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Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways

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Abstract. Artificial additions of nutrients of differing forms such as salmon carcasses and analog pellets (i.e. pasteurized fishmeal) have been proposed as a means of stimulating aquatic productivity and enhancing populations of anadromous and resident fishes. Nutrient mitigation to enhance fish production in stream ecosystems assumes that the central pathway by which effects occur is bottom-up, through aquatic primary and secondary production, with little consideration of reciprocal aquatic-terrestrial pathways. The net outcome (i.e. bottom-up vs. top-down) of adding salmon-derived materials to streams depend on whether or not these subsidies indirectly intensify predation on *in situ* prey via increases in a shared predator or alleviate such predation pressure. We conducted a 3-year experiment across nine tributaries of the N. Fork Boise River, Idaho, USA, consisting of 500-m stream reaches treated with salmon carcasses (n = 3), salmon carcass analog (n = 3), and untreated control reaches (n = 3). We observed 2–8 fold increases in streambed biofilms in the 2–6 weeks following additions of both salmon subsidy treatments in years 1 and 2 and a 1.5-fold increase in standing crop biomass of aquatic invertebrates to carcass additions in the second year of our experiment. The consumption of benthic invertebrates by stream fishes increased 110–140% and 44–66% in carcass and analog streams in the same time frame, which may have masked invertebrate standing crop responses in years 3 and 4. Resident trout directly consumed 10.0–24.0 g·m⁻²·yr⁻¹ of salmon carcass and <1–11.0 g·m⁻²·yr⁻¹ of analog material, which resulted in 1.2–2.9 g·m⁻²·yr⁻¹ and 0.03–1.4 g·m⁻²·yr⁻¹ of tissue produced. In addition, a feedback flux of terrestrial maggots to streams contributed 0.0–2.0 g·m⁻²·yr⁻¹ to trout production. Overall, treatments increased annual trout production by 2–3 fold, though density and biomass were unaffected. Our results indicate the strength of bottom-up and top-down responses to subsidy additions was asymmetrical, with top-down forces masking bottom-up effects that required multiple years to manifest. The findings also highlight the need for nutrient mitigation programs to consider multiple pathways of energy and nutrient flow to account for the complex effects of salmon subsidies in stream-riparian ecosystems.

Key words: Idaho; indirect effects; Pacific salmon; resource subsidies; salmon carcass analog; trophic control.

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INTRODUCTION

Globally, salmon have declined as a consequence of habitat degradation and harvest (Lichatowich 1999, Montgomery 2004), and in the Pacific Northwest they have been eliminated from approximately 40% of their historic range (NRC 1996). Declines in salmon abundance have caused a corresponding decrease in the transport of nutrients and organic matter from marine to freshwater environments, with only an estimated 6–7% of historical levels of nutrients being returned to natal streams by spawning runs (Gresh et al. 2000). Early recognition of the ecological importance of nutrient deposition to lakes by returning salmon led to a series of fertilization experiments aimed at enhancing populations and harvest (Juday et al. 1932, Stockner 2003, Hyatt et al. 2004), and similar programs were later adapted to streams (Naiman et al. 2002). These practices were initially developed as a means of stock enhancement, but more recently applied as a management approach for improving anadromous and resident fish populations and to benefit other aquatic and terrestrial organisms that historically utilized salmon-derived resource subsidies (Hyatt et al. 2004, Compton et al. 2006). Managers are turning to compensatory nutrient mitigation to potentially offset the negative effects of dams and other stressors on salmon populations, however, key assumptions of this approach remain largely unevaluated (Collins et al. 2015).

Nutrient mitigation as a management tool is rooted in assumptions that additions are needed to compensate for reduced returns of adult salmon, that added nutrients will “jump-start” productivity at multiple trophic levels, and that this ultimately will benefit an array of fishes. Though anadromous salmonids are typically the focus, nutrient mitigation may benefit resident fishes that would have historically utilized salmon-derived subsidies (e.g., Jaacks and Quinn 2014). In practice, nutrient additions are achieved by directly adding salmon carcasses, inorganic fertilizers, or pelletized salmon tissue (commonly referred to as carcass “analog”; Pearsons et al. 2007). Conceptually, such fertilization programs are based upon the assumption that the delivery of nutrients by adult salmon is necessary to sustain greater productivity of juvenile salmon because these nutrients stimulate aquatic primary

productivity, and are subsequently transferred to fishes via aquatic invertebrates (Nelson and Edmondson 1955, Stockner 2003, Collins et al. 2015). Yet, there are alternate pathways by which salmon-derived subsidies may subsidize stream food webs and influence fishes, such as the direct consumption of salmon tissues (i.e., carcass tissue, eggs, or fry; Scheuerell et al. 2007, Denton et al. 2009). In addition, carcasses are frequently removed (e.g., by bears) to adjacent riparian habitats, where a variety of organisms readily consume, convert, and transport the marine-derived energy and nutrients throughout the landscape (Hocking and Reimchen 2006, Quinn et al. 2009, Collins and Baxter 2014). This leads to the potential for reciprocal feedback to stream ecosystems, for instance through increased inputs of terrestrial arthropods, which, in turn, may contribute to sustaining stream fish populations (Wipfli and Baxter 2010). However, the occurrence of these terrestrial-aquatic feedbacks in response to nutrient mitigation has not been experimentally evaluated.

If nutrient additions are to achieve goals of mitigation, it is necessary to understand pathways by which salmon-derived subsidies flow through food webs, and how these changes influence responses of prey and predators. Based upon ecological theory (i.e., Fretwell 1977, Power 1992, Borer et al. 2006), the effects of fertilization on stream organisms across trophic levels should arise from a complex dynamic between bottom-up effects that originate from stimulation of primary producers and top-down influences of predation, though this dynamic may also depend upon the timescales of subsidy inputs, the duration of subsidy availability, and the timing of subsidy responses (Sears et al. 2004, Takimoto et al. 2009, Spiller et al. 2010). Although a spawning event may be relatively ephemeral, salmon-derived subsidies can have bottom-up effects on stream food webs, influencing algal biomass and primary production (Verspoor et al. 2010, Ebel et al. 2014) that may subsequently translate into increased aquatic invertebrate growth rates (Chaloner and Wipfli 2002, Minakawa et al. 2002) and elevated levels of invertebrate biomass or density that may persist through the weeks and months following spawning and carcass deposition (Wipfli et al. 1998, Verspoor et al. 2011). As stream fishes also directly consume materials

derived from salmon (Bilby et al. 1998, Scheuerell et al. 2007, Denton et al. 2009), this may improve their growth and condition (Wipfli et al. 2004, Guyette et al. 2013), but it is uncertain how long these may persist or if these changes influence the potential top-down effects of these fish. Moreover, the net outcome may be complicated because subsidies of salmon can affect responses of both prey and predators, and may depend on whether salmon-derived subsidies indirectly intensify predation on *in situ* prey via increases in a shared predator (apparent competition; Holt 1977), or alleviate such predation pressure (e.g., by providing an alternate prey source; Abrams and Matsuda 1996). In any case, the responses of organisms to artificial additions of salmon-derived subsidies may depend on the relative strength of responses of consumers across trophic levels, the net effect emerging from co-occurring top-down and bottom-up forces (Borer et al. 2006), as well as the efficiency of predators and their regulating influence on prey (Power 1992). Longer term, multitrophic levels studies are required to address these possibilities.

Nutrient mitigation treatments of different physical forms are added to streams, including dissolved or pelletized inorganic fertilizers (Wipfli et al. 2010), salmon carcasses added artificially, and pelletized salmon tissue (Kohler et al. 2008, 2012, Guyette et al. 2013). Variation in subsidy form may have implications for the pathways of energy and nutrient flow through the recipient community and influence how effective the tool is at achieving desired goals. From a mitigation policy perspective, these are currently considered analogous to one another because the quantities and ratios of nitrogen, phosphorus and other micronutrients may be similar (Pearsons et al. 2007); however, the treatment forms may have very different effects on organisms across trophic levels, and the extent to which effects propagate among habitats and influence stream-riparian linkages might differ as well. For instance, responses to carcasses vs. analog pellets may differ due to duration of persistence, palatability to consumers, and potential for translocation to terrestrial habitats. Particularly owing to the growing and widespread use of the analog pellets, there is need for experimental tests of responses to additions of salmon carcasses compared to the “analog” that address the extended suite of potential interactions and feedbacks in stream-riparian food webs.

Here, we present the results of a 4 year, manipulative experiment aimed at testing a suite of hypotheses regarding the effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways in streams of central Idaho that historically received returns of Pacific salmon. Specifically, we hypothesized that salmon subsidies increase the productivity of resident fishes through multiple pathways including (1) the bottom-up pathway through the stream biofilm and their aquatic invertebrate prey, (2) direct consumption of salmon-derived subsidies (i.e., tissue) by these fishes, and (3) amplified inputs of arthropod prey from terrestrial habitats. As salmon subsidies can affect multiple trophic levels simultaneously, we also hypothesized that the net effect of salmon subsidies on bottom-up and top-down processes across trophic levels would be asymmetrical. Finally, we hypothesized that the efficacy of mitigation tools (carcass vs. analog pellet) would differ due to varied pathways by which these subsidies influence recipient food webs.

METHODS

Study area

We conducted this experiment in nine 1st–3rd order streams located in the North Fork Boise River drainage in central Idaho, USA (Fig. 1, Table 1). This 980 km² drainage ranges in elevation from 1060–2990 m.a.s.l., is entirely contained within the Boise National Forest, and is located on the Idaho Batholith, a large geologic formation in central Idaho comprised primarily of granites, resulting in very low geologic inputs of nutrients. This region also experiences some of the lowest atmospheric nutrient deposition rates in the country (NADP 2012), resulting in nutrient poor, low conductivity, poorly buffered surface water. Studies in other streams draining the Idaho Batholith, including the North Fork Boise River, have demonstrated that stream biofilms are typically limited by N or co-limited by N and P (Marcarelli and Wurtsbaugh 2007, Sanderson et al. 2009, Marcarelli et al. 2014). The annual hydrograph of the North Fork Boise River is dominated by a spring snowmelt pulse peaking in late May, followed by a prolonged base flow period beginning in mid-late July. Although

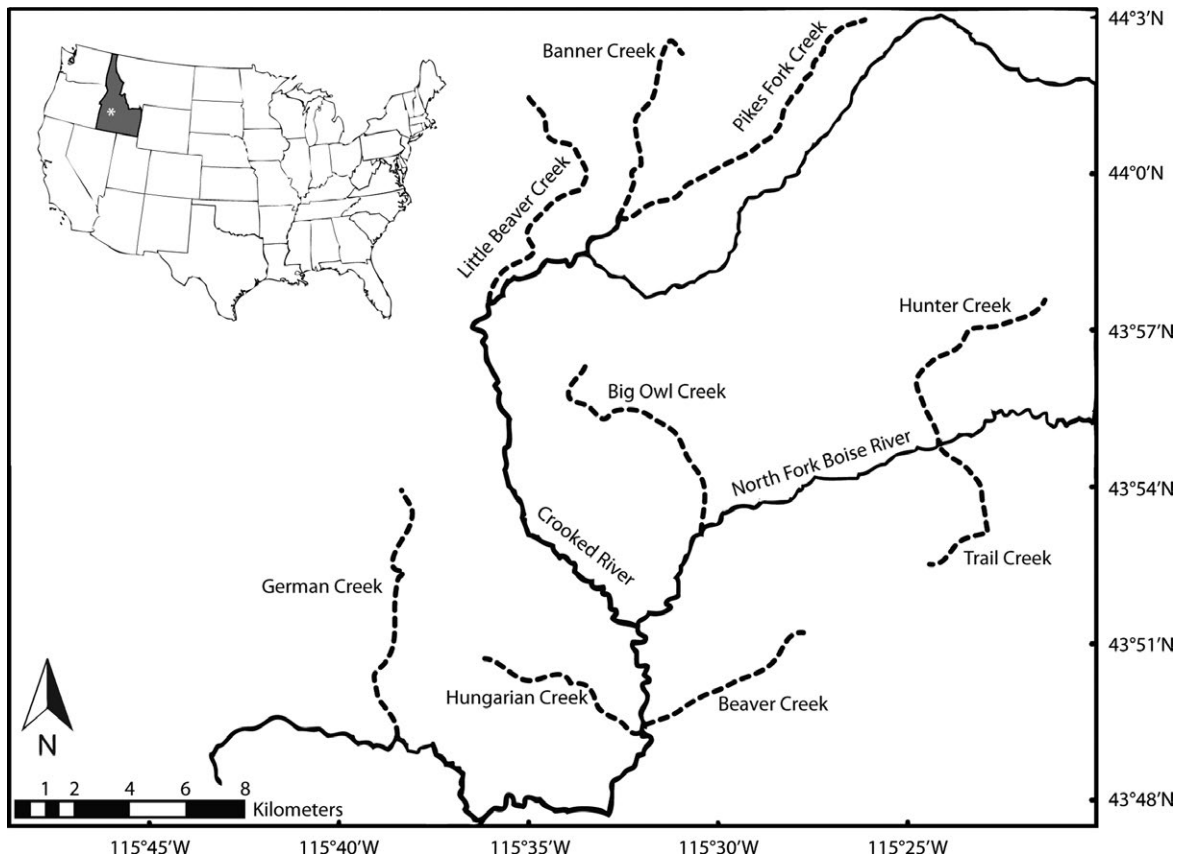


Fig. 1. Map of experimental streams and study area in the North Fork Boise River drainage, Idaho, United States. Dashed lines indicate study streams.

Table 1. Stream reach characteristics at each of nine streams in the North Fork Boise River drainage, Idaho, United States. Salmon carcasses and salmon analog pellets were added to the same 500-m reaches each year.

Treatment	Stream	Drainage area (km ²) [†]	Median particle size (mm) [‡]	Q (L/s) [§]	Volume in pools (m ³)	Volume in riffles and runs (m ³)	Large woody debris (no./100 m)
Control	Banner Cr.	23	30	66.4	56.6	64.0	0
	Beaver Cr.	15	45	32.7	0	29.1	0
	Hungarian Cr.	11	15	52.4	1.0	18.7	49
Carcass	Trail Cr.	20	75	66.5	2.7	32.0	16
	Little Beaver Cr.	6	10	26.9	18.9	35.6	7
	Big Owl Cr.	18	20	39.5	9.0	31.9	3
Analog	German Cr.	23	55	109.8	15.0	59.1	7
	Hunter Cr.	16	60	60.4	5.7	42.7	0
	Pikes Fork Cr.	28	30	61.2	28.1	99.9	21

[†] Area above the downstream end of the study reaches, determined using USGS StreamStats, <http://water.usgs.gov/osw/streamstats/>.

[‡] Estimated from 100 point counts in the downstream 100 m of the study reaches.

[§] Q Stream discharge, averaged across all measurements in the stream between 2008 and 2011.

^{||} Riffle and run volume determined in the downstream 100 m of the study reach in association with annual electrofishing surveys.

anadromous fishes including Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*) were historically abundant in this tributary of the Snake River (NWPCC 2004), the Boise River was blocked by the construction of three dams between 1906 and 1915, such that salmon migrations have been eliminated for over a century. Populations of resident fishes may have been negatively affected by these losses, and the potential for benefits to them were a key part of the rationale for experimental addition of salmon subsidies. Within our study sites, fish assemblages were dominated by rainbow trout (*O. mykiss*), non-native brook trout (*Salvelinus fontinalis*), and shorthead sculpin (*Cottus confusus*). Bull trout (*S. confluentus*) were also present, but so rare that we were unable to evaluate any treatment effects.

Experimental treatments and design

We evaluated two commonly used nutrient mitigation tools in our experiment: annual additions of pasteurized salmon carcasses (*O. mykiss*, *O. tshawytscha*) obtained from regional fish hatcheries, and pelletized salmon carcass material, or “analog”. To address concerns highlighted by Compton et al. (2006) that transporting salmon carcasses between basins may facilitate the spread of fish disease, all salmon carcasses were frozen for storage then pasteurized (internal temperature of 60°C for 20 min). The freezing and pasteurization process was implemented to kill fish pathogens (e.g., whirling disease, *Myxobolus cerebralis*), as is required by the State of Idaho and U.S. Fish and Wildlife Service. Because of the logistical difficulty of handling, transporting, and pasteurizing fish carcasses, salmon carcass analog is an increasingly popular mitigation tool in streams of the Pacific Northwest (Pearsons et al. 2007, Kohler et al. 2012), including central Idaho (Kohler et al. 2008, Ebel et al. 2014). This material is also pasteurized and pathogen-free, and it is manufactured from fish meal so it contains nutrient content similar to salmon carcasses, but it can also be manipulated so that its nutrient content matches that of naturally spawning fish (Pearsons et al. 2007). Several studies have shown that stream producers and consumers utilize nutrients from analog pellets (Wipfli et al. 2004, Kohler et al. 2012, Marcarelli et al.

2014). We chose these two treatments because they are considered the most realistic mimics of material delivered by naturally spawning salmon (but see Collins et al. 2015), and include a full suite of nutrients including carbon, nitrogen, phosphorus, trace metals and other micronutrients. Moreover, these two treatments are being applied and considered as mitigation activities throughout the region.

We used a randomized experimental design in which reaches of nine streams were selected that were typical for the region (e.g., lithology, geomorphology, vegetation and history of wildfire; Dunham et al. 2007), spanned a range of sizes that historically would have been used by spawning salmon and steelhead (IDFG 1985), and had similar resident fish assemblages. At all of these sites, we made additional measures of several habitat characteristics known to influence periphyton, invertebrates and fishes, and though these varied among streams (see Table 1), neither stream size nor these added habitat measures differed systematically by treatment (ANOVA, d.f., 2, 6; discharge, particle size, drainage area, habitat volume, $P > 0.05$). Carcass loading rates were based on a target of 0.5 salmon carcasses m^{-2} of wetted stream channel, chosen to reflect a high spawner density based upon historical data for streams of this region (IDFG 1985). Analog treatment rates were adjusted to match P application rates from salmon carcasses at 5.5 g $P m^{-2}$. Differences in N content of carcasses and analog resulted in an N application rate of 27 g $N m^{-2}$ to analog-treated streams and 50 g $N m^{-2}$ to carcass-treated streams (Table 2; Marcarelli et al. 2014, Wheeler et al. 2014). Carcass or analog treatments were applied annually to the same 500 m reaches of their respective streams during the first week of August for three consecutive years (2008–2010). Crews walked along untreated control streams to mimic the disturbance to treated streams during treatment deployment.

Measurement of periphyton and benthic invertebrate biomass

We quantified responses of periphyton and benthic invertebrate biomass within riffles of all study streams. We sampled periphyton standing crop biomass prior to and 2 and 6 weeks following treatment application in 2008, prior to and 1 month following treatment application

Table 2. Annual loading rates (g m^{-2}) of salmon carcass and analog pellets to streams. Loading rates were based on wetted widths. Loading rates of N from salmon carcasses were estimated based on a composition of 11.7% N. Loading rates of N from analog pellets were estimated based on a composition of 9% N. Salmon carcasses and salmon analog pellets were added to the same 500-m reaches each year.

Treatment	Site	Treatment (g m^{-2})			N (g m^{-2})		
		2008	2009	2010	2008	2009	2010
Carcass	Trail	333.1	336.0	337.7	49.6	50.1	50.3
	Little Beaver	275.2	275.7	274.7	50.5	50.6	50.4
	Big Owl	335.9	335.5	339.5	49.6	49.5	50.1
Analog	Hunter	78.1	49.1	78.1	39.5	24.8	25.1
	Pikes Fork	61.2	55.4	61.2	27.6	25.0	25.1
	German	80.8	81.6	80.8	24.7	25.0	25.0

in 2009 and 2010, and 1 year following the final application in 2011 at seven random locations within the downstream half of each treatment reach (0–250 m). Standing crop biomass was estimated as chlorophyll *a* and ash-free dry mass (AFDM) using standard methods (APHA 2005). Planar rock area was determined by tracing the rocks onto paper and weighing the cutout (Bergey and Getty 2006). To evaluate inter-annual responses, benthic macroinvertebrates were sampled at the same seven random locations as periphyton, once per year prior to treatment applications. Here, we quantified inter-annual responses of benthic invertebrates, which matched the annual sampling of fish populations. Interannual responses of benthic invertebrates are less represented in the ecological literature than short-term responses (see review by Collins et al. 2015), which have been reported extensively in prior studies of salmon nutrient mitigation (e.g., Wipfli et al. 1998, Minakawa et al. 2002, Kohler and Taki 2010, and others). We sampled riffle habitats with a Surber sampler (0.09 m^2 , $250 \mu\text{m}$ mesh size) to a substrate depth of approximately 10 cm. In the laboratory, macroinvertebrates were separated from detritus, identified to genus, and then measured to the nearest 0.5 mm. The biomass of each taxon was then calculated using length-weight relationships obtained from the literature (Benke et al. 1999).

Resident fish gut contents, abundance, biomass, and annual production

From 2008–2011, 1438 trout and sculpin were tagged (passive integrated transponder [PIT] tags), with 863 recaptures. Here, we refer to

responses by resident trout instead of individual species because rainbow and brook trout were sympatric in a subset of streams and comparisons showed their responses were similar. Likewise, sculpin were present in a subset of streams, and we present their responses separately. Sampling of fishes for growth rate estimation and gut contents was always conducted in the same sampling reach over the duration of the experiment, and occurred during annual sampling events (2008–2011), as well as in the weeks following annual treatment additions (2008 – 2, 6 weeks post treatment application; 2009 and 2010 – 2, 4, 6 weeks post treatment application). Due to the elevation of sites, snow and ice covered streams prevented access for growth rate and gut content sampling from late autumn through early spring. Changes in weight of tagged and recaptured fishes between sampling periods were used to determine rates of growth. Short-term growth responses were measured during the first 0–6 weeks immediately after treatment applications of each year. Overwinter growth rates accounted for periods of time from early October, through winter, to sampling periods occurring in July. The gut contents from a subset ($n = 10\text{--}15$ per species) of fishes from each stream were nonlethally collected during each sample period using gastric lavage. Samples were stored in 90% ethanol until processed. In the laboratory, macroinvertebrates (identified to Family; classified as aquatic or terrestrial), salmon carcass tissue, resident fishes, analog material, and eggs in gut samples were dried and weighed.

Density and biomass of stream fishes were estimated annually prior to experimental treatment additions. At each stream, fishes were sampled within a 100 m section of the study reach using a backpack electrofisher (~500 V, 45 Hz). The 100 m sections were blocked at the upstream and downstream ends with 6 mm diameter mesh netting. After each pass, all fish were measured (Salmonidae, fork length; Cottidae, total length), weighed, and tagged. We estimated fish age using length-frequency graphs (Isely and Grabowski 2007). Using the removal module with program CAPTURE, we estimated population size for each age class (White et al. 1982). We then calculated density and biomass for each age class by dividing abundance by reach area. To account for fishes not collected during the multipass removal sampling, biomass was calculated by multiplying the average weight of fish within each age class by the density of the same age class. Annual production was estimated at each stream using the increment summation method for each age class based upon the population estimates and growth rates (Newman and Martin 1983, Hayes et al. 2007). Sculpin (likely shorthead sculpin, *Cottus confusus*, though taxonomy of this group is in active revision; e.g., Lemoine et al. 2014) were present in only six of the nine study streams, one of which was a control stream, which precluded statistical analysis of their responses. Although sculpin were not present in all streams, we report their annual production because they are an often-underrepresented yet important component of stream food webs (Swain et al. 2014).

Trophic basis of trout production and annual consumption of benthic invertebrates

To quantify the different pathways of organic matter flow to trout and sculpin, and how they were affected by subsidy additions, we used the trophic basis of production approach (Benke and Wallace 1980). This approach accounts for both the quality and quantity of a diet item in its contribution to production. Production ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) and gut content (proportion of mass) data were used to quantify the production attributable to diet items (i.e., treatment material, benthic invertebrates, terrestrial maggots) consumed by trout and the annual quantity of each item consumed (Benke and Wallace 1980, Cross et al. 2013). Proportions of diet items

consumed during our experiment were averaged for each sample period for each stream. The portion of production attributed to a given diet item (F_i) was calculated as:

$$F_i = (G_i \times AE_i \times NPE)$$

where G_i is the proportion of food type i in the consumers diet, AE_i is the assimilation efficiency of food type i , and NPE is the net production efficiency (Bellmore et al. 2013, Cross et al. 2013). We used the following assimilation efficiencies for resident trout and sculpin: 0.75 for benthic aquatic invertebrates, 0.70 for terrestrial invertebrates, and 0.95 for fish tissue and brook trout eggs (Warren and Davis 1967, Elliott 1976). Net production efficiency was 0.21 and 0.12 for age 0 and age 1+ to account for allometric relationships between fish consumption and growth with fish size (Donner 2011, Bellmore et al. 2013). To determine the relative contribution of each diet item to fish production for each sampling interval, we used:

$$PF_{ij} = \frac{F_i}{\sum_{i=1}^n F_i} \times P_j$$

where P_j is the total sum of production estimates for each fish species. Finally, to determine the total annual consumption of benthic invertebrates by trout and sculpin, annual flows from each food type i to consumer j were calculated by dividing PF_{ij} by the product of AE_i and NPE for each sampling period.

Statistical analyses

To evaluate the hypothesis that salmon subsidies take multiple pathways (i.e., bottom-up, direct consumption, terrestrial feedbacks) through food webs to influence resident fishes, we quantified responses across trophic levels and through time. Data were analyzed using repeated-measures analysis of variance (rmANOVA) with treatment (carcass, analog, control) as the fixed factor and stream biofilm, benthic invertebrate biomass (total biomass and by Order), fish biomass and density, annual consumption of invertebrates, and annual production of resident trout as response variables.

To evaluate the hypothesis that subsidies would asymmetrically affect both bottom-up (biofilm, invertebrates) and top-down processes, such that shorter lived organisms may exhibit responses quickly and longer lived taxa may require longer periods of time for effects to manifest, we used the treatment \times time interaction to assess the responses of organisms across trophic levels. Finally, to test the hypothesis that the efficacy of mitigation tools (carcass vs. analog pellet) would differ because of the range of food web pathways influenced and the magnitude of responses through each pathway, *a priori* contrasts between treatments and control were conducted for all main treatment effects. For all statistical tests, P -values < 0.05 were considered significant, and those between 0.05 and 0.1 were considered marginally significant, though of potential ecological meaning given the low replication and statistical power of this large scale field experiment. All response variables were log transformed to correct for non-normality of residuals and heteroscedasticity. Analyses were conducted using SAS v.9.2 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Periphyton and insect biomass

Overall responses of chlorophyll *a* (Treatment, $F_{2,6} = 1.35$, $P = 0.328$) and AFDM (Treatment, $F_{2,6} = 2.59$, $P = 0.154$) to subsidy additions were not detected. However, 2–6 fold increases in chlorophyll *a* biomass (Treatment \times Time, $F_{3,50} = 7.41$, $P = 0.0003$) and AFDM (Treatment \times Time, $F_{3,50} = 3.68$, $P = 0.0179$) were observed in the short term (2–6 weeks) following treatment additions. Short-term increases occurred in 2008–2010 for analog and 2008 and 2009 for carcass treatments (Fig. 2a, b). However, these short-term increases did not carry-over to the following year, such that streams that were treated with salmon subsidies the previous year did not have significantly elevated periphyton biomass the following summer (Fig. 2a, b).

Overall, treatment additions increased total benthic invertebrate biomass (Treatment, $F_{2,6} = 9.79$, $P = 0.012$), with carcasses having the strongest effect (Carcass vs. control, $F_{1,6} = 18.46$,

$P = 0.005$; Carcass vs. analog, $F_{1,6} = 9.41$, $P = 0.022$), but in general responses became dampened with each subsequent year of the experiment. Benthic invertebrate biomass positively increased following the first year of salmon carcass additions (Year \times Treatment, $F_{6,18} = 2.68$, $P = 0.048$); however, this pattern was not observed in streams treated with analog, nor were the effects of either treatment detected in 2010 or 2011 (Fig. 3). During 2009, standing crop biomass of invertebrates in streams treated with salmon carcasses was two times that of control and analog streams (Fig. 3). Within the aquatic insect assemblage, biomass of Diptera larvae increased in these carcass-treated streams (Treatment, $F_{2,6} = 8.37$, $P = 0.018$), doubling from 2008 to 2009, 1 year after the initial treatment additions (Treatment \times Year, $F_{6,18} = 2.37$, $P = 0.073$), however, this pattern was not observed in 2010 or 2011. When analyzed individually, we detected no significant overall treatment effects or treatment by year interactions for the Orders Plecoptera, Coleoptera, Trichoptera, or Ephemeroptera (rmANOVA, $P > 0.1$).

Biomass, density, growth rates, and annual production of resident fishes

Contrary to our expectations, we detected no overall effects of treatment additions on the standing crop biomass (Treatment, $F_{2,6} = 2.34$, $P = 0.177$) or density (Treatment, $F_{2,6} = 0.39$, $P = 0.694$) of resident trout, nor were any treatment effects detected across years (Year \times Treatment, $P > 0.05$; Fig. 4a, b). In addition, no effect of treatment ($P > 0.05$), year ($P > 0.05$), or treatment by year interaction ($P > 0.05$) was detected on standing crop biomass or density for any age class. The average weight of trout collected during annual samplings (July) did not differ by treatments for age-1 (Treatment, $F_{2,6} = 1.02$, $P = 0.416$), age-2 (Treatment, $F_{2,6} = 1.78$, $P = 0.247$), or age-3+ (Treatment, $F_{2,6} = 0.26$, $P = 0.782$; Fig. 5a, b, c). On the other hand, the rate of growth of individual trout was strongly influenced by treatments (Fig. 6). In the weeks following treatment additions, growth rates of age 1 + trout were five times greater than controls (Treatment, $F_{2,6} = 7.44$, $P = 0.023$) and three to six times greater for age 3 + trout (Treatment, $F_{2,6} = 14.84$, $P = 0.004$; Fig. 6). In general, these increases

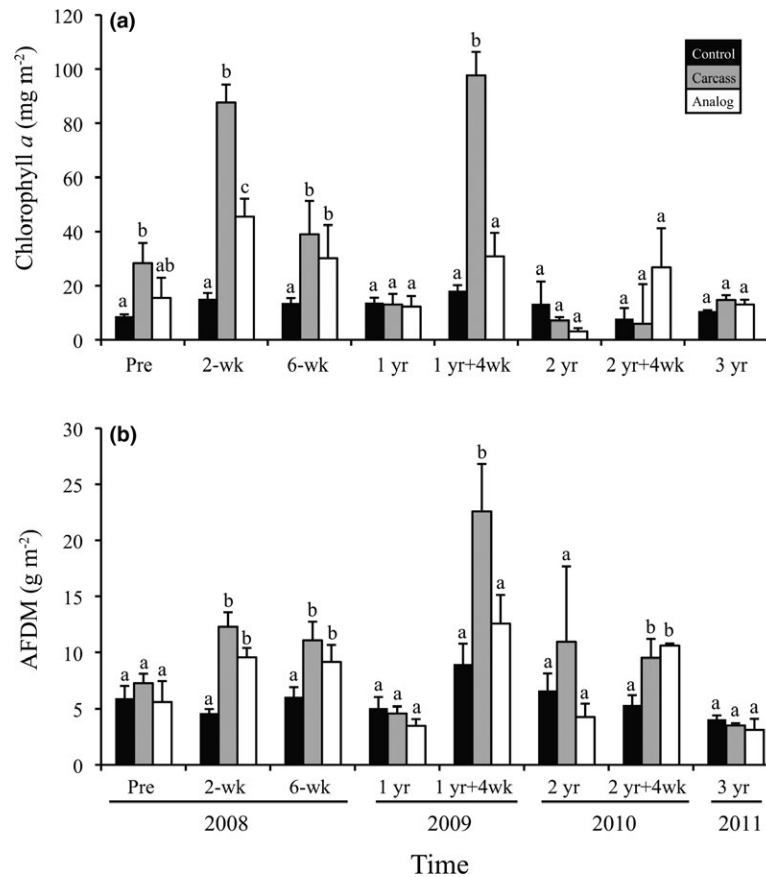


Fig. 2. Chlorophyll *a* (a) and ash-free dry mass (AFDM) (b) of stream biofilms sampled prior to (Pre, 2008), and the weeks and years following annual treatment additions from 2008–2011. Groups of columns represent treatments and control for specific sampling periods. Samples 1, 2 and 3 yr represent inter-annual sampling that occurred prior to annual treatment additions. Treatment additions occurred during August of 2008–2010. Error bars are ± 1 SE ($n = 3$). Differing lower case letters denote differences between treatments. For additional biofilm responses, please refer to Marcarelli et al. (2014).

in growth rates did not differ between carcass and analog treatments for age 1+ trout (carcass vs. analog, $F_{1,6} = 0.18$, $P = 0.685$), however, among the largest trout (age-3+) the carcass treatment had the larger effect (carcass vs. analog, $F_{1,6} = 20.49$, $P = 0.004$). In addition, rates of growth calculated for the over-winter period were greater for age 1+ trout (Treatment, $F_{2,6} = 8.41$, $P = 0.018$) in carcass (carcass vs. control, $F_{1,6} = 14.46$, $P = 0.008$) and analog (analog vs. control, $F_{1,6} = 10.45$, $P = 0.017$) treatments relative to control streams. In contrast, overwinter growth rates of age-3+ trout did not differ from controls in either carcass or analog treatments (Treatment, $F_{2,6} = 3.18$, $P = 0.114$; Fig. 6).

In contrast to the lack of response in terms of trout density or biomass, but consistent with the observed increases in growth, treatment additions caused 2–3 fold increases in estimates of annual trout production (Fig. 7a; Treatment, $F_{2,6} = 12.23$, $P = 0.007$). Within control streams, trout production ranged from 3.1 to 4.2 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ over the duration of our experiment (Fig. 7a), whereas within analog and carcass-treated streams it ranged from 6 to 8 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ and 8 to 12.5 $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$, respectively. Contrasts indicated that trout production in both carcass (carcass vs. control, $F_{1,6} = 20.60$, $P = 0.002$) and analog (analog vs. control, $F_{1,6} = 10.47$, $P = 0.017$) treated streams differed from those in control streams, but not from one another (carcass vs. analog, $F_{1,6} = 2.63$, $P = 0.155$).

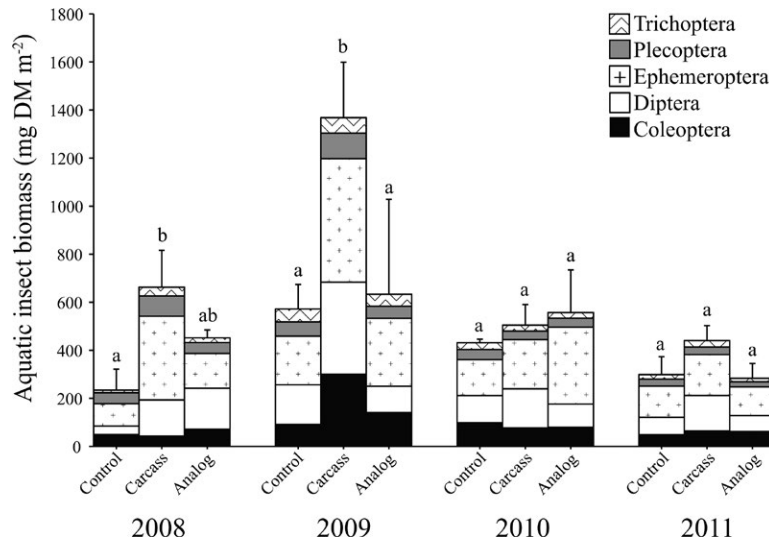


Fig. 3. Annual biomass of larval aquatic insects sampled from 2008 to 2011. Insect biomass increased significantly during summer 2009 in carcass treatments, but not in 2010 or 2011. Error bars are ± 1 SE ($n = 3$). DM = dry mass. Differing lower case letters denote statistically significant differences between treatments.

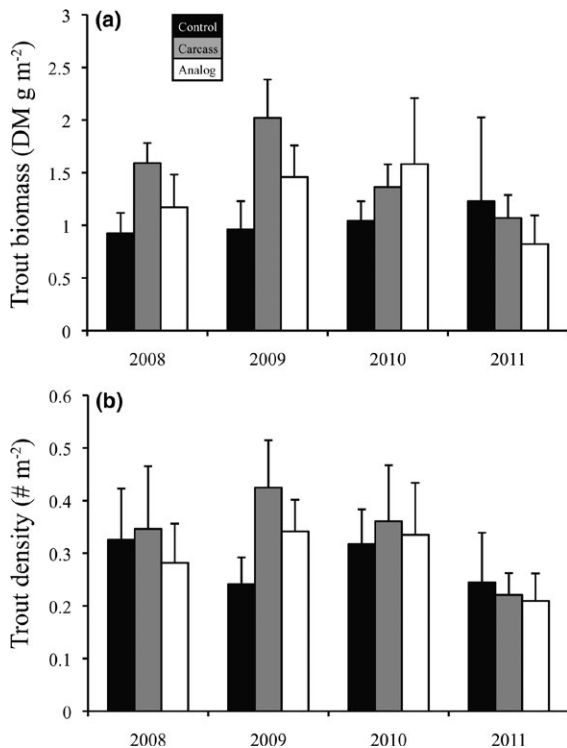


Fig. 4. Biomass (a) and density (b) of trout in streams of the North Fork Boise basin during annual sampling events for years 2008–2011. Error bars are ± 1 SE ($n = 3$).

Sculpin production at both Banner Cr. (Control: 2.15–5.11 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, SD: 1.48) and Little Beaver Cr. (Carcass: 1.40–4.01 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, SD: 1.49) fluctuated over the years of the experiment, initially increasing, then decreasing, whereas their production at Pikes Fork Cr. (Analog: 1.01–4.08 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, SD: 1.64) declined over the duration of the experiment. In contrast, sculpin production at German (Analog: 0.01–0.33 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, SD: 0.16), Trail (Carcass: 0.63–4.91 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, SD: 2.21), and Big Owl creeks (Carcass: 1.08–4.94 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, SD: 1.96) all increased through time.

Trophic basis of trout production and annual consumption of benthic invertebrates

The trophic basis of production of resident trout was influenced by salmon subsidies through direct consumption of the materials added, and via both aquatic and terrestrial pathways. Across treated streams, trout populations directly consumed 10–24 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ of salmon carcass tissue and <1–11 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ of analog material during the weeks it was available. This consumption accounted for an estimated 3–5% of the carcass material added and 4–11% of analog material added, and fueled 17% and 6% of trout annual production, respectively (Fig. 8). Unexpectedly, other forms of piscivory by trout (i.e.,

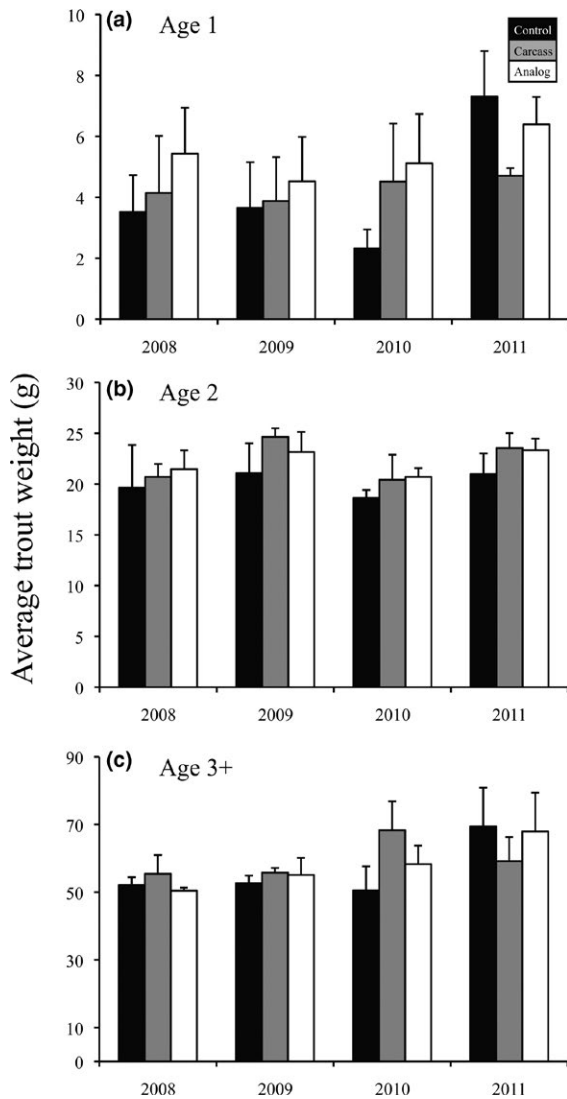


Fig. 5. Average weight of (a) age 1, (b) age 2, and (c) age 3 + trout sampled during annual (July) population surveys for years 2008–2011. Error bars are ±1 SE (n = 3).

consumption of sculpin, rainbow trout fry, brook trout eggs) were 2.6–7.6 times greater in analog ($0.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) and carcass ($2.3 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) treatments, respectively, than in controls ($0.3 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). Collectively, piscivory accounted for 8% of resident trout production in control streams. In contrast, piscivory accounted for 36% and 17% of trout production in carcass and analog treatments. Allochthonous inputs of terrestrial invertebrates (i.e., adult flies, maggots) accounted for approximately 14% of annual

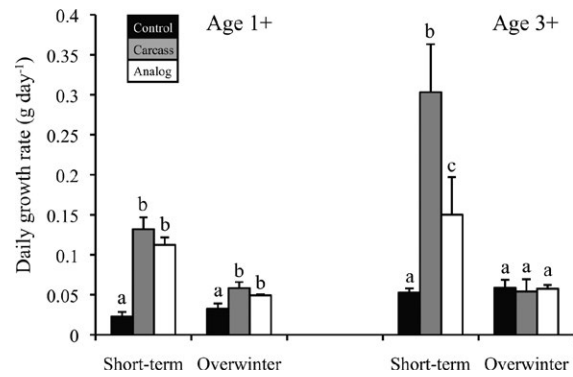


Fig. 6. Growth rates of resident trout for age 1+ and age 3+ trout. Short-term responses occurred in the 0–6 weeks post treatment applications of each year. Overwinter growth rates account for periods of time from early October, through winter, to sampling periods occurring in July. Error bars are ±1 SE (n = 3). Differing lower case letters denote statistically significant differences between treatments.

production in carcass treatments, 10% in analog treatments, and 5% in controls. The occurrence of maggots of terrestrial Diptera was highly variable among streams that were treated with carcasses, and they did not occur in control or analog-treated streams. In turn, trout production attributable to consumption of maggots ranged from 0 to $2.09 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (SD: 1.08), or 7% of annual trout production in streams treated with salmon carcasses.

The annual consumption of aquatic invertebrates by trout and sculpin was greatest in treatment streams, based on our estimates of the annual flows of aquatic invertebrate biomass required to fuel the fish production we observed (Treatment, $F_{2,6} = 6.28$, $P = 0.033$; Fig. 7). Overall, consumption of aquatic invertebrates in both carcass (carcass vs. control, $F_{1,6} = 14.96$, $P = 0.008$) and analog (analog vs. control, $F_{1,6} = 5.17$, $P = 0.063$) was greater than control streams, but did not differ between treatments (carcass vs. analog, $F_{1,6} = 2.54$, $P = 0.161$). Consumption of aquatic invertebrates by resident fishes did not differ between treatment and control streams during the first year of the experiment. However, in the following 2 years consumption of aquatic invertebrates increased 110–140% and 44–66% in carcass and analog streams, respectively.

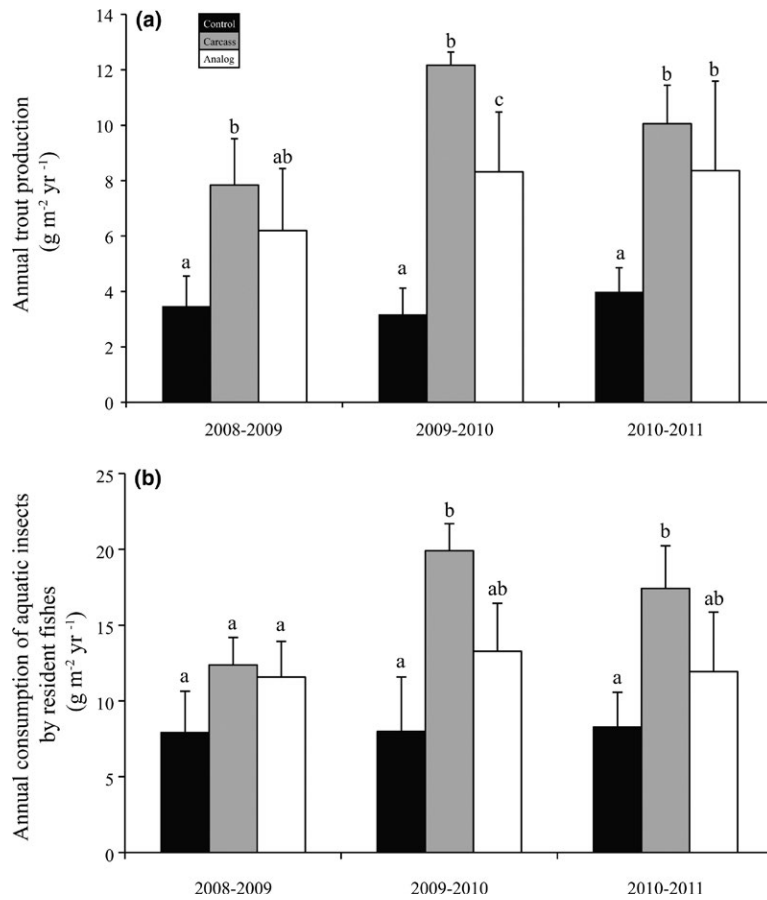


Fig. 7. (a) Annual production of resident trout and (b) the estimated consumption of benthic invertebrates by resident fishes over the duration of the experiment. Error bars are ± 1 SE ($n = 3$). Differing lower case letters denote statistically significant differences between treatments.

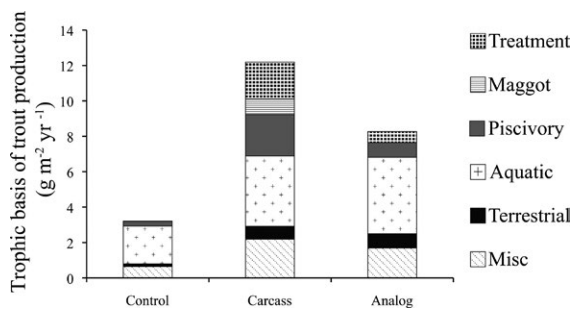


Fig. 8. Trophic basis of trout production for aquatic, terrestrial, and salmon-subsidy diet items. Treatment additions increased the trophic basis of trout production through the consumption of benthic invertebrates, piscivory, and direct consumption of both salmon carcass and salmon carcass analog material.

DISCUSSION

Our field experiment showed that the direct and propagating effects of salmon-derived subsidies through food web pathways that crossed land-water boundaries resulted in increased growth and production (though not local abundance) of resident stream fishes, which, in turn, strengthened top-down control of stream invertebrates. In addition, the magnitude of bottom-up and top-down responses of organisms to experimental additions of these subsidies was influenced by the form of the subsidy (i.e., carcass vs. analog pellet). Moreover, the removal of salmon carcasses from the stream and subsequent utilization by terrestrial organisms resulted in increased allochthonous inputs of

terrestrial arthropods back into the stream. Such effects were not observed for analog pellets, which were not removed from streams due to their physical form. Taken together, these findings indicate resident fishes may respond to attempts to mitigate for the loss of salmon-derived nutrients, but that the form of additions and diversity of associated food web pathways are important to consider when implementing such management tools.

A primary goal of nutrient mitigation is to increase productivity of salmonid fishes (e.g., resident, anadromous) by producing more and larger fish (Stockner 2003, Collins et al. 2015). Our findings suggest a disparity may occur between the measured response of individuals vs. those of populations, and different metrics used to evaluate population-level changes may yield different perspectives. We observed individual fish readily responded to subsidy additions in the short term, which contributed to strong increases in their annual production, yet we did not detect responses in fish standing crop biomass or density, metrics that are much more commonly assessed than production. Standing crop biomass and density of fishes represent a snapshot in time. We hypothesize that increased short-term growth increased the metabolic requirements of fishes, resulting in a cropping of invertebrates through late fall, winter, and spring, which reduced food resources and allowed density-dependent factors to regulate biomass and abundance of resident fishes in the reaches we monitored. Although we did not quantify immigration and emigration by trout, our treatment additions may have contributed to emigration by subsidized fishes to potentially more profitable habitats with less competition located outside of the study reaches, as has been observed in other studies of subsidy effects on fish populations (Denton et al. 2009). Larger fish may have moved throughout the river network, thus distributing any demographic responses and making them less detectable in our study reaches. Studies at larger (e.g., sub-watershed) scales may be needed to better address demographic responses to subsidies from salmon, whether added as mitigation efforts or associated with natural runs. For instance, in a coastal British Columbia river, inorganic nitrogen and phosphorus fertilizers were continuously (May–September) added to a 29 km stretch over

multiple years, resulting in bottom-up stimulatory effects across trophic levels that ultimately increased outmigration of salmon smolts, ocean survival, and returns of adults (Slaney et al. 2003, Ward et al. 2003). Moreover, multiple generations of resident fishes may need to experience these annual subsidies to induce a local effect on a population. However, the timescales necessary to encompass multiple trout generations exceeded the duration of our 3-year experiment.

The direct consumption of subsidy materials by stream fishes provided a direct and efficient linkage from subsidy to fish. Both carcass and analog material were readily consumed in the weeks when it was available to fishes. Trout consumed more carcass than analog material, and in turn, exhibited more production. Others have documented the direct consumption of salmon-derived subsidies by fishes, suggesting their direct utilization is commonplace (Scheuerell et al. 2007, Denton et al. 2009). We detected additional pathways of piscivory, specifically the consumption of sculpin, brook trout eggs, and rainbow trout fry in both treatments, and more of this occurred in streams treated with salmon carcasses than those treated with analog material. The mechanisms driving increased piscivory may be increased growth rates and gape size of predators, increased recruitment of sculpin populations, shifts in foraging modes, or some combination of processes. Sculpin production increased through time in two of three streams treated with carcasses. The absence of sculpin in some of the study streams precluded rigorous statistical analyses of their density or biomass responses to treatment applications. Nevertheless, our trophic basis calculations indicated that more trout production was attributable to the consumption of sculpin in streams treated with salmon carcasses relative to control streams. To our knowledge, this is the first evidence of increased piscivory through multiple pathways due to salmon-derived subsidies.

Salmon-derived subsidies entered food webs across multiple trophic levels, with effects that propagated through aquatic and terrestrial environments in a manner more complex than the simplified bottom-up pathway that presently informs most salmon nutrient mitigation efforts (Stockner 2003, Collins et al. 2015). Terrestrial insects responded to subsidy materials exposed near the wetted margins of the stream

or carcasses removed entirely from the stream by bears. Consideration of such terrestrial responses falls outside the scope of most mitigation efforts focused on nutrients, however, our findings indicate that short-term responses by terrestrial insects had substantial effects on trout production. Terrestrial Diptera larvae (i.e. maggots, Family: Calliphoridae) have been observed in the diets of salmonids (Scheuerell et al. 2007, Denton et al. 2009), but the overall contribution of these allochthonous inputs to annual production has not previously been determined in the context of salmon mitigation. Our results indicated that, on average, the allochthonous input of Diptera maggots accounted for 7% of annual trout production when salmon carcasses were present. This pathway did not occur in streams treated with analog because the pellets were not removed from the stream and therefore could not be colonized by flies. Allochthonous inputs of terrestrial arthropods (excluding maggots) contributed to 6 and 9% of annual trout production in carcass and analog treatments, respectively, a slight increase from the 4% observed in controls. In a related study, the presence of both salmon carcasses and analog acted as an attractant, drawing aerial insects towards the riparian zone (Collins and Baxter 2014), and based on our observations, the decomposition of analog material also smelled “fishy,” suggesting that a similar odor drew adult flies to these sites. The role of salmon carcasses as both attractant and substrate for colonization indicates that subsidy form can impact both the magnitude and mechanism (i.e., behavioral, demographic) of consumer responses in adjacent habitats.

The bottom-up responses we observed to salmon subsidy treatments across trophic levels were generally consistent with findings of previous studies (Chaloner et al. 2007, Verspoor et al. 2010, 2011). Stream biofilms increased in the short-term following treatment additions during the first 2 years of the experiment, however, no carry-over effects were observed in the following summer (prior to the following annual treatment addition) for either treatment (for more detail regarding biofilm and stream nutrient chemistry responses, see Marcarelli et al. 2014). Standing crop biomass of benthic invertebrates doubled after the first year in streams treated with salmon carcasses and was highly variable among

streams treated with analog. Although biomass of benthic insects was elevated in streams treated with carcasses in 2011, no treatment effects were detected in the final 2 years of the experiment.

The net outcome of co-occurring, bottom-up effects of fertilization and increased top-down effects of predation appeared to result in a complex dynamic, whereby subsidized fishes masked responses of subsidized aquatic invertebrates. We suspect that this was due, in large part, to the fact that salmon subsidies entered food webs at multiple trophic levels. The asymmetrical outcome we observed between bottom-up and top-down responses is consistent with results of other enrichment experiments summarized by Borer et al. (2006). In addition, our experiment demonstrated that the observed asymmetries required multiple years to manifest, suggesting a potential ‘priming’ effect of subsidy additions across years, as trophic levels compensated to a new and annual source of energy and nutrients. In fact, the pattern appeared to be the result of increased production by resident fishes and their corresponding efficiency in consuming available resources. These lagged responses echo those of other multiyear enrichment experiments (albeit outside the scope of salmon restoration or nutrient mitigation) that have demonstrated that treatment effects may require several years to manifest and can change over time (Slavik et al. 2004, Cross et al. 2006, Davis et al. 2010). Bottom-up treatment effects on aquatic invertebrates manifested in the second year, but were not detected in the following 2 years. Had we made these measures alone, we might have concluded that treatments had no effect during these years. However, estimates of annual production (i.e., accrual of biomass per year) of resident trout increased 125–282% and 78–161% in carcass and analog treatments, respectively, over the duration of the experiment. Furthermore, by quantifying the annual consumption of aquatic invertebrates by fishes, we reconciled the lack of detectable response of aquatic invertebrate biomass in the latter years of our experiment, such that the increased production of stream fishes apparently culled invertebrate biomass down to levels near those of control streams, masking treatment effects. The specific mechanisms influencing this pattern are uncertain because we did not evaluate shifts in foraging behaviors of

trout, although both feeding on drifting insects and picking insects from the benthos probably contributed. The presence of gravel in the diets of trout suggests the latter likely occurred in concert with the interception of drifting insects (S. F. Collins, *personal observation*).

We observed that the strength of organism responses to experimental addition of salmon subsidies varied between forms, with stronger responses to additions of carcasses vs. so-called “analog” pellets. Some of our observations were similar to those reported from other studies evaluating the effects of analog pellets elsewhere in Idaho (Kohler et al. 2008, Ebel et al. 2014) and comparisons of analog and carcasses in Alaska (Wipfli et al. 2004). However, we also found that the interaction of salmon carcasses with aquatic and terrestrial consumers provided both more and enhanced pathways of material flow that ultimately enhanced fish production. Although similar with respect to the content of organic and inorganic nutrients, the use of nutrients as a common denominator could not account for the differences between the two in terms of the suite of responses across aquatic and terrestrial habitats. Although we cannot rule out the effects of different N loading rates on the differences observed between treatments in our study, it is clear that the form of the treatment added mediated the magnitude to which it was incorporated into food webs via direct vs. indirect pathways. Our study focused primarily on responses aquatic organisms. However, assemblages of other semi-aquatic (e.g., amphibians) and many terrestrial (e.g., birds, mammals) organisms may also benefit from subsidies associated with salmon, though they are not typically targeted as part of nutrient mitigation efforts.

Experimental evaluation of the efficacy of nutrient mitigation will yield more realistic management goals and expectations and better inform future policy. To ensure that assumptions are justified, mitigation programs should be nested within an adaptive management framework (Walters and Holling 1990) so that feedbacks occur regarding the effectiveness of such projects and, if needed, point to the need for new strategies. It is apparent that salmon-derived subsidies have complex ecological effects through multiple habitat types. Simple conceptions of “bottom-up” effects are not wrong necessarily, but fail to encompass the potential suite of food web respons-

es. Gross oversimplification of these processes may then transfer to policy, to a detriment. For instance, differences in the ecological effects of analog pellets and salmon carcasses indicate that the “analog” is not analogous to a salmon carcass. Extending this thought, it is reasonable to expect that the pasteurized salmon carcasses used in our experiment could differ in their effects compared to those of unaltered salmon carcasses. Furthermore, there are numerous characteristics of real salmon runs that are not mimicked by artificial additions of any kind (Collins et al. 2015). Comparisons of responses like those we measured, but in a design that includes natural salmon runs, would be instructive, but even a study like ours that involved only the additions of dead salmon or their pelletized tissues reveals that salmon are more than simple vectors of nutrients. This perspective should be reflected in the value placed upon conserving not only healthy runs of wild salmon but also the management practices we employ in efforts to replace or restore them.

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