear throughout the Columbia River basin. We chose this species and location because Chinook salmon populations are declining in the Columbia River basin (Williams et al. 1999; Gayeski et al. 2018), and spawning rivers in the basin are frequent targets of carcass addition efforts aimed at enhancing population productivity (Kohler et al. 2012, 2013). The model simulates freshwater food webs and salmon population dynamics at a daily time scale and was run for 20 or more years.

Life cycle model

The dynamics of the Chinook salmon population were modeled similar to a stage-based Lefkovich matrix model (Lefkovich 1965). The life cycle for one cohort takes 4 years and considers six life history stages: eggs, juveniles, smolts, first year ocean residency, second year ocean residency coupled with adult migration, and adults at spawning grounds (Fig. 1). Each stage has a hard-set duration, and individuals were advanced to the next stage after accounting for stage-based mortality (Table 1). The life cycle was initialized with adult salmon entering the spawning grounds 1 July, holding for 2 months, and eventually spawning on 1 September. We assumed that juveniles spend 1 year in fresh water before migrating to the ocean as smolts and that adults have a 2-year residency in the ocean before returning to spawn. Although we acknowledge that Chinook salmon exhibit variability in life histories, evaluating the influence of salmon carcass additions on these myriad strategies was outside the scope of our analyses.

Food web model

To model the dynamics of the freshwater food web, we used the Aquatic Trophic Productivity (ATP) model, which has been described in detail elsewhere, including a comprehensive list of parameter values, sensitivity analyses, coding, and comparisons with empirical data (Benjamin and Bellmore 2016; Bellmore et al. 2017; Whitney et al. 2019). Briefly, the ATP model simulates the capacity of river ecosystems to sustain fishes via the transfer of organic matter among different components of a simplified river food web. This model mechanistically links the dynamics of the food web, and the resultant performance of different web members, to (i) the physical and hydraulic conditions of the stream, (ii) the structure and composition of the adjacent riparian zone, and (iii) marine nutrient subsidies delivered by adult salmon.

The ATP model consists of five biomass stocks: periphyton (e.g., algal community), terrestrial detritus (e.g., leaf litter), aquatic invertebrates, juvenile Chinook salmon, and nontarget fishes (Fig. 1). In the model, periphyton and terrestrial detritus are con-

sumed by aquatic invertebrates, and invertebrates (aquatic and terrestrial) are consumed by fish. Selection of prey items by a predator are a function of the prey quality (i.e., assimilation efficiency; Table A1) and quantity (i.e., biomass; see Bellmore et al. 2017; Whitney et al. 2019 for details). The nontarget fish stock represents the remaining fish in the community that may compete with (e.g., whitefish, sculpin (*Cottus* spp.)) or prey upon (e.g., bull trout (*Salvelinus confluentus*), sculpin) juvenile Chinook salmon. All biomass stocks, except for juvenile Chinook salmon, are governed by mass balance equations (for details see Benjamin and Bellmore 2016; Bellmore et al. 2017; Whitney et al. 2019). For juvenile Chinook salmon, the model tracks both fish abundance and average individual mass (see below).

The dynamics of the modeled food web are controlled by the environmental conditions of the river reach. These environmental conditions include river discharge, channel morphology, water temperature, water clarity, dissolved nitrogen and phosphorus concentrations, light availability, and riparian vegetation structure. In the model, water temperature influences the bioenergetics of fishes and aquatic invertebrates (consumption and respiration rates) and decay rates of periphyton and terrestrial detritus. Water clarity (e.g., turbidity and water depth) and nutrient concentrations influence the amount of light and nutrients available to fuel periphyton at the base of the food web. Riparian vegetation contributes leaf litter and terrestrial invertebrates to the stream and filters incoming solar radiation. Channel morphology (bank-full width, bank-full depth, and gradient) and discharge affects channel hydraulics, such as water depth, width, flow velocity, and shear stress acting on the streambed. In turn, channel width influences the wetted area available for biological production; and water velocity, shear stress, and benthic sediment size influence the mobilization, transport, and retention of benthic organisms and organic matter.

Within the ATP model, returning adult salmon provide a source of marine nitrogen, phosphorus, and organic matter that are incorporated into the food web. The magnitude of nutrients and organic matter from adult salmon are proportional to the number or biomass of adults that return to the modeled river reach to spawn. We assumed an adult salmon returning to spawn, as well as experimentally added carcasses, was 5 kg (Quinn 2005). Upon returning, live salmon contribute dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) through excretion that can increase periphyton production (Bellmore et al. 2014). During the spawning event, salmon contribute eggs that can be available for consumption by juvenile Chinook salmon and nontarget fishes. In addition, the model accounts for the process of bioturbation, whereby salmon detach aquatic invertebrates and organic matter by scouring the stream bed during nest construction (Bellmore et al. 2014). The detached invertebrates and organic

Table 2. Percentage of the simulations that had a 5% increase, 5% decrease, or no change in adult densities during and after carcass addition compared with precarcass addition adult densities.

Carcass addition (carcass·m ⁻²)	During addition			After addition		
	Negative	No change	Positive	Negative	No change	Positive
0.1	2.6	28.6	68.8	3.5	96.1	0.4
0.2	5.5	18.0	76.5	4.1	95.4	0.5
0.5	6.0	14.3	79.7	6.2	93.3	0.5
1.0	8.9	10.0	81.1	6.9	92.7	0.4
2.0	10.2	7.0	82.8	9.6	89.7	0.7
4.0	16.4	4.3	79.3	16.2	83.1	0.7
6.0	17.5	4.2	78.3	16.5	83.1	0.4
8.0	16.5	4.6	78.9	17.1	82.9	0.0
10.0	22.5	4.1	73.4	23.6	76.0	0.4

Note: One carcass was assumed to be 5 kg.

matter can be consumed by predators or exported from the treatment reach. Once salmon are dead, DIN and SRP are leached out of carcasses during decomposition (Naiman et al. 2002; Janetski et al. 2009), and the carcasses themselves become direct food sources for aquatic invertebrates and fishes. All salmon carcass biomass, either from postspawning salmon or experimentally added carcasses, entering the stream are subject to export, decay, and stranding on terrestrial habitat (Janetski et al. 2009). Carcasses that become stranded in terrestrial habitats can be colonized by terrestrial invertebrates (e.g., dipteran larvae), which increases the flux of terrestrial invertebrates to the stream and available for fish consumption (Collins et al. 2016). Carcasses in the stream may not be immediately available for consumption by aquatic invertebrates and fish (Cleason et al. 2006). Thus, we included a time-lag to account for conditioning of carcasses by microorganisms and locating of carcasses by consumers. We assumed that carcass biomass becomes available to consumers at a rate of 1% of carcass biomass per day. For example, if 5000 g of carcass is added to the stream, 50 g would be available for consumption by aquatic invertebrates and fishes on day 1, and another 1% of the remaining carcass material on day 2, and so on until all remaining carcass biomass — that has not decayed or been exported downstream — is available to consumers.

Linking the salmon life cycle to food web dynamics

We focused the linked life cycle and food web models on the freshwater stages. The initial number of juvenile Chinook salmon to be incorporated into the river food web was based on the number of eggs that survive to hatching. Once in the food web model, the growth and survival of juvenile Chinook salmon depends on bottom-up and top-down processes, including (i) food availability and (ii) competition with and predation by the nontarget fishes.

Both the size and abundance of juvenile Chinook salmon are simultaneously simulated within the linked model. Juvenile salmon growth is a function of water temperature, food availability, and fish density (see Bellmore et al. 2017). Fish growth is bounded by temperature-dependent consumption and respiration rates calculated using a Wisconsin bioenergetic model parameterized for Chinook salmon (Hanson et al. 1997). Consumption is also a function of food availability and fish density; consumption rate is high when food is abundant and juvenile salmon densities are low and becomes more constrained as food becomes limiting and juvenile densities increase (greater intraspecific competition; Bellmore et al. 2017). A similar approach was used to calculate consumption rates for nontarget fishes and aquatic invertebrates in the model (Bellmore et al. 2017).

Based on the daily weight (g) of a juvenile salmon, we simultaneously simulated three sources of mortality: (i) predation, (ii) starvation, and (iii) size-based, density-independent mortality (Table 1). Predation mortality is the consumption of juvenile Chinook salmon by the nontarget fish stock. We assumed that smaller fish were more

likely to be preyed upon than larger fish (Keeley and Grant 2001). Starvation mortality occurs when metabolic costs (respiration) exceed energy intake via consumption, which causes fish to lose mass. We used condition factor (K) to estimate starvation mortality following Railsback et al. (2009), which assumes that as K decreases with weight loss, more fish succumb to starvation. We assumed that starvation mortality would indirectly mimic density-dependent competition for food because more fish in the reach would translate to less food available per individual and vice versa. Size-based, density-independent juvenile salmon mortality assumed that fish size influences the susceptibility to density-independent causes of death (e.g., disease, scouring flows). We assumed smaller fish were more likely to experience mortality from these sources (Railsback et al. 2009). Juvenile Chinook salmon abundance at time t is a function of the cumulative mortality from these three sources during time $t - 1$.

Mortality rate for smolts was dependent on their size (Ward and Slaney 1988; Passolt and Anderson 2013). The size of smolts leaving freshwater habitats was linked to downstream migrant survival using the length-based mortality equation from Zabel and Achord (2004; Table 1). Survival during the smolt stage accounts for dam passage, as well as other sources of mortality (e.g., avian, pinniped), and ends with entrance into the estuary. We applied constant survival values from the literature for all other life stages (estuary survival, ocean survival, upstream adult migrant survival, and prespawn survival; Table 1).

Model parameterization

To parameterize the model, we used environmental information from streams where Chinook salmon spawn and rear in the Columbia River basin and where carcass or analog additions are frequently conducted (see Table A1; Fig. A1 for ambient conditions). For several environmental inputs, we took the average of conditions found across numerous streams (Kohler et al. 2012). Thus, the model was not coded for a specific stream, but rather represents the general conditions found in streams where carcass additions have occurred. For those environmental conditions that are temporally dynamic (e.g., water temperature, discharge, nutrient concentrations), the model uses the same daily inputs for each year of the simulation, with exceptions noted in the scenario descriptions below. Because we wanted to simulate the consequences of adding carcasses on dynamics of salmon populations without the interference of habitat quality or other factors that can affect salmon, we assumed that 90% of the modeled reach was suitable for spawning and juvenile rearing.

Scenarios, model simulations, and uncertainty analyses

We conducted two series of model scenarios to explore whether salmon carcass additions can result in more adults returning to spawn. In each series, we conducted simulations with different densities of added carcass (0 (henceforth baseline), 0.1, 0.2, 1, 2, 4,

6, 8, or 10 carcasses·m⁻²; Table 2). Each carcass added was assumed to be 5 kg wet weight (Quinn 2005). In the first series, we added carcasses each year for 20 years. From these simulations, we addressed the questions regarding the consequences of carcass additions on salmon populations and the mechanistic food web pathways by which carcasses may affect salmon population dynamics. In the second series of model simulations, we explored the consequences of salmon populations following the cessation of carcass additions (e.g., before, during, and after). To do this, we ran simulations for a 40-year time frame, with 10 years precarcass addition, 20 years of annual carcass addition, and 10 years post-carcass addition. We recognize that the duration of our simulations may be unrealistic because resources required for carcass augmentation may be unsustainable for the long term, but our goal was to ensure that any effect of carcass additions on salmon population dynamics was fully realized before additions were ceased. In addition, we recognize that some of the loading biomasses of carcasses may be unattainable or rarely occur naturally under current conditions. However, it is possible that these values of available marine-derived nutrients occurred naturally (Thurrow et al. 2020). Regardless, our goal with the high values of carcass additions was to identify a potential amount, if any, of supplementation needed to recover salmon populations.

To estimate how uncertainty in the value of different model parameters influenced the modeled abundance of salmon and food web dynamics, we ran 2000 simulations to calculate confidence intervals of model outputs using Latin hypercube sampling (Ford and Flynn 2005). We identified 39 parameters to concurrently vary in our uncertainty analysis (Table A1). These parameters were chosen because (i) they have been previously shown to be influential in ATP model simulations (Bellmore et al. 2017), (ii) they directly influence the effect of adult salmon or carcasses on the food web (e.g., nutrients excreted by adults or leached by carcasses, assimilation efficiency of carcasses and eggs), or (iii) they directly control survival and abundance of salmon life stages in the life cycle model (e.g., mortality of eggs or ocean resident fish, female salmon fecundity). All parameters used in the Latin hypercube sampling were adjusted by $\pm 25\%$ of the mean value using a uniform distribution. All simulations were done in Stella Architect 1.5 (ISEE Systems, Lebanon, New Hampshire, USA).

From the 2000 simulations, we categorized outcomes as negative, positive, or no change. This was done both during carcass addition and after carcass addition. Positive responses exhibit $>5\%$ increase in spawning adult abundance relative to precarcass addition, negative responses exhibit $>5\%$ decrease, and “no change” represents all simulations where salmon densities stay within 5% of precarcass addition values.

We present mass of carcasses and smolts in grams of wet weight to allow for direct comparisons of model output with empirical studies. In contrast, we present the biomass of the food web stocks (e.g., periphyton, invertebrates, fish) in grams ash-free dry mass (AFDM) because it eliminates the variability in water content between stocks, and this unit of measure is more comparable among stocks. We used a conversion factor of 0.2 g AFDM per 1.0 g wet weight (Whitney et al. 2019).

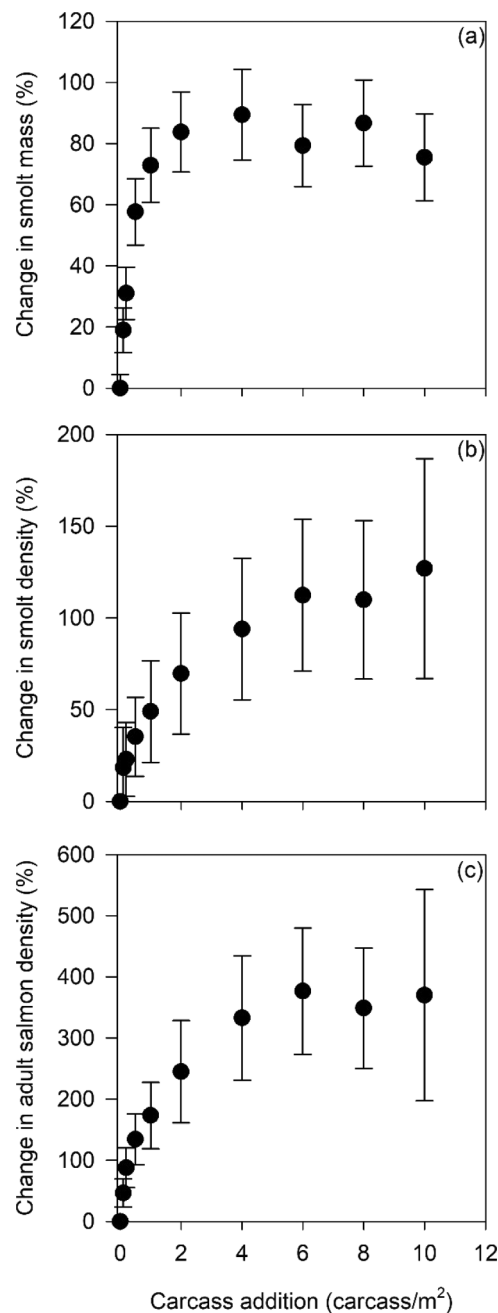
Results

Response of salmon during carcass addition

When no carcasses were added to the model (i.e., baseline conditions), the simulated density of salmon returning to spawn was 0.005 adults·m⁻² (0.002–0.056 adults·m⁻²; 10–90 percentiles). Mortality for juveniles rearing in the modeled river section was 0.75 (0.47–0.99). The density of smolts migrating downstream was 0.40 smolts·m⁻² (0.08–1.35 smolts·m⁻²), with a mass of 8.3 g (5.0–15.8 g) and a mortality of 0.56 (0.25–0.94).

When carcasses were added to the model, the mass of an individual smolt, as well as the densities of salmon smolts and adults

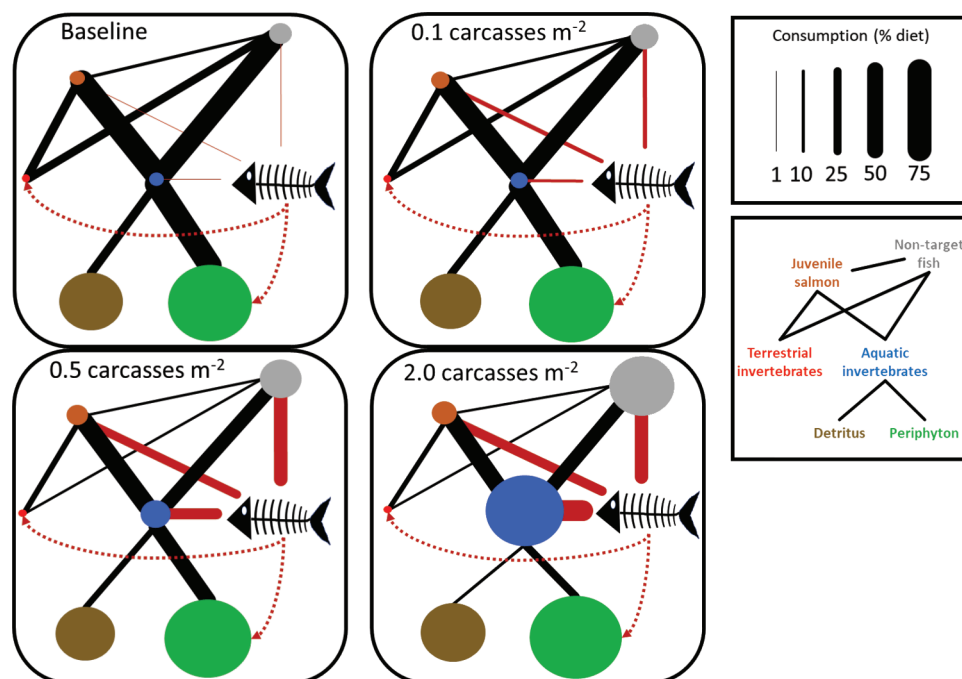
Fig. 2. Change ($\pm 95\%$ confidence bounds) in smolt mass (a), smolt density (b), and adult density (c) to various carcass additions (0, 0.1, 0.2, 0.5, 1, 2, 4, 6, 8, and 10 carcasses·m⁻²) compared with no additions. One carcass was assumed to be 5 kg.



increased (Fig. 2). Compared with baseline, the mass of a smolt increased from 19% to 84% with additions of 0.1–2.0 carcasses·m⁻² (0.5–10 kg·m⁻²). Similar results were simulated for smolt and adult densities with increases up to $\sim 49\%$ and 173% , respectively. Additions above 2.0 carcasses·m⁻² (10 kg·m⁻²) produced little additional increase in smolt and adult abundance, and a threshold was suggested.

Adult densities in most (69%–82%) of the 2000 simulations had a positive response to carcass additions (Table 2). Some simulations, however, had no response (4%–28%) or a negative response (3%–22%). As the density of carcasses added increased, fewer simulations exhibited no response in adult density, but the percentage of simulations with a negative response increased. Parameters most

Fig. 3. Flow diagrams showing the flow of organic matter between consumers and resources (lines; consumption in percent) and biomass stocks (circles; annual average g AFDM·m⁻²) for baseline and during carcass addition at 0.1, 0.5, and 2.0 carcasses·m⁻². Black lines represent the percent consumption of food web members, and red lines represent the influence of carcasses on periphyton and terrestrial invertebrates (dashed) or the consumption of carcass material (solid). One carcass was assumed to be 5 kg. [Colour online.]



influential to these responses included water temperature during juvenile rearing, consumption rate of nontarget fishes, juvenile starvation, and estuary mortality (Fig. A2).

Response of food web during carcass addition

Changes in juvenile salmon abundance and size were a result of changes in the pathways and magnitudes of organic matter flow through the river food web (Fig. 3). When no carcasses were added, organic matter flowed in a chain of strong interactions from periphyton to aquatic invertebrates to fish, with the bulk of the invertebrate biomass fueling both juvenile Chinook salmon (73% of diet) and nontarget fish biomass (67% of diet). Without additional carcasses, the subsidy of terrestrial invertebrates was also important (26% and 23% for juvenile salmon and nontarget fishes, respectively), whereas the subsidy from returning salmon adults provided relatively little energy flow (1% of carcass material; <0.5% of salmon eggs of diet).

With the addition of salmon carcasses, the annual biomass (g AFDM·m⁻²·year⁻¹) of stocks increased, and diets shifted to take advantage of the additional carcass material (Fig. 3). The average annual biomass of juvenile Chinook salmon increased up to 81%, at 2.0 carcasses·m⁻² (10 kg·m⁻²), as did the annual biomass of nontarget fishes (up to 221% increase) and aquatic invertebrates (up to 570%), owing to a substantial increase in the direct consumption of carcass material (up to 32% of diet for juvenile salmon; 48% for nontarget fishes; 66% for aquatic invertebrates). The consumption of eggs of spawning salmon remained relatively low (<0.5% for both fish species). With the increase in the carcass subsidy, the percentage of invertebrates in the diet composition of fish decreased for both aquatic (down to 55% for juvenile salmon; 44% for nontarget fishes) and terrestrial (down to 13% for juvenile salmon; 4% for nontarget fishes) invertebrates. Similarly, a 7% decline in percent consumption of periphyton and 7% decline in detritus consumed by aquatic invertebrates also occurred. Carcass addition only minimally boosted annual periphyton biomass (generally <10% increase), largely because nutrient contributions (nitrogen and phosphorus) from spawners and carcasses were in-

sufficient to significantly alleviate nutrient limitation. Furthermore, although invertebrates consumed less periphyton on a per-capita basis, overall consumption of periphyton — top-down control — was greater because of increased aquatic invertebrate biomass.

Response of salmon after carcass addition

When carcasses were no longer added to the stream each year, adult densities in most scenarios returned to baseline or precarcass addition levels within 5 to 10 years regardless of the density of carcasses added (Fig. 4; Table 2). Similar results were found for modeled smolt densities.

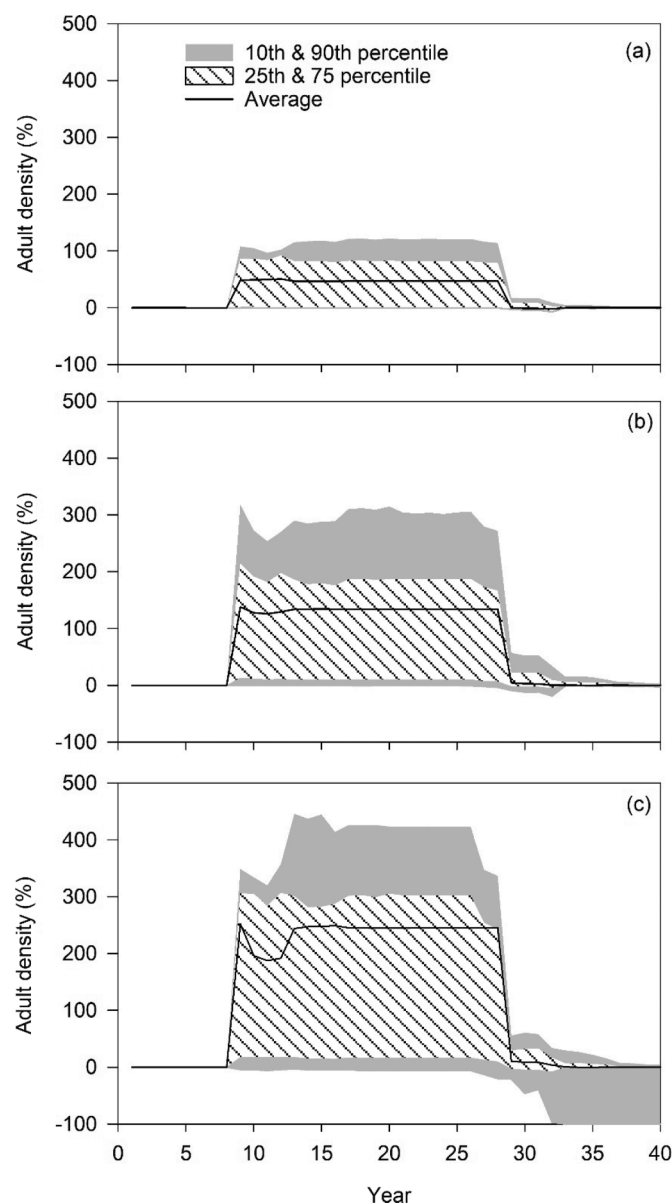
A small percentage of the simulations had posttreatment adult densities that were 5% different than pretreatment densities (Table 2). Our simulations do suggest the potential for carcass addition to have lasting effects even after carcass additions have ceased. However, the percentage of simulations that exhibited lasting positive responses in juvenile and adult salmon was very small (i.e., <1%). In contrast, many more simulations suggested the potential for population declines, including extirpation, once carcass additions cease. The most influential model parameters affecting postcarcass addition responses were water temperature during juvenile rearing, consumption rate of nontarget fishes, juvenile starvation, and estuary mortality (Fig. A2).

Similar to the response of salmon, the biomass of periphyton, aquatic invertebrates, and nontarget fishes also generally returned to baseline values. However, in a few instances, the biomass of nontarget fishes remained elevated (3%–20% relative to baseline) following cessation of carcass additions. This generally occurred in simulations where juvenile salmon biomass declined. Notably, nontarget fish biomass would also increase when salmon densities increased.

Discussion

One of the objectives of adding salmon carcasses or an analog to a river is to increase the number of salmon smolts migrating to

Fig. 4. Change in the density of spawning salmon adults compared with baseline (no carcass addition) for before, during, and after carcass additions at 0.1 (a), 0.5 (b), and 2.0 carcasses·m⁻² (c). Carcasses were added for 20 years starting on year 5 and ending on year 25. One carcass was assumed to be 5 kg.



the ocean and adults returning to natal spawning and rearing habitat. The assumed mechanism is that carcasses will increase aquatic primary and secondary productivity, thus improving growth and survival of juvenile salmon through direct and indirect pathways. The objective is to rekindle the positive feedback of pulsed marine nutrients that may have occurred historically with large salmon runs. Our simulations suggest that adding salmon carcasses to rivers may temporarily increase aquatic productivity and the abundance of juvenile and adult salmon. However, we found limited evidence that responses to carcass addition persist if supplementation efforts stop. Once carcass supplementation ceased, freshwater productivity and salmon populations quickly returned to (or even declined below) pre-addition levels. Although our model analysis hints at the possibility of positive responses persisting following carcass supplementation, these lasting positive effects occurred in less than 1% of the simulations. If true,

these findings should temper expectations for the capacity of nutrient supplementation efforts to recover salmon populations.

A number of studies have observed positive effects of natural spawning salmon or added carcasses on primary and secondary production (see Janetski et al. 2009 for a review). During carcass additions, the density of smolts and returning adults increased in our model simulations and began to level at a density of 2.0 carcasses·m⁻² (10 kg·m⁻²). At densities higher than 2.0 carcasses·m⁻², there was a diminishing return with more carcasses added, suggesting a threshold where the percentage of negative responses begins to increase. This is consistent with mesocosm experiments that found up to 60% increase in juvenile salmon mass with carcass additions that leveled off after ~1.0 carcass·m⁻² (5 kg·m⁻²; Wipfli et al. 2003; but see Kiffney et al. 2018). Based on our modeling results, the percentage of negative responses also begins to increase after the 2.0 carcasses·m⁻², further supporting the potential of a threshold limit. Although the lower addition densities (0.1 and 1.0 carcasses·m⁻²) may be more feasible given limited resources, they did have a higher percentage of simulations with no effect, as has been observed (Harvey and Wilzbach 2010; Wheeler et al. 2017).

The primary factor driving the response of salmon was the size and growth of juveniles. In general, juvenile salmon that could take advantage of the subsidized marine-derived nutrient from added carcasses were capable of attaining a larger size and retaining it throughout their freshwater life stage. The subsidy allowed them to better avoid mortality owing to starvation during colder winter months, as well as better avoid predation by nontarget fishes. The larger size attained also reduced mortality risk during the smolt stage. In contrast, simulations with a negative response to carcass addition had colder water temperature (<2000 °C in degree days) that restricted growth of juveniles, thus making them more vulnerable to starvation, downstream mortality, and predation by subsidized populations of nontarget fish. The influence of marine-derived nutrients on growth has been attributed to both positive and negative changes in abundance and survival of fish in a number of studies (Janetski et al. 2009; Gerwing and Plate 2019), as well as adult returns (Slaney et al. 2003). Results of this study provide further mechanistic insights as to how this variability can arise.

In our model simulations, salmon carcass additions primarily benefited salmon through direct consumption of carcass material by juvenile fish, a pathway consistent with previous observations (Bilby et al. 1996; Kiernan et al. 2010; Collins et al. 2016) and modeling efforts (Bellmore et al. 2017). Indirect pathways of carcasses incorporated into the modeled food web were also demonstrated but were less important. For example, carcass material was directly consumed by aquatic invertebrates, resulting in modeled increases in invertebrate biomass available for fish consumption. An increase in periphyton biomass was minimal, contrary to some empirical evidence, which suggests that nutrients provided by returning adults (Levi et al. 2013; Benjamin et al. 2016) or added carcasses (Wipfli et al. 1998; Marcarelli et al. 2014) may stimulate primary production. A lack of periphyton response was in part due to top-down suppression of periphyton by larger invertebrate populations. Moreover, within the modeled river section, we allowed adult salmon to spawn on nearly all (90%) of the stream bed, which reduced periphyton biomass via bed scour during redd building (Holtgrieve and Schindler 2011; Bellmore et al. 2014). Lastly, predation by nontarget fishes on juvenile salmon, as well as competition, can influence the response of salmon to restoration actions, including nutrient mitigation (Bellmore et al. 2017). For instance, in our simulations subsidized populations of nontarget fishes sometimes resulted in negative responses for salmon after carcass additions ceased. This mainly occurred when the consumption rate by nontarget fishes, selected in our sensitivity analysis, was higher than average (Table A1), suggesting that carcass additions could have unintended negative impacts when conducted in the presence of predators.

The hypothesis that additions of salmon carcasses can restore salmon populations by improving freshwater conditions is not supported by our model findings. Although carcass addition increased returning salmon numbers by up to 400%, this was still a relatively low adult density ($\sim 0.1\text{--}0.2$ adults·m⁻²), which in most of our simulations was insufficient to sustain higher populations after carcass addition ceased. Similar results have been observed for other nutrient addition (Ericksen et al. 2009; Wilson and Corsi 2016) and mitigation efforts (Sharma et al. 2006; Venditti et al. 2017). In the context of our model, populations returned to baseline levels due to environmental factors that affect the growth and size of juvenile salmon. Without the subsidy of carcasses, juvenile fishes were more susceptible to starvation during cold winter temperatures (Ebersole et al. 2006). Those that survived were smaller in size and more vulnerable to predation by nontarget fishes and experienced greater out-of-basin mortality (Zabel and Achord 2004; Duffy and Beauchamp 2011). Interestingly, those few simulations that maintained higher salmon densities frequently had lower out-of-basin mortality, suggesting that the positive feedback spawners contribute to population growth might operate if downstream circumstances were different (e.g., lower smolt migration and ocean mortality). Simulations that showed a negative response following carcass additions were mainly owing to extreme density dependence, whereby large numbers of juveniles no longer had adequate resources to support their growth and thus experienced high juvenile and smolt mortality.

Our model is a simplified representation of lotic ecosystems and food webs and may not account for some mechanisms that can influence or be influenced by salmon. First, salmon carcasses and nutrient mitigation can influence species in different ways. For example, chironomid midges often have a strong positive response to salmon carcasses, whereas responses can be variable for other aquatic invertebrate taxa (Wipfli et al. 1998; Kiffney et al. 2018). Similarly, variable responses have been observed among and within fish species (Collins et al. 2015; Gerwing and Plate 2019). For the purposes of our model, we represent the entire aquatic macroinvertebrate community in one stock, likewise for nontarget fishes. However, we believe that the general magnitude and direction of response by Chinook salmon, which was our focal species, would be similar if species-specific responses were incorporated for macroinvertebrates and nontarget fishes. Second, the timing of carcass additions or multiple salmon species may have different and emergent contributions (e.g., Twining et al. 2017). Similarly, the phenology of the size, growth, and migration timing of salmon can influence populations trajectories (Campbell et al. 2019; Flitcroft et al. 2019) and the magnitude of marine-derived nutrient subsidies (Armstrong et al. 2019). These complexities of salmon life history expression were beyond the scope of this study but offer pathways for future studies. Third, we did not directly account for nutrient retention (O'Keefe and Edwards 2002) or uptake (Naiman et al. 2002) beyond that of the periphyton stock, which can further influence the positive feedback by salmon.

Our results have important implications for expected outcomes of using carcass and nutrient additions as a means of restoring salmon. First, nutrient mitigation is likely a benefit to salmon only during treatments, except in rare occasions, and managers might conclude that resources may be better used for alternative actions that may be more likely to provide long-lasting benefits. Given this limitation and others (Collins et al. 2015), nutrient addition as a means of restoration deserves measured expectations. Second, because the consequences to carcass addition primarily occurred during the action suggests that other factors may be restricting salmon recovery. For example, restoring or reconnecting floodplain habitat could have a greater benefit on juvenile salmon compared with nutrient supplementation (Bellmore et al. 2017), although this is likely context-dependent (Whitney et al., in press). Third, if carcass or nutrient additions are implemented, then coupling it with other recovery actions may improve resto-

ration outcomes. For example, our results suggest that out-of-basin mortality can strongly complement the consequences of carcass additions on returning adult salmon. Thus, coupling nutrient mitigation with improving downstream conditions may benefit the population over the long term. Moreover, making changes downstream can have a greater impact that will benefit multiple populations. Fourth, no single action will overcome the consequences of other deleterious effects. Critically questioning, assessing, and addressing the ecological needs and limitations of the species (Gayeski et al. 2018), as well as a focus on the natural processes that support ecosystem function (Beechie et al. 2010), are necessary to achieve meaningful recovery and sound management of aquatic and terrestrial resources.

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References

- Adkison, M.D. 2010. Models of the effects of marine-derived nutrients on salmon (*Oncorhynchus* spp.) population dynamics. *Can. J. Fish. Aquat. Sci.* **67**(1): 5–15. doi:10.1139/F09-161.
- Armstrong, J.B., Schindler, D.E., Cunningham, C.J., Deacy, W., and Walsh, P. 2019. Watershed complexity increases the capacity for salmon–wildlife interactions in coastal ecosystems. *Conserv. Lett.* **13**(2): e12689. doi:10.1111/conl.12689.
- Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., et al. 2010. Process-based principles for restoring river ecosystems. *Bioscience*, **60**(3): 209–222. doi:10.1525/bio.2010.60.3.7.
- Bellmore, J.R., Fremier, A.K., Mejia, F., and Newsom, M. 2014. The response of stream periphyton to Pacific salmon: using a model to understand the role of environmental context. *Freshw. Biol.* **59**(7): 1437–1451. doi:10.1111/fwb.12356.
- Bellmore, J.R., Benjamin, J.R., Newsom, M., Bountry, J.A., and Dombroski, D. 2017. Incorporating food web dynamics into ecological restoration: a modeling approach for river ecosystems. *Ecol. Appl.* **27**(3): 814–832. doi:10.1002/eaap.1486. PMID:28078716.
- Benjamin, J.R., and Bellmore, J.R. 2016. The aquatic trophic productivity model—a decision support model for river restoration planning in the Methow River, Washington. US Geological Survey Open-File Report 2016-1075, Reston, Virginia.
- Benjamin, J.R., Bellmore, J.R., and Watson, G.A. 2016. Response of ecosystem metabolism to low densities of spawning Chinook Salmon. *Freshw. Sci.* **35**(3): 810–825. doi:10.1086/686686.
- Bilby, R.E., Fransen, B.R., and Bisson, P.A. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can. J. Fish. Aquat. Sci.* **53**(1): 164–173. doi:10.1139/f95-159.
- Campbell, E.Y., Dunham, J.B., Reeves, G.H., and Wondzell, S.M. 2019. Phenology of hatching, emergence, and end-of-season body size in young-of-year coho salmon in thermally contrasting streams draining the Copper River Delta, Alaska. *Can. J. Fish. Aquat. Sci.* **76**(2): 185–191. doi:10.1139/cjfas-2018-0003.
- Chaloner, D.T., Martin, K.M., Wipfli, M.S., Ostrom, P.H., and Lamberti, G.A. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: evidence from artificial and natural streams. *Can. J. Fish. Aquat. Sci.* **59**(8): 1257–1265. doi:10.1139/f02-084.
- Chaloner, D.T., Lamberti, G.A., Merritt, R.W., Mitchell, N.L., Ostrom, P.H., and Wipfli, M.S. 2004. Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. *Freshw. Biol.* **49**(5): 587–599. doi:10.1111/j.1365-2427.2004.01213.x.
- Cleason, S.M., Li, J.L., Compton, J.E., and Bisson, P.A. 2006. Response of nutrients, biofilm, and benthic insects to salmon carcass addition. *Can. J. Fish. Aquat. Sci.* **63**(6): 1230–1241. doi:10.1139/f06-029.
- Collins, S.F., Marcarelli, A.M., Baxter, C.V., and Wipfli, M.S. 2015. A critical assessment of the ecological assumptions underpinning compensatory mitigation of salmon-derived nutrients. *Environ. Manage.* **56**(3): 571–586. doi:10.1007/s00267-015-0538-5. PMID:25968140.
- Collins, S.F., Baxter, C.V., Marcarelli, A.M., and Wipfli, M.S. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. *Ecosphere*, **7**(3): e01248. doi:10.1002/ecs2.1248.
- Duffy, E.J., and Beauchamp, D.A. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Can. J. Fish. Aquat. Sci.* **68**(2): 232–240. doi:10.1139/F10-144.
- Ebersole, J.L., Wigginton, P.J., Jr., Baker, J.P., Cairns, M.A., Church, M.R., Hansen, B.P., et al. 2006. Juvenile coho salmon growth and survival across

- stream network seasonal habitats. *Trans. Am. Fish. Soc.* **135**(6): 1681–1697. doi:10.1577/T05-144.1.
- Ericksen, R., Anders, P.J., Lewandowsky, C., and Siple, J. 2009. Status of kokanee populations in the Kootenai River in Idaho and Montana and South Arm Kootenay Lake, British Columbia [online]. Report prepared for Kootenai Tribe of Idaho. Available from https://www.researchgate.net/profile/Paul_Anders/publication/242236465_Status_of_Kokanee_Populations_in_the_Kootenai_River_in_Idaho_and_Montana_and_South_Arm_Kootenay_Lake_British_Columbia/links/0f31753b4355275697000000.pdf.
- Flitcroft, R., Lewis, S., Arismendi, I., Davis, C., Giannico, G., Penaluna, B., et al. 2019. Using expressed behavior of coho salmon (*Oncorhynchus kisutch*) to evaluate the vulnerability of upriver migrants under future hydrological regimes: management implications and conservation planning. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **29**(7): 1083–1094. doi:10.1002/aqc.3014.
- Ford, A., and Flynn, H. 2005. Statistical screening of system dynamics models. *Syst. Dyn. Rev.* **21**(4): 273–303. doi:10.1002/sdr.322.
- Gayeski, N.J., Stanford, J.A., Montgomery, D.R., Lichatowich, J., Peterman, R.M., and Williams, R.N. 2018. The failure of wild salmon management: need for a place-based conceptual foundation. *Fisheries*, **43**(7): 303–309. doi:10.1002/fsh.10062.
- Gerwing, T.G., and Plate, E. 2019. Effectiveness of nutrient enhancement as a remediation or compensation strategy of salmonid fisheries in culturally oligotrophic lakes and streams in temperate climates. *Restor. Ecol.* **27**(2): 279–288. doi:10.1111/rec.12909.
- Gresh, T., Lichatowich, J., and Schoonmaker, P. 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. doi:10.1577/1548-8446(2000)025<0015:AEHAC>2.0.CO;2.
- Gustafson, R.G., Waples, R.S., Myers, J.M., Weitkamp, L.A., Bryant, G.J., Johnson, O.W., and Hard, J.J. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. *Conserv. Biol.* **21**(4): 1009–1020. doi:10.1111/j.1523-1739.2007.00693.x. PMID:17650251.
- Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish bioenergetics 3.0. University of Wisconsin, Sea Grant Institute, WISCU-T-97-001, Madison.
- Harvey, B.C., and Wilzbach, M.A. 2010. Carcass addition does not enhance juvenile salmonid biomass, growth, or retention in six Northwestern California streams. *North Am. J. Fish. Manage.* **30**(6): 1445–1451. doi:10.1577/M10-022.1.
- Holtgrieve, G.W., and Schindler, D.E. 2011. Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology*, **92**(2): 373–385. doi:10.1890/09-1694.1. PMID:21618917.
- Honea, J.M., Jorgensen, J.C., McClure, M.M., Cooney, T.D., Engie, K., Holzer, D.M., and Hilborn, R. 2009. Evaluating habitat effects on population status: influence of habitat restoration on spring-run Chinook salmon. *Freshw. Biol.* **54**: 1576–1592. doi:10.1111/j.1365-2427.2009.02208.x.
- Janetski, D.J., Chaloner, D.T., Tiegs, S.D., and Lamberti, G.A. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia*, **159**(3): 583–595. doi:10.1007/s00442-008-1249-x. PMID:19132408.
- Keeley, E.R., and Grant, J.W.A. 2001. Prey size of salmonid fishes in streams, lakes, and oceans. *Can. J. Fish. Aquat. Sci.* **58**(6): 1122–1132. doi:10.1139/f01-060.
- Kiernan, J.D., Harvey, B.N., and Johnson, M.L. 2010. Direct versus indirect pathways of salmon-derived nutrient incorporation in experimental lotic food webs. *Can. J. Fish. Aquat. Sci.* **67**(12): 1909–1924. doi:10.1139/F10-110.
- Kiffney, P.M., Naman, S.M., Cram, J.M., Liermann, M., and Burrows, D.G. 2018. Multiple pathways of C and N incorporation by consumers across an experimental gradient of salmon carcasses. *Ecosphere*, **9**(4): e02197. doi:10.1002/ecs2.2197.
- Kohler, A.E., Pearsons, T.N., Zandt, J.S., Mesa, M.G., Johnson, C.L., and Connolly, P.J. 2012. Nutrient enrichment with salmon carcass analogs in the Columbia River basin, USA: a stream food web analysis. *Trans. Am. Fish. Soc.* **141**(3): 802–824. doi:10.1080/00028487.2012.676380.
- Kohler, A.E., Kusnierz, P.C., Copeland, T., Venditti, D.A., Denny, L., Gable, J., et al. 2013. Salmon-mediated nutrient flux in selected streams of the Columbia River basin, USA. *Can. J. Fish. Aquat. Sci.* **70**(3): 502–512. doi:10.1139/cjfas-2012-0347.
- Lefkovich, L. 1965. The study of population growth in organisms grouped by stages. *Biometrics*, **21**(1): 1–18. doi:10.2307/2528348.
- Lessard, J.A., Merritt, R.W., and Berg, M.B. 2009. Investigating the effect of marine-derived nutrients from spawning salmon on macroinvertebrate secondary production in southeast Alaskan streams. *J. N. Am. Benthol. Soc.* **28**(3): 683–693. doi:10.1899/08-141.1.
- Levi, P.S., Tank, J.L., Rüegg, J., Janetski, D.J., Tiegs, S.D., Chaloner, D.T., and Lamberti, G.A. 2013. Whole-stream metabolism responds to spawning Pacific salmon in their native and introduced ranges. *Ecosystems*, **16**(2): 269–283. doi:10.1007/s10021-012-9613-4.
- Marcarelli, A.M., Baxter, C.V., and Wipfli, M.S. 2014. Nutrient additions to mitigate loss of Pacific salmon: consequences for stream biofilm and nutrient dynamics. *Ecosphere*, **5**(6): 69. doi:10.1890/ES13-00366.1.
- Moore, J.W., Hayes, S.A., Duffy, W., Gallagher, S., Michel, C.J., and Wright, D. 2011. Nutrient fluxes and the recent collapse of coastal California salmon populations. *Can. J. Fish. Aquat. Sci.* **68**(7): 1161–1170. doi:10.1139/f2011-054.
- Naiman, R.J., Bilby, R.E., Schindler, D.E., and Helfield, J.M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*, **5**(4): 399–417. doi:10.1007/s10021-001-0083-3.
- Nehlsen, R.J., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries*, **16**(2): 4–21. doi:10.1577/1548-8446(1991)016<0004:PSATCS>2.0.CO;2.
- O'Keefe, T.C., and Edwards, R.T. 2002. Evidence for hyporheic transfer and removal of marine-derived nutrients in a sockeye stream in southwest Alaska. *Am. Fish. Soc. Symp.* **33**: 99–107.
- Passolt, G., and Anderson, J.J. 2013. A model linking ocean survival to smolt length. *North Pac. Anadromous Fish Comm. Tech. Rep.* **9**: 184–190.
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Wash.
- Railsback, S.R., Harvey, B.C., Jackson, S.K., and Lamberson, R.H. 2009. InSTREAM: the individual-based stream trout research and environmental model. General Technical Report, PSW-GTR-218. US Department of Agriculture, Forest Service, Albany, Calif.
- Rinella, D.J., Wipfli, M.S., Stricker, C.A., Heintz, R.A., and Rinella, M.J. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. *Can. J. Fish. Aquat. Sci.* **69**(1): 73–84. doi:10.1139/f2011-133.
- Sharma, R., Morishima, G., Wang, S., Talbot, A., and Gilbertson, L. 2006. An evaluation of the Clearwater River supplementation program in western Washington. *Can. J. Fish. Aquat. Sci.* **63**(2): 423–437. doi:10.1139/f05-228.
- Slaney, P.A., Ward, B.R., and Wightmans, J.C. 2003. Experimental nutrient addition to the Keogh River and application to the Salmon River in coastal British Columbia. In *Nutrients in salmonid ecosystems: sustaining production and biodiversity*. Edited by J. Stockner. American Fisheries Society, Bethesda, Md. pp. 111–126.
- Stockner, J.G. (Editor). 2003. Nutrients in salmonid ecosystems: sustaining production and biodiversity. American Fisheries Society, Bethesda, Md.
- Thurrow, R.F., Copeland, T., and Oldemeyer, B.N. 2020. Wild salmon and the shifting baseline syndrome: application of archival and contemporary red counts to estimate historical Chinook salmon (*Oncorhynchus tshawytscha*) production potential in the central Idaho wilderness. *Can. J. Fish. Aquat. Sci.* **77**(4): 651–665. doi:10.1139/cjfas-2019-0111.
- Twining, C.W., Palkovacs, E.P., Friedman, M.A., Hasselman, D.J., and Post, D.M. 2017. Nutrient loading by anadromous fishes: species-specific contributions and the effects of diversity. *Can. J. Fish. Aquat. Sci.* **74**(4): 609–619. doi:10.1139/cjfas-2016-0136.
- Uchiyama, T., Finney, B.P., and Adkison, M.D. 2008. Effects of marine-derived nutrients on population dynamics of sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **65**(8): 1635–1648. doi:10.1139/F08-085.
- Venditti, D.A., Kinzer, R.N., Apperson, K.A., Barnett, B., Belnap, M., Copeland, T., et al. 2017. Effects of hatchery supplementation on abundance and productivity of natural-origin Chinook salmon: two decades of evaluation and implications for conservation programs. *Can. J. Fish. Aquat. Sci.* **75**(9): 1495–1510. doi:10.1139/cjfas-2016-0344.
- Ward, B.R., and Slaney, P.A. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Can. J. Fish. Aquat. Sci.* **45**(7): 1110–1122. doi:10.1139/f88-135.
- Wheeler, K., Miller, S.W., and Crowl, T.A. 2017. Adfluvial salmonids have engineering but not fertilization impacts in tributaries of central Utah reservoir. *Can. J. Fish. Aquat. Sci.* **75**(3): 389–401. doi:10.1139/cjfas-2016-0462.
- Whitney, E.J., Bellmore, J.R., and Benjamin, J.B. 2019. User manual for the aquatic trophic productivity model: a river food web simulation model for management and research. Gen. Tech. Rep. PNW-GTR-973. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Ore.
- Whitney, E.J., Bellmore, J.R., Benjamin, J.B., Jordan, C.E., Dunham, J.B., Newsom, M., and Nahorniak, M. [In press.] Beyond sticks and stones: integrating both abiotic and biotic factors into watershed restoration assessments. *Food Webs*.
- Williams, R.N., Bisson, P.A., Bottom, D.L., Calvin, L.D., Coutant, C.C., Erho, M.W., Jr., et al. 1999. Return to the river: scientific issues in the restoration of salmonid fishes in the Columbia River. *Fisheries*, **24**(3): 10–19. doi:10.1577/1548-8446(1999)024<0010:RTTRES>2.0.CO;2.
- Wilson, S.M., and Corsi, M.P. 2016. Dworshak Reservoir nutrient enhancement research, 2007–2015, project completion report. Idaho Department of Fish and Game, Boise, Idaho, USA.
- Wipfli, M.S., Hudson, J., and Caouette, J. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. *Can. J. Fish. Aquat. Sci.* **55**(6): 1503–1511. doi:10.1139/f98-031.
- Wipfli, M.S., Hudson, J., Caouette, J., and Chaloner, D.T. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. *Trans. Am. Fish. Soc.* **132**(2): 371–381. doi:10.1577/1548-8659(2003)132<0371:MSIFES>2.0.CO;2.
- Zabel, R.W., and Achord, S. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. *Ecology*, **85**(3): 795–806. doi:10.1890/02-0719.

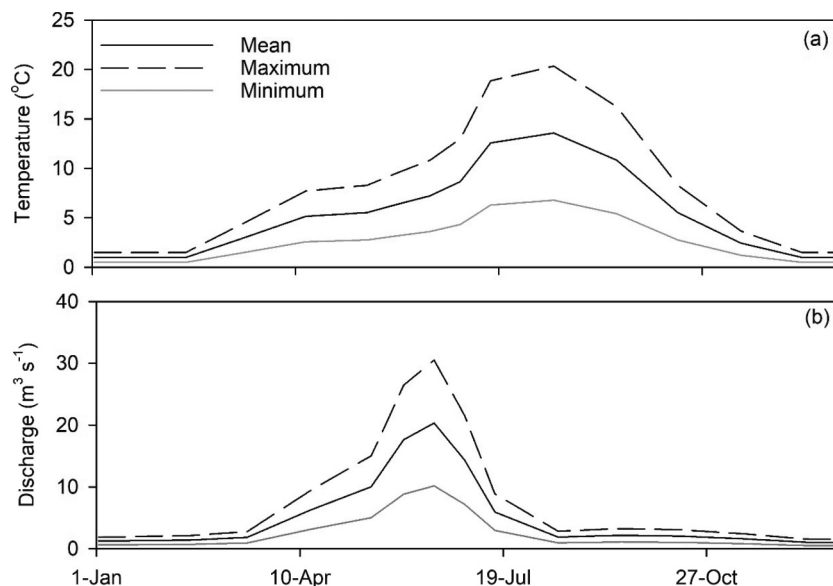
Appendix A

Appendix Table A1 and Figs. A1 and A2 appear on the following pages.

Table A1. Parameter descriptions, mean values used, and response of salmon smolt density from the Latin hypercube analysis to estimate model uncertainty.

Category	Parameter description	Value
Nutrients	Nitrogen excretion from live salmon ($\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	0.161
	Phosphorus excretion from live salmon ($\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	0.032
	Nitrogen leaching from dead salmon ($\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	0.016
	Phosphorus leaching from dead salmon ($\text{mg}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	0.003
Salmon eggs and carcass	Proportion of carcasses stranded in terrestrial habitats	0.5
	Coefficient for decay rate*	1.11
	Slope of export rate for salmon carcasses	14
	Slope of export rate for salmon eggs	18
Aquatic invertebrates	Salmon carcass assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)	0.7
	Periphyton assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)	0.4
	Maximum consumption rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	0.5
	Mortality rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)*	0.017
Nontarget fishes	Self-interaction parameter	9
	Salmon carcass assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)	0.3
	Salmon egg assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)	0.95
	Mortality rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	0.005
Periphyton	Aquatic invertebrate assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)*	0.75
	Fish assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)*	0.9
	Self-interaction parameter*	4
	Maximum consumption rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)*	0.16
Juvenile salmon	Maximum growth at optimum temperature ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	1.1
	Slope of export rate	10
	Half saturation level for density ($\text{g}\cdot\text{m}^{-2}$)*	4
	Half saturation level for phosphorus ($\text{mg}\cdot\text{L}^{-1}\cdot\text{day}^{-1}$)	0.005
Life cycle model	Salmon carcass assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)	0.3
	Salmon egg assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)	0.95
	Aquatic invert assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)	0.75
	Terrestrial invertebrate assimilation efficiency ($\text{g}\cdot\text{g}^{-1}$)*	0.7
Environmental	Self-interaction parameter*	3
	Egg mortality	0.4
	Coefficient of smolt mortality*	1.013
	Estuary mortality*	0.94
Environmental	Ocean mortality	0.2
	Prespawn mortality	0.1
	Female fecundity ($\text{eggs}\cdot\text{female}^{-1}$)*	3900
	Exponent of starvation mortality function*	7.5
Environmental	Degree days ($^{\circ}\text{C}$)*	See Fig. A1
	Discharge ($\text{m}^3\cdot\text{s}^{-1}$)	See Fig. A1
	Ambient dissolved inorganic nitrogen ($\text{mg}\cdot\text{L}^{-1}$)	0.06
	Ambient soluble reactive phosphorus ($\text{mg}\cdot\text{L}^{-1}$)*	0.006
	Channel gradient ($\text{m}\cdot\text{m}^{-1}$)	0.007

Note: Values were adjusted $\pm 25\%$ to determine uncertainty. An asterisk (*) identifies the fifteen most influential parameters to model results (see Fig. A1).

Fig. A1. Minimum, mean, and maximum annual temperature (a) and discharge (b) used in model simulation and sensitivity analysis.**Fig. A2.** Relative importance of different model parameters in determining the density of adult salmon during and after carcass addition based upon random forest analysis. Parameters not shown were relatively unimportant. See Table A1 for description of parameters.