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**Bioenergetic calculations evaluate changes to habitat quality for salmonid
fishes in streams treated with salmon carcass analog**

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Abstract

Nutrient supplementation in oligotrophic streams is proposed as a means of mitigating losses of marine-derived subsidies from declining or extirpated populations of anadromous fishes. One of the central predictions of nutrient addition is an increased production of fish through bottom-up increases in invertebrate abundance. Such changes in food availability may increase growth and production rates for stream fishes by increasing habitat quality. In this study we apply bioenergetic calculations to estimate changes to habitat quality based on predicted increases in net energy intake. We compared invertebrate drift abundance and estimated changes in energy availability in streams treated with salmon carcass analog versus untreated controls. Our results revealed a 2-3 fold increase in invertebrate drift abundance following the addition of salmon carcass analog; however, this effect appeared to be short-term. Measures of the energetic profitability of stream habitat for salmonid fishes revealed small, yet significant increases in net energy availability in streams that received analog additions, but only after controlling for differences in physical habitat features such as temperature and stream flow.

Keywords: habitat quality, bioenergetics, salmon carcass, invertebrate drift, food availability.

Introduction

The availability of habitat that meets the minimum requirements to sustain individuals over time is arguably one of the most important factors limiting populations. Habitat alteration and fragmentation are commonly cited as primary factors causing the decline of natural populations because the loss of habitat that meets the minimum requirements for growth and reproduction has become increasingly limited in many areas (Andrn 1994; Turlure et al. 2010; Bergerot et al. 2012). As a result, degraded and isolated habitats often experience significant declines in populations and concordant declines in biodiversity (Chapin et al. 2000). While efforts to recover populations in decline have often focused on habitat quality in order to establish self-sustaining populations over time, the success of such programs relies on identifying critical elements of habitat quality or connectivity that can be restored sufficiently to achieve population viability (Miller and Hobbs 2007).

In western North America, anadromous fishes have declined over significant portions of their range (Gustafson et al. 2007). Changes to habitat quality and the amount of accessible habitat are principal factors that are commonly thought to threaten anadromous fishes (Gregory and Bisson 1997; Parrish et al. 1998). As anadromous salmonids may have a significant influence on freshwater ecosystems via the delivery of marine-derived nutrients from spawning fishes, declines in anadromous populations can further accelerate changes to habitat quantity and quality (Gende et al. 2002). The resulting loss of marine-derived organic matter and nutrients can limit primary and secondary production of stream organisms (Naiman et al. 2002) and reduce or eliminate the physical effect of bioturbation (Moore et al. 2007). Declines in primary and secondary production in association with altered food webs and functional processes may then further exacerbate changes to habitat quantity and quality (Naiman et al. 2012). Given that

food abundance is often viewed as a limiting factor for salmonid populations (Mason 1976; Ensign et al. 1990; Utz and Hartman 2009; Alldredge et al. 2015), declines in food abundance and availability as a result of diminished stream invertebrate production may drive fish populations to lower levels of productivity by a feedback loop occurring through a loss of marine-derived organic matter and nutrients (Cederholm et al. 1999).

Nutrient supplementation (or fertilization) of stream and lake ecosystems has long been proposed as a means of increasing salmonid production through bottom-up increases in food abundance (Stockner and MacIsaac 1996; Slaney and Ashley 1999). In oligotrophic aquatic habitats, the addition of nutrients has produced dramatic increases in primary production as well as their secondary consumers (Johnston et al. 1990; Slavik et al. 2004). While significant increases in salmonid fish production have been observed in fertilized lakes (Stockner and MacIsaac 1996), the effect on salmonid production in streams has been equivocal. In some instances inorganic nutrient (Johnston et al. 1990), salmon carcass (Bilby et al. 1998; Wipfli et al. 2003, 2010), or salmon carcass analog (Kohler et al. 2012) addition has led to increases in the growth or abundance of salmonids; whereas in other studies, organic matter and nutrient addition (i.e., salmon carcass) has had little to no effect on salmonid growth or abundance (Wilzbach et al. 2005; Harvey and Wilzbach 2010; Cram et al. 2011). Furthermore, in instances where increases in salmonid abundance are detected, they are relatively weak in comparison to the increases at lower trophic levels (Grant et al. 1998).

If organic matter and nutrient addition to streams provides increases in habitat quality to stream salmonids, an unanswered question is whether such treatments result in increases in habitat quality from: 1) increased invertebrate abundance serving as food for drift feeding fishes, 2) direct consumption of marine-derived subsidies (i.e., carcass or analog materials) by stream

fishes, or 3) a combination of both direct and indirect pathways. As salmonids in streams are primarily drift-feeding predators, they acquire energy by capturing invertebrates drifting in the water column (Keeley and Grant 1995; Macneale et al. 2010; Gunnarsson and Steingrímsson 2011). Assessing changes to habitat quality for drift-feeding predators in streams can be complicated by seasonal changes in water flow, temperature, and drift abundance that may constrain significant portions of the year where fish can acquire energy and grow (Rosenfeld 2003). Understanding how these primary factors interact to influence whether a positive energy budget is achieved in habitats available to stream salmonids is critical to understanding whether potential improvements to habitat quality, such as nutrient supplementation, will yield significant benefits.

As is the case for almost all ectothermic animals, metabolic rate, energy consumption, and growth in salmonid fishes are strongly dependent on temperature conditions that fluctuate seasonally and daily in natural habitats (Elliott 1994). Bioenergetic models offer a way of capturing how temperature, food availability, and energetic costs of foraging in flowing water interact to influence habitat quality for salmonids in streams. Bioenergetic models for stream fishes evaluate the energetic trade-offs that exist from foraging in flowing water environments, such that individuals seek to maximize the energy they obtain from the environment in an attempt to increase their fitness through improved growth, survival, and reproductive rates. By applying energetic calculations to such estimates, measures of habitat quality can be used to determine whether habitat conditions fall within a range needed for metabolic processing of food and production of growth (Jenkins and Keeley 2010; Urabe et al. 2010).

In this study, we applied bioenergetic calculations to estimate habitat quality for salmonid fishes in streams. As nutrient addition studies are commonly predicted to improve habitat

conditions for salmonids by increasing food abundance, we first tested whether the addition of supplemental organic matter and nutrients from salmon carcass analog (Pearsons et al. 2007) increased the abundance of drifting aquatic invertebrates. We then evaluated changes to the energetic quality of stream habitat for salmonid fishes by comparing streams treated with salmon carcass analog versus similar untreated control streams.

Methods and materials

Experimental design and study sites

This study was designed as an upstream-downstream, before-after comparison that incorporated the experimental introduction of salmon carcass analog (SCA) to investigate the response of stream habitat quality to organic matter and nutrient enrichment. The study involved dividing each of six study streams into 3 km upstream and downstream segments with no separation between segments. Upstream and downstream segments were then longitudinally stratified into upper, middle, and lower reaches. Each 1 km stream reach was then further subdivided into 10, 100 m sub-sections, with one sub-section randomly chosen and used continuously throughout the study to represent a specific stream reach. In order to measure habitat characteristics within each stream reach, data was collected from transects located at the upstream boundary, mid-point, and downstream boundary of each sub-section. The habitat data from the three stream reaches, within each segment, was used to provide an average for each upstream and downstream segment for every stream in the study. Hence, the unit of replication used in response variables for this study was based on average values for each segment of the six study streams.

We selected six streams in the Salmon River basin of central Idaho, USA, to test the effect of increased organic matter and nutrient levels on bioenergetic measures of habitat quality

for stream-dwelling salmonid fishes. Segments of Cape Horn Creek, Basin Creek, Panther Creek, and Moyer Creek were used as treatment streams that received SCA; whereas, Elk Creek and Musgrove Creek were monitored as control streams and did not receive SCA (Fig. 1). Each of the streams is a spawning and rearing area for populations of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*). Of the four experimentally treated streams, only the downstream segment received SCA treatment with the upstream segment monitored as controls and left untreated. Two treatment streams, Cape Horn Creek (treated on August 9 and August 11 in 2010 and 2011 respectively) and Panther Creek (treated on August 18 and August 16 in 2010 and 2011 respectively), received a stocking density of $0.15 \text{ kg}\cdot\text{m}^{-2}$ of bank-full channel width (high treatment), with the two other treated streams, Basin Creek (treated on August 12 and August 8 in 2010 and 2011 respectively) and Moyer Creek (treated on August 18 and August 16 in 2010 and 2011 respectively), receiving a loading density of $0.03 \text{ kg}\cdot\text{m}^{-2}$ of bank-full channel width (low treatment). Two additional streams, Elk Creek and Musgrove Creek, were included as control streams and did not receive treatment with SCA, but were divided into study segments and monitored in the same way as treatment streams (see Supplemental Table 1 for stream characteristics). Application treatments of SCA were based on previous evaluations that used comparable loading rates for the low treatment (Kohler et al. 2008) and a higher loading rate ($0.15 \text{ kg}\cdot\text{m}^{-2}$) to evaluate the potential for differential responses to variable application rates, higher loads applied in other studies (Kohler et al. 2012), and to better approximate historical returns of anadromous salmonid biomass to Idaho streams. Treatments were applied manually in a spatially uniform, albeit patchy, manner across the downstream segment of each treatment stream. Disturbance to the stream benthos during the application process was minimal and associated with wading into haphazard locations along the

stream segment to soak and empty SCA bags during application. Treatment materials (i.e., SCA pellets) subsequently dispersed over short distances and within minutes were either observed to be retained by coarse substrate and woody matter or settled into depositional habitats (e.g., pools). The SCA used as treatment in this study was produced using marine fish bone meal and based on the formulation described by (Pearsons et al. 2007). This pasteurized product is in a pelletized form, each pellet weighing approximately 1 g and measuring 9 mm in diameter. Pellets contained approximately 50% crude protein, 7% crude fat, 9% nitrogen (N), and 1.8% phosphorus (P) by mass. For comparison, approximately 1.86 kg of pelletized SCA material is equivalent to a 5.5 kg adult Chinook salmon (using N content equivalent for calculations). As such, our treatments correspond to the addition of roughly 157-234 Chinook salmon carcasses per km (0.05 kg·m⁻² of bankfull channel width) for the low SCA treatment and 641-1,182 Chinook salmon carcasses per km (0.24 kg·m⁻² of bankfull channel width) for the high SCA treatment. Pellets were observed to degrade over a 2-6 week post-treatment period.

Parent geology of the study streams are cretaceous granite, quartz diorite, and Idaho batholith (Omernik 1987). General upland vegetation patterns consist primarily of lodge-pole pine (*Pinus contorta*) with riparian vegetation dominated by red-osier dogwood (*Cornus sericea*) and willow (*Salix* spp.). The availability of N in central Idaho streams is limited by the slow weathering of granitic rock and a dearth of N-fixing riparian species (Henderson et al. 1978). Precipitation to the region arrives largely from winter snowfall and peak stream flows generally occur during spring runoff in May and June, with base flows returning from August to April.

Bioenergetic modeling

We estimated the energetic profitability of stream habitat for salmonid fishes by applying bioenergetic calculations on study segments from treatment and control streams. We adapted

177 previous approaches to energetic measures of stream habitat based on estimates of net energy
178 intake (NEI) rates (Hughes and Dill 1990; Guensch et al. 2001). Net energy intake can be viewed
179 as the amount of energy available per unit time minus the costs associated with capturing and
180 processing that source. For salmonid fishes in streams, the primary source of food or energy
181 intake comes from capturing drifting aquatic invertebrates. Salmonids typically maintain
182 foraging stations in streams by swimming against the stream current and scanning the water
183 column for drifting prey items. Once suitable prey are detected, a foraging fish moves to capture
184 and handle the prey item, and then repeats the process for the next available prey item. Hence,
185 individual fish acquire energy by capturing food items, but also expend energy by maintaining
186 position in the stream current, moving to intercept prey, and then metabolically processing those
187 food items (Fausch 1984; Hughes and Dill 1990).

188 The net amount of energy available for a fish at any particular location in a stream will
189 depend on the integration of many different factors. Bioenergetic models of energy availability
190 depend on estimating a number of primary factors thought to capture the critical elements
191 necessary to estimate NEI. The first component in modeling energy intake can be based on a
192 foraging fish scanning the water column for prey items and seeing an area or 'window' of
193 capture that is defined by the maximum capture area (MCA). For salmonids in streams, that area
194 is typically modeled as the area of a half circle with a radius defined by the maximum capture
195 distance (MCD_i) indexed by prey size class i . The amount of food energy that flows through the
196 capture area, or gross energy intake (GEI), is simply the invertebrate drift density (DD) passing
197 through the capture area per unit time. If drift density is constant across a habitat, then GEI will
198 increase with current velocity until current speeds make capture of invertebrates impossible and
199 decrease the probability of prey capture. Gross energy intake for a foraging fish can then be

modified by subtracting the costs of capturing and processing food. Costs integrated into foraging models for salmonids in streams estimate measures of swimming costs (SC), costs of capturing the prey (CC), as well as metabolic costs associated with digestion and excretion. As ectothermic animals, metabolism is strongly related to environmental temperatures and body size, whereas costs associated with swimming increase with increasing current velocity.

For drift feeding fishes, NEI can be estimated by summing estimates of energy gain for all size classes of invertebrates drifting through a given area of habitat, minus losses. As salmonids are one of the most intensively studied groups of fishes, many different functional relationships have been developed for different aspects of their ecology. We followed past applications of NEI to stream salmonids largely based on the studies of Hughes and Dill (1990) and used the model developed by Addley (1993) and then tested by Guensch et al. (2001) and later by Jenkins and Keeley (2010). We used Elliott's (1976) model of maximum food ration for trout as an upper limit or maximum amount of energy (C_{max}) that could be ingested by a salmonid of a given size over an eight hour period of foraging. If $GEI < C_{max}$, NEI can then be estimated by:

$$NEI = \frac{\sum_{i=1}^{20} MCA_i \cdot V_{ave} \cdot DD_i \cdot PC_i \cdot (E_i - CC_i) - SC}{1 + \sum_{i=1}^{20} t_i \cdot MCA_i \cdot V_{ave} \cdot DD_i}$$

If $GEI \geq C_{max}$, then: $NEI = C_{max} \cdot E_i - SC$. For each prey size class i , we entered: the maximum capture area (MCA_i), average velocity at a fish focal point (V_{ave}), the drift density (DD_i), the probability of prey capture (PC_i), the energy acquired from a food item (E_i), the cost of capturing the prey item (CC_i), the swimming costs associated with holding position in the stream (SC), and the time spent handling a prey item (t_i). In our study we used 20 size classes of prey, ranging in length from 0.5 to 10 mm in length. The maximum capture area is represented by the area of a

half circle of a radius determined by the maximum capture distance (MCD_i), which is determined by the reactive distance to prey size class i (Hughes and Dill 1990). In instances where water depth in the stream was shallower than the reactive distance, MCA was truncated to reflect the smaller area available. The amount of energy available from a given class of prey can be estimated based on prey size (Smock 1980), and adjusted for the cost of digesting the prey as well as energetic losses from excretion (Elliott 1976; Brett and Groves 1979). Swimming costs (SC) and costs of capturing prey (CC) can also be estimated based on fish size, temperature, and water velocity at a location in the stream (Addley 1993). Time required to capture a prey item t_i was estimated at 5 s (Bachman 1984). A detailed list of formulae to estimate different components of the model is provided in Supplemental Table 2. Also, see Guensch et al. (2001) for a similar description of the model parameters and mathematical proof.

In order to estimate energy availability across study locations, measures of the habitat conditions are also needed as input to model calculations. As estimates of invertebrate drift abundance (DD), invertebrates were sampled each month and at each sampling location using a drift net. Drift samples collected in July (2010 and 2011) and August (2010 only) represent pre-treatment periods prior to SCA applications. Drift samples collected in August (2011 only; 6-17 days after SCA applications), September (2010 and 2011; 27-45 days after SCA applications), and October (2010 and 2011; 56-76 days after SCA applications) represent post-treatment periods. At each sampling location, a drift net (25 cm width x 25 cm height x 75 cm length, mesh size 300 μ m) was anchored into the stream bottom by two metal stakes and then faced upstream into the stream current with the top of the net above the water surface. A single drift sample was collected at each 100 m study sub-section for each month (July to October) in both study years (144 total drift samples in 2010 and 144 total drift samples in 2011). Average drift abundance for

a single study stream was then estimated by averaging abundance across samples for a single treatment or control stream segment. Invertebrate collections occurred no less than two hours after dawn or two hours before dusk to reduce the effect of the diel periodicity of invertebrate drift (Smock 1996) and to include the time of day when salmonids are actively feeding on drifting invertebrates. At the center of the drift nets, current velocity ($\pm 1 \text{ cm} \cdot \text{s}^{-1}$) and the depth ($\pm 1 \text{ cm}$) of the water flowing through the net were recorded to determine the volume of water sampled by each net over a 30 minute sampling period. After a sample was collected, the catch was transferred to a plastic bag and preserved in 5% formalin. To compare the size and abundance of invertebrates across sites and over time, samples were sorted to remove detritus and retain intact invertebrates. To estimate size and abundance of invertebrates in a sample, individual invertebrates were identified to the order or family level of taxonomy and then measured for length and width ($\pm 0.01 \text{ mm}$) using a dissecting microscope equipped with a digitizing system.

As estimates of the physical habitat characteristics within study sites, we sampled stream habitat at monthly intervals across all study sites. We measured the availability of stream habitat by transecting the stream at three locations in each study section (see experimental design above). We measured current velocity ($\pm 1 \text{ cm} \cdot \text{s}^{-1}$) and stream depth ($\pm 1 \text{ cm}$) across the width of each transect at 25 cm intervals using a calibrated wading rod and current velocity meter.

Estimates of NEI and the proportion of suitable habitat

As foraging area, prey size, and energetic demands are strongly related to body size in our bioenergetic calculations, we estimated NEI rates for three size classes of salmonids (5 cm, 10 cm, and 15 cm) in treatment and control streams. Because the study streams were used as representative rearing streams for juvenile Chinook salmon and steelhead trout, we used these

fish sizes to approximate the range of body size when these two species use the streams for rearing purposes. To estimate the NEI experienced by a fish at a given foraging location, we used the bioenergetic calculations with month specific temperatures and drift abundance, along with the stream depth and current velocity for each habitat measurement location along a transect. To represent responses in treatment and control streams, we calculated mean NEI values for each of the three transects within a single 100 m sub section, then averaged values again for each of the 3 - 100 m sub sections within a treatment or control segment, producing a single observation for each control or treatment stream. At sites within a transect where NEI was estimated to be negative, we assigned NEI = 0 (Urabe et al. 2010). We also evaluated changes to habitat quality based on the proportion of sites within a transect where NEI was estimated to be positive (NEI > 0). Following the calculations for mean NEI values, we averaged proportions for NEI > 0 across transects within each 100 m sub section site and then sites within streams to represent the response in each control versus SCA treated stream. In addition to the proportion of sites with NEI > 0, we also calculated the proportion of sites that met the requirement for a reduced ration (as opposed to a maximum ration) based on Elliott's (1975) empirically derived equations for brown trout (*Salmo trutta*) as a general proxy for the caloric requirements of salmonids living in the study streams. NEI estimates were used to estimate the number of sites along a transect capable of provisioning a fish with a reduced ration level of food intake. We converted the minimum mass of food required to achieve a reduced ration intake level into energy units (NEI; joules·hr⁻¹) using the following equation:

$$\text{NEI}(\text{J} \cdot \text{hr}^{-1}) = \frac{1}{8(\text{feeding hours} \cdot \text{day}^{-1})} \cdot \text{ration}(\text{mg} \cdot \text{day}^{-1}) \cdot 4.438(\text{cal} \cdot \text{mg}^{-1}) \cdot 4.1868(\text{J} \cdot \text{cal}^{-1}) \cdot 0.58,$$

where the required ration size (mg·day⁻¹) and conversion to calories (cal·mg⁻¹) are based on

Elliott (1976), whereas the energy assimilation fraction (0.58) is from (Gustafson et al. 2007) and

Elliott (1976). We used 8 h as a conservative estimate for the average amount of time that a fish would have to effectively forage over the course of a day and acquire sufficient energy to meet a reduced ration level of intake. These calculated estimates of energy requirements were then used to assess the proportion of habitat with NEI values from treatment and control streams capable of supplying at least a reduced ration for fish of three size classes. As before, we averaged proportions across transects within each 100 m sub section site and then sites within streams to represent the response in each control versus SCA treated stream for statistical analyses.

Statistical analyses

We evaluated changes to response variables over the four month monitoring period (July to October) in 2010 and 2011 using a mixed-model repeated-measures analysis of variance (RM-ANOVA). As we considered the response over two years, using two four-month periods, we treated the difference between years as a random effect in our statistical model and treatment categories (control, low SCA, or high SCA) as well as specific months of the year as fixed factors. We modeled the covariance structure across repeated observations on the same experimental units assuming a correlated covariance structure (CS), uncorrelated (UN), first-order autoregressive (AR), or heterogeneous first-order autoregressive (ARH) variance structure and selected the best model fit among candidate models using a corrected Akaike's information criterion (AICc) following the procedures described by Littell et al. (2006) and implemented in the mixed procedure from SAS 9.3 (SAS Institute 2011).

We compared measures of invertebrate drift abundance to estimate potential changes of food abundance in treatment versus control stream segments. Measures of invertebrate abundance were $\log_{10}$ transformed to provide best model fit. Changes in NEI rates between control and treatment streams were compared by mean NEI values observed over the four

months in treatment (low and high SCA levels) and control streams. We also evaluated changes to habitat quality by estimating the proportion of habitat with NEI values > 0 , as well as the proportion of habitat that met the criterion for a reduced ration based on Elliott's (1976) model for brown trout. Proportional measures of habitat availability were arcsin-square root transformed to provide best model fit.

In order to estimate the sensitivity of the primary factors influencing the bioenergetic estimate of suitable habitat, we used site and month specific values for temperature and stream discharge, in addition to treatment and any potential between-year effects in a multiple regression analysis. We estimated the proportion of variation in suitable habitat (as defined by Elliott's 1976 criterion) accounted for by temperature, stream discharge, between year effects, and treatment levels, by considering each factor as an independent variable in a multiple regression model. The effect of each individual factor was evaluated after controlling for all other factors in the regression model using a type III sum of squares and tests of significance based on $\alpha = 0.05$ (SAS Institute 2011). By doing so, we estimated the unique proportion of variation in suitable habitat accounted for by each of the factors for all size classes of fish examined.

Finally, we examined how simulated increases in drift abundance may further affect the availability of habitat with NEI values > 0 , by modeling increases in drift abundance that were two to ten times higher than the responses observed in SCA treatment over control streams.

Results

Over the course of the four months of monitoring in 2010 and 2011, invertebrate drift abundance did respond to the treatment effect of SCA addition. Invertebrate drift abundance was higher in treated streams over control streams, but was only significantly different during

September, one month after treatment with SCA ($F_{2, 55.4} = 6.09$, $P = 0.0041$). Invertebrate drift abundance increased significantly then declined over the four month period when averaged across treatment and control streams (Fig. 2, RM-ANOVA, $F_{3, 37.3} = 6.54$, $P = 0.0011$). We did not detect any significant interaction between treatment levels and time (RM-ANOVA, $F_{6, 40.1} = 1.51$, $P = 0.20$), or any between year effect on invertebrate drift abundance (RM-ANOVA, $z = 1.05$, $P = 0.15$). Six invertebrate categories made up about 86% of the invertebrates captured in the drift samples, and included Chironomidae (14.1%), Diptera (38.9%, adults and pupae), Trichoptera (3.7%), Ephemeroptera (17.6%), Coleoptera (4.8%), Plecoptera (2.0%), and Simuliidae (4.8%). Another 14% of the drift was composed of small proportions of other categories, including, Arachnida, Collembolla, Copepoda, Haplotaxida, Hemiptera, Lepidoptera, Megaloptera, Nematoda, Odonata, and Orthoptera. Abundance of Chironomidae mirrored the overall increases and then decline of invertebrates from July to September - October (Fig. 3a, RM-ANOVA, $F_{3, 35.6} = 8.13$, $P = 0.0003$). Chironomidae abundance in treated streams showed a peak over control streams in September (Fig. 3a, $F_{2, 49} = 4.42$, $P = 0.017$). Similar changes were observed for Diptera adult and pupal stages over the four months (Fig. 3b, RM-ANOVA, $F_{3, 38.8} = 8.47$, $P = 0.0002$), with a significant peak during September in SCA treated streams over control streams (Fig. 3b, $F_{2, 58.9} = 4.42$, $P = 0.0038$). Of the remaining taxa that made up the predominant proportions in the drift, no others indicated a significant response to SCA addition over control streams (Fig. 3c to g; RM-ANOVA, treatment effect: all F values < 1.22 , all P-values > 0.15 ; treatment by month effect: all F values < 1.80 , all P-values > 0.18). Trichoptera and Simuliidae invertebrate drift did increase then declined significantly over the four month period when averaged across all stream types (Fig. 3c and g; Trichoptera: RM-ANOVA, $F_{3, 43.3} = 7.28$, $P = 0.0005$; Simuliidae: RM-ANOVA, $F_{3, 35.1} = 7.80$, $P = 0.0004$). Collectively, other taxa

that made up smaller proportions of the invertebrate drift, appeared to increase in September in SCA treated streams, but not significantly (Fig. 3h, RM-ANOVA, treatment effect: $F_{3, 22.3} = 0.51$, $P = 0.61$; treatment by month effect: $F_{6, 51.5} = 0.97$, $P = 0.46$). When averaged across treated and control streams, all other taxa increased then declined over the four month period (Fig. 3h. RM-ANOVA, $F_{3, 50.3} = 5.05$, $P = 0.0039$).

Average NEI values in treatment and control streams declined over the course of four months for 5 cm (Fig. 4a; RM-ANOVA, $F_{3,15} = 30.76$, $P < 0.0001$), 10 cm (Fig. 4b; RM-ANOVA, $F_{3,15} = 23.01$, $P < 0.0001$), and 15 cm fish (Fig. 4c; RM-ANOVA, $F_{3,15} = 32.29$, $P < 0.0001$). Prior to SCA addition in July and August, NEI estimates were largely overlapping between stream categories. Although NEI values for SCA treated streams tended to increase over control streams following fertilization in September and October, we could not detect any difference among streams as a result of treatment conditions for 5 cm (Fig. 4a; RM-ANOVA, $F_{2,17} = 0.22$, $P = 0.81$), 10 cm (Fig. 4b; RM-ANOVA, $F_{2,17} = 0.01$, $P = 0.99$), or 15 cm fish (Fig. 4c; RM-ANOVA, $F_{2,17} = 0.89$, $P = 0.52$). No significant interactions between month and treatment conditions were detected for any size class of fish (Fig. 4a –c, RM-ANOVA, all F -values ≤ 0.44 , all P -values ≥ 0.09) or any significant between year effects (RM-ANOVA, all z -values ≤ 1.34 , all P -values ≥ 0.49).

The mean proportion of habitat available that had NEI values > 0 were similar across treatment and control streams, but tended to increase slightly following the introduction of SCA in treatment streams during September (Fig. 5a-c). Despite this increase, there was no significant effect of SCA on the proportion of foraging sites with NEI values > 0 for 5 cm (Fig. 5a; RM-ANOVA, $F_{2,17} = 0.45$, $P = 0.65$), 10 cm (Fig. 5b; RM-ANOVA, $F_{2,17} = 1.23$, $P = 0.32$), or 15 cm fish (Fig. 5c; RM-ANOVA, $F_{2,17} = 0.68$, $P = 0.52$). The proportion of sites with NEI > 0 did

change significantly over the four months for 5 cm (Fig. 5a; RM-ANOVA, $F_{3,15} = 17.31$, $P < 0.0001$), and 10 cm fish (Fig. 5b; RM-ANOVA, $F_{3,15} = 6.76$, $P = 0.0042$), but not for 15 cm fish (Fig. 5c; RM-ANOVA, $F_{3,15} = 2.06$, $P = 0.15$). There was no significant interaction between month and treatment effects (Fig. 5a–c, RM-ANOVA, all F-values ≤ 1.99 , all P-values ≥ 0.12) or any significant between year effects (RM-ANOVA, all z-values ≤ 1.27 , all P-values ≥ 0.10).

When we used NEI calculations to estimate the proportion of suitable habitat that met the requirements for a reduced ration level of energy intake, we could not detect any effect of SCA addition to treatment over control stream sites. The proportion of habitat that met the requirements for a reduced ration of energy intake did not differ among treatment and control streams, whether we considered this for 5 cm (Fig. 6a, RM-ANOVA, $F_{2,17} = 0.46$, $P = 0.64$), 10 cm (Fig. 6b, RM-ANOVA, $F_{2,17} = 0.49$, $P = 0.62$) or 15 cm fish (Fig. 6c, RM-ANOVA, $F_{2,17} = 0.47$, $P = 0.63$). Although the proportion of suitable habitat did decline significantly over the course of the four months for 5 cm (Fig. 6a, RM-ANOVA, $F_{3,15} = 29.33$, $P < 0.0001$), 10 cm (Fig. 6b, RM-ANOVA, $F_{3,15} = 62.35$, $P < 0.0001$), and 15 cm fish (Fig. 6c, RM-ANOVA, $F_{3,15} = 72.89$, $P < 0.0001$), there was no significant interaction between month and treatment levels for all size classes of fish (Fig. 6a–c, RM-ANOVA, all F-values ≤ 1.59 , all P-values ≥ 0.21). Similarly, there was no significant between year effect for all size classes of fish compared (RM-ANOVA, all z-values ≤ 0.15 , all P-values ≥ 0.44).

When we investigated the effect of stream flow, temperature, treatment levels, and year on the availability of suitable habitat that met a maintenance ration criterion, a significant proportion of the variability in energetically suitable habitat was accounted for by each of these factors based on a partial regression analysis. Temperature was positively correlated with the availability of suitable habitat, after controlling for the effects of stream discharge, SCA

405 treatment, and year for 5 cm (Fig. 7a, partial $r^2 = 0.44$, $P < 0.0001$), 10 cm (Fig. 7a, partial $r^2 =$
406 0.41 , $P = 0.0001$), and 15 cm fish (Fig. 7a, partial $r^2 = 0.42$, $P < 0.0001$). Similarly, after
407 controlling for the effects of temperature, SCA treatment, and year; stream discharge was
408 significantly correlated with the availability of suitable habitat for 5 cm (Fig. 7d, partial $r^2 = 0.19$,
409 $P < 0.0001$), 10 cm (Fig. 7e, partial $r^2 = 0.13$, $P < 0.0001$), and 15 cm fish (Fig. 7f, partial $r^2 =$
410 0.064 , $P = 0.0013$). In contrast to temperature, the availability of suitable habitat decreased with
411 increasing stream discharge across all three size classes of fish. When we compared the
412 availability of suitable habitat by SCA treatment categories after controlling for the effects of
413 temperature, stream discharge, and year, we detected a significant effect of SCA treatment on the
414 availability of suitable habitat. Streams treated with SCA tended to have a higher proportion of
415 suitable habitat than control streams for 5 cm (Fig. 7g, partial $r^2 = 0.053$, $P = 0.0071$), 10 cm
416 (Fig. 7h, partial $r^2 = 0.062$, $P = 0.0028$), and 15 cm fish (Fig. 7i, partial $r^2 = 0.054$, $P = 0.0028$).
417 Finally, differences in study streams between years also accounted for a significant proportion of
418 the availability of suitable habitat for 5 cm (partial $r^2 = 0.033$, $P = 0.033$), 10 cm (partial $r^2 =$
419 0.11 , $P < 0.0001$), and 15 cm fish (partial $r^2 = 0.15$, $P < 0.0001$). AICc values for all models
420 indicated best model fit with the inclusion of temperature, discharge, treatment effects, and year
421 effects for the three size classes of fish examined.

422 While temperature, stream discharge, and SCA treatment were all significantly correlated
423 with the amount of suitable habitat available over the course of the study, how great a proportion
424 in the variation in suitable habitat, in some cases, depended on which size class of fish was
425 considered (Fig. 8). Temperature variation accounted for the largest proportion of the variation in
426 suitable habitat for all size classes of fish, but was relatively equal among size classes. Stream
427 discharge had the biggest effect on the smallest size class of fish with the effect decreasing with

increasing fish size. SCA treatment accounted for a significant proportion in the variation in suitable habitat, but was smaller than other factors considered and much more equal across size classes of fish. When we compared the variation in the amount of suitable habitat by year (2010 and 2011), an additional component of variation was explained by this factor, mainly for the 10 and 15 cm size classes of fish (Fig. 8).

Application of low SCA treatment resulted in a 10 to 20% increase over control streams in the number of foraging sites with positive NEI values in September for all size classes of fish (Fig 9a-c). Higher levels of SCA application resulted in a 20 to 35% increase for the three size classes of fish in September (Fig. 9d-f). Little or no effect of SCA treatment was estimated in October, due to the constraining effect of cold water temperatures. Simulated changes in invertebrate drift abundance above the levels measured from experimental treatment responses indicated larger responses in the proportion of habitat with positive NEI values. Simulated two to ten-fold increases in invertebrate drift over the low SCA treatment dramatically increased the number of sites with $NEI > 0$, with a 40 to 50% increase over control streams in September (Fig. 9 a-c), and more moderate increases of 1 to 5% for October (Fig. 9 a-c). Simulated two to ten-fold increases in invertebrate drift over the high SCA treatment also appeared to increase the number of sites in September; however, increases tended to level off after a four-fold increase in drift abundance (Fig. 9d-f). Slightly higher increases in October were estimated for high SCA treatment conditions in comparison to the low SCA treatment (Fig. 9d-f).

Discussion

In this study, we examined the effect of organic matter and nutrient supplementation from SCA on invertebrate drift abundance and the energetic quality of stream habitat for salmonid fishes. We found that after SCA was introduced into treatment streams invertebrate drift

abundance increased up to 148%, relative to control streams, but the effect largely declined 60 days after treatment application. Bioenergetic estimates of habitat quality could not detect any increases in habitat quality in streams treated with SCA over control streams without controlling for physical factors. Temperature and stream discharge appeared to have a much bigger influence on the availability of suitable habitat for juvenile salmon and trout in Salmon River streams relative to SCA; however, after statistically removing the effect of differences in physical habitat features, SCA application provided a small, but significant increase in habitat quality for drift-feeding salmonids.

Food availability is thought to be an important factor limiting the abundance of salmonids in streams (Chapman 1966; Gibson 1988). While experimental studies have demonstrated the influence of food availability on the abundance of salmonids under controlled conditions (Keeley 2001; Imre et al. 2004), the relationship between food abundance and salmonid abundance in natural streams is less clear. Although few would question that individuals and populations are ultimately limited by food supply, many factors can reduce the proximate importance of food availability in limiting animal abundance (Boutin 1990). As salmonids are commonly viewed as drift-feeding predators in streams, increasing invertebrate drift abundance should lead to increasing salmonid abundance. However, only a few studies have examined the relationship between salmonid abundance and invertebrate drift abundance, and have either failed to detect any significant correlation between the two, or were only weakly correlated (Gibson and Galbraith 1975; Johansen et al. 2005). It may be that these past studies have primarily examined a relatively narrow range of invertebrate drift abundance and a much wider range of natural food availability would be necessary to detect the strong effect observed in experimental studies (Slaney and Northcote 1974; Keeley 2001; Imre et al. 2004). Interestingly, studies incorporating

invertebrate drift abundance into estimates of NEI have found positive correlations between salmonid abundance and energy intake rates (Jenkins and Keeley 2010; Urabe et al. 2010). Alternatively, other factors that influence habitat quality may be more important in constraining the availability of suitable habitat for salmonids in streams.

Although measurements of invertebrate drift has a long history in studies of stream ecosystems, a better understanding of what constitutes high or low drift abundance, as well as size composition and temporal and spatial variability, is greatly needed to better understand its effect as a food resource for salmonids. In our study streams, daytime invertebrate drift abundance from July to October was measured in the range of 0.5 to 3 invertebrates per m³ of water, with streams treated with SCA about two to three times higher in September than controls streams. Our data indicate that even with SCA treatment, observed invertebrate drift abundance in our study streams was at the low end of invertebrate drift abundance reported in past studies examining food availability for salmonids in streams. Comparable studies that have measured daytime invertebrate drift indicate drift abundance in the range of 1 to 5 invertebrates per m³ to as high as 20 to 50 invertebrates per m³ (Allan 1978; Wilzbach and Hall 1985; Leung et al. 2009; Jenkins and Keeley 2010). Hence, a much stronger and sustained response in invertebrate drift production may be needed to have a larger benefit for habitat quality for salmonids. However, our evaluations were predicated on increased quantities of invertebrate drift to evaluate potential changes to habitat quality and did not consider changes to benthic invertebrate abundance and biomass as food for stream-dwelling fishes. Benthic invertebrate samples collected in the same study streams showed increases in abundance and biomass, as well as increased $\delta^{15}\text{N}$ content, following SCA additions, suggesting that marine-derived subsidies enrich macro-invertebrate tissue and have the potential to enhance the quality (i.e., nutritional content) of food available to

stream fishes in addition to increasing their abundance (A. Kohler, unpublished data). Understanding how chemical, physical, and biological processes influence drift abundance and how changes to invertebrate abundance and quality affect food availability and nutritional status for salmonids is still largely unexplored. Future studies may improve our understanding of food availability for salmonids by quantifying prey size, nutritional content, and abundance over a wide range of stream productivity.

The addition of inorganic nutrients to oligotrophic streams has long been proposed as a means of providing bottom-up increases in stream productivity with the goal of increasing fish production (Slaney and Ashley 1999). Whether through the application of liquid agricultural fertilizer, pelletized forms of slow release fertilizer, or even from the addition of sucrose as a source of nutrients, nutrient addition has often led to large increases in stream periphyton and benthic invertebrate abundance (Warren et al. 1964; Johnston et al. 1990; Slavik et al. 2004). Effects on the abundance of salmonids have been detected in the form of increased growth and abundance in some instances (Ward et al. 2003), but not others (Wipfli et al. 2010; Harvey and Wilzbach 2010). More recent studies have focused on the importance of organic matter and marine-derived nutrient subsidies provided by spawning salmon through excretion and carcass deposition (Levi et al. 2013). In other studies, applying salmon carcasses or SCA has increased salmonid abundance or growth in some cases (Bilby et al. 1998; Wipfli et al. 2003; Guyette et al. 2013), but not others (Harvey and Wilzbach 2010). As is the case in studies that have experimentally manipulated food abundance and observed large effect sizes, experimental studies that have added salmon carcasses or SCA to controlled conditions generally find significant increases in growth or abundance (Wipfli et al. 2004).

Our data indicate that increases in invertebrate drift abundance one month after SCA additions improved habitat quality for stream salmonids; however, this effect was short-term and only evident after controlling for physical factors (i.e., temperature and discharge). Short-term increase in invertebrate abundance and biomass, especially pronounced in multivoltine taxa (e.g., some Chironomidae), is commonly observed in studies evaluating benthic invertebrate response to marine-derived subsidies such as salmon carcasses and SCA additions (Wipfli et al. 1998; Kohler et al. 2012; Kiffney et al. 2014). For example, Wipfli et al. (1998) observed benthic invertebrate densities that peaked 20-30 days following salmon carcass additions and then declined over time, similar to our observations of invertebrate drift abundance. Furthermore, companion studies evaluating benthic invertebrate response in our study streams observed similar increases, also one month after SCA additions (A. Kohler, unpublished data). To our knowledge, this is the first study to intensively evaluate changes to invertebrate drift abundance available to stream-dwelling salmonids following the addition of marine-derived subsidies such as salmon carcass materials or SCA.

Our results are based on the consumption of invertebrate drift and the associated bio-physical factors that influence growth. In studies of salmon carcass addition, direct consumption of tissue from carcass material (Bilby et al. 1998) provides an alternative mode of feeding that is not captured by estimating habitat quality based on invertebrate drift-feeding models. Similarly, SCA additions across Columbia River basin streams significantly increased salmonid stomach fullness and growth measures, suggesting that fishes directly ingested particulate SCA material (Kohler et al. 2012). Bottom-up increases from organic matter and nutrient addition may only provide marginal increases in food availability from invertebrate drift because salmonids capture invertebrates from the stream current one at a time and may be constrained by the maximum rate

of capture. Although alternative foraging modes such as direct consumption of SCA and carcass tissue and consumption of benthic invertebrates may offer additional energy intake pathways, if the goal of SCA addition is to provide increases in habitat quality for salmonid fishes by increasing invertebrate drift availability, then larger increases in drift abundance will be needed before bioenergetics modeling predicts significant gains in NEI and associated habitat quality. We suggest future studies incorporate both indirect (e.g., increased invertebrate drift) and direct (e.g., consumption of carcass or analog material) pathways into evaluations of habitat quantity and quality.

Unlike the changes we observed for invertebrate drift abundance, stream discharge and temperature accounted for a much larger proportion of the variability in habitat quality for salmonids than was evident when comparing the change in habitat quality over the course of a growing season. The amount of energetically suitable habitat tended to decrease with increasing stream discharge for all size classes of fish. High discharge rates may decrease the availability of suitable habitat because water velocity can exceed the swimming and prey capture abilities for fish of a given size. Smaller fish, in particular, tended to be more strongly constrained by discharge, probably because they are often limited to the slower margins of stream flow. Larger fish have stronger swimming abilities and can exploit a wider range of current velocities, but they too may be unable to exploit the fastest areas of stream current if the costs of capturing prey are too high (Bjornn and Reiser 1991). In each year of our study, temperature constrained habitat quality, particularly in October when cold water limited the metabolic scope of fish to process food. As ectotherms, salmonids can be limited to the seasonal window where water temperature is warm enough to permit fish growth, typically this is thought to occur when warmer temperatures arrive in spring and lasts until late summer or early fall (Ultsch 1989; Cunjak et al.

1998). Based on our bioenergetic calculations, juvenile salmon in the Salmon River basin of central Idaho experience reduced opportunities for growth once water temperatures decline in October.

Although the development of bioenergetics models for stream salmonids began more than 30 years ago (Fausch 2014; Piccolo et al. 2014), their application in evaluating measures of habitat quality has been more recent (Guensch et al. 2001; Rosenfeld and Taylor 2009; Urabe et al. 2010). Bioenergetic approaches of measuring habitat quality for stream ecosystems are attractive because of the ability to integrate seasonal changes in temperature and stream flow as well as differences in prey size and abundance. All of which are critical components in measuring the energetic profitability of habitat for foraging salmonids in a seasonally variable environment. However, widespread use and improvements of bioenergetic estimates of habitat quality for stream salmonids may be difficult to achieve because of the complexity in developing algorithms for such calculations, uncertainty in model parameters (Rosenfeld et al. 2014), and the barrier these factors create for new users. Perhaps the solution to such issues lies in creating open source software where new users can easily input habitat, temperature, and prey abundance data to estimate NEI, with default model parameters that can also be modified with new or alternate equations. By doing so, users can explore how different combinations of habitat factors alter habitat quality, change energy intake or introduce new limiting factors (e.g. predation risk, turbidity) without having to completely invent an analytic procedure of their own. A similar approach has been widely used for bioenergetic analyses of fishes usually applied to lentic and marine habitats (Chipps and Wahl 2008).

Our study revealed that SCA addition to streams increased invertebrate drift abundance by up to 148% relative to control streams, but the effect declined over time. Bioenergetic

estimates of habitat quality for salmonid fishes revealed small yet significant increases in streams treated with SCA; however, such effects could only be detected after changes in stream flow and temperature were accounted for. Energetic estimates of habitat quality may provide valuable insight in evaluating how multiple factors can interact with each other in dynamic stream ecosystems.

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Fig. 1. Location of study streams within the Salmon River basin of central Idaho, USA. Streams labeled as C/T refer to treatment streams with upstream control (C) segments and downstream treatment (T) segments that received salmon carcass analog additions. Streams labeled as C/C refer to control streams with upstream and downstream segments that did not receive salmon carcass analog additions. Inset map indicates the location of the upper Salmon River watershed (shaded polygon) in the western United States.

215x166mm (300 x 300 DPI)

Fig. 2. Log₁₀ least squares mean (± 1 SE) invertebrate drift abundance according to three types of study streams over four months. Open circles and dashed line represent control streams. Closed triangles and circles represent streams treated with low or high levels of salmon carcass analog. Right-hand vertical axis provided as reference for conversion to untransformed values of invertebrate drift.

Fig. 3. Log₁₀ least squares mean (± 1 SE) invertebrate drift abundance according to three types of study streams over four months by the following different taxonomic categories: (a) Chironomidae, (b) Diptera (adults and pupae), (c) Trichoptera, (d) Ephemeroptera, (e) Coleoptera, (f) Plecoptera, (g) Simuliidae, or (h) other (all remaining taxa, see text). Open circles and dashed line represent control streams. Closed triangles and circles represent streams treated with low or high levels of salmon carcass analog. Right-hand vertical axis provided as reference for conversion to untransformed values of invertebrate drift.

293x386mm (300 x 300 DPI)

Fig. 4. Least squares mean (± 1 SE) net energy intake (NEI) for foraging sites in three stream categories. Open circles and dashed line represent control streams. Closed triangles and circles represent streams treated with low or high levels of salmon carcass analog. Foraging sites with negative NEI values were set to zero by default.

286x578mm (300 x 300 DPI)

Fig. 5. Least squares mean (± 1 SE) proportion of suitable habitat based on net energy intake (NEI) values > 0 for (a) 5 cm, (b) 10 cm, or (c) 15 cm fish. Open circles and dashed line represent control streams. Closed triangles and circles represent streams treated with low or high levels of salmon carcass analog. Data are arcsine-square root transformed.
272x527mm (300 x 300 DPI)

Fig 6. Least squares mean (± 1 SE) proportion of suitable habitat capable of meeting or exceeding a reduced ration, according to three types of study streams for (a) 5 cm, (b) 10 cm, or (c) 15 cm fish. Open circles and dashed line represent control streams. Closed triangles and circles represent streams treated with low or high levels of salmon carcass analog. Data are arcsine-square root transformed.
272x527mm (300 x 300 DPI)

Fig. 7. Residual variation in the proportion of suitable habitat capable of meeting a reduced ration from a multiple regression model controlling for discharge, SCA treatment, and year effects versus temperature for (a) 5 cm, (b) 10 cm, or (c) 15 cm fish. Residual variation in the proportion of suitable habitat from a multiple regression model controlling for temperature, SCA treatment and year effects versus discharge for (d) 5 cm, (e) 10 cm, or (f) 15 cm fish. Residual variation in the proportion of suitable habitat from a multiple regression model controlling for temperature, discharge and year effects versus SCA treatment for (g) 5 cm, (h) 10 cm, or (i) 15 cm fish. Open circles represent control sites. Closed triangles and circles represent streams treated with low or high levels of salmon carcass analog. Data are arcsine-square root transformed.

213x163mm (300 x 300 DPI)

Fig. 8. Proportion of variation in suitable habitat capable of meeting a reduced ration and accounted for by SCA treatment (hatched bars), temperature (black bars), discharge (open bars), and between year effects (stippled bars) for three size classes of fish.
158x120mm (300 x 300 DPI)

Fig. 9. Percent change in the proportion of habitat with NEI > 0 in comparison to control streams following the application of **low** SCA treatment conditions in September (open squares) and October (closed squares) for (a) 5 cm fish, (b) 10 cm fish, and (c) 15 cm fish, and the estimated percent change based simulated increases in invertebrate drift as a two to ten-fold multiple of measured experimental responses. Percent change in the proportion of habitat with NEI > 0 in comparison to control streams following the application of **high** SCA treatment conditions in September (open squares) and October (closed squares) for (d) 5 cm, (e) 10 cm, and (f) 15 cm fish, and the estimated percent change based on simulated increases in invertebrate drift as a two to ten-fold multiple of measured experimental responses.
151x82mm (300 x 300 DPI)