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**Thermal constraints on stream consumer responses to a
marine resource subsidy**

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Title: Thermal constraints on stream consumer responses to a marine resource subsidy

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Running Head: Temperature and marine subsidies

Abstract:

Spawning migrations of Pacific salmon (*Oncorhynchus spp.*) to coastal watersheds provide a rich resource subsidy to freshwater consumers. However, variation in thermal regimes and spawning activity across the landscape constrain the ability of poikilothermic consumers to assimilate eggs and carcasses. We investigated how sockeye salmon (*O. nerka*) spawning density and stream temperature affect the growth, body condition, and fatty acid composition of juvenile coho salmon (*O. kisutch*), a known egg predator, in 7 tributaries of the Wood River in southwest Alaska. We compared mean body size of juvenile coho salmon in late summer among 3-7 years per stream and found that the largest mean size occurred in warm streams where sockeye salmon spawned, though overall subsidy magnitude (spawner density) had no effect on consumer body size. Individuals that consumed more salmon eggs (estimated from $\delta^{15}\text{N}$) were larger, and had altered fatty acid composition, but did not have higher relative body condition. These results indicate that effects of marine subsidies on freshwater consumers depend both on local habitat conditions and on individual variation in energy allocation.

41 Introduction:

42 Resource subsidies between ecosystems, for example from ocean to land, or from forests
43 to freshwaters, are ubiquitous and increasingly well-described, with much focus applied to
44 quantifying subsidy magnitudes (Marczak et al. 2007). These efforts have resulted in the
45 realization that the effects of subsidies on recipient ecosystems vary according to food web
46 structure, consumer life histories, and local environmental conditions (Marczak et al. 2007, Yang
47 et al. 2010). Interactions between local conditions and ecosystem responses to subsidies occur
48 across diverse geographic regions and taxonomic groups. For example, nutrient additions from
49 seabird guano to South Pacific island soils enhance tree growth only after strong El Niño rains,
50 which cause seabirds to abandon nesting colonies, thereby relieving trees from the damage they
51 cause (Molina-Montenegro et al. 2013). Abundance of alternative food sources can also mediate
52 consumer responses to subsidies—migratory geese subsidize Arctic fox reproduction in tundra
53 environments, but only make up a significant portion of fox cub diets when local rodent
54 populations are low (Giroux et al. 2012). Despite emerging evidence for strong interactions
55 between local ecological conditions and consumer responses to subsidies, many studies are
56 conducted at coarse scales that integrate across local variation, and are designed primarily to
57 quantify effects of different subsidy magnitudes (Marczak et al. 2007).

58 Returns of Pacific salmon (*Oncorhynchus spp.*) to spawning grounds along the west coast
59 of North America provide a substantial marine-derived resource subsidy to aquatic and terrestrial
60 consumers such as bears, birds, insects, and resident fishes (Gende et al. 2002, Schindler et al.
61 2003). Consumption of salmon eggs and carcasses enhance growth and productivity of many
62 stream organisms (Chaloner et al. 2002, Scheuerell et al. 2007, Bentley et al. 2012, Swain et al.
63 2014). However, even in regions with high overall salmon returns, spawning occurs patchily

across space and time, constraining the ability of consumers to access marine-derived resources. In SW Alaska, landscape features such as the presence of nursery lakes determine suitable spawning habitat for sockeye salmon (*O. nerka*), and therefore create spatial variation in access to eggs and carcasses. Sockeye returns to individual spawning sites can also vary by orders of magnitude among years (Rogers and Schindler 2008). Large, mobile consumers such as bears and birds track variation in salmon resources across space and time (Schindler et al. 2013), but less mobile consumers such as insects and small fishes likely cannot, potentially creating differences in growth and condition among populations and individuals.

Salmon eggs and carcasses are more nutrient and energy rich than other food sources available to stream predators in high latitude streams (Gende et al. 2004). As a result, consumption of salmon resources should increase growth and fat accumulation in stream organisms, and ultimately improve their survival at subsequent life stages. Experimental addition of salmon eggs and carcasses to stream reaches or enclosures often induce rapid, positive changes in growth and lipid composition of consumers (Wipfli et al. 2003, Heintz et al. 2004). Poly-unsaturated fatty acids (PUFA) such as docosahexaenoic acid (DHA), eicosapentaenoic acid (EPA), and arachidonic acid (ARA) are chemical precursors for a range of important cellular components and hormones and cannot be synthesized de novo by most vertebrates, therefore adequate dietary inputs of these lipids are crucial for fish development and growth (Ahlgren, Vrede, and Goedkoop 2009). Adult salmon tissues, like many other marine fishes, are much higher in DHA, EPA, and ARA than freshwater organisms, making them an important potential source of these lipids for stream consumers (Heintz et al. 2010).

The strong positive effects of egg and carcass consumption on growth and body condition observed in small-scale experiments demonstrate the potential benefits of salmon resources to

stream consumers, but complexity in natural environments may mediate these effects in wild populations (Armstrong et al. 2010). At high latitudes, temperature acts as an additional constraint on the capacity for ectotherms to exploit resource subsidies. By strongly mediating metabolic rate, temperature affects the serial processes in the food-to-fuel pathway, spanning from foraging to fat deposition and somatic growth (Weiner 1992). For example, cold temperatures can generate digestive constraints on foraging when food is abundant (Elliott and Persson 1978). Armstrong et al. (2013) showed that juvenile coho salmon are digestively constrained when foraging on salmon eggs, and that these constraints were especially severe when temperatures were reduced from 10 °C to 6°C. Therefore even if high quality resources such as salmon eggs are present, low water temperatures may limit the benefits that cold-blooded consumers derive from them.

In this study we investigated how local environmental conditions (i.e., water temperature) regulate the ability of juvenile coho salmon (*O. kisutch*), a known egg predator, to capitalize on resource subsidies provided by spawning sockeye salmon. Streams within our study watershed (Wood River system, southwest Alaska) differ significantly in their thermal regimes due to variation in geomorphic conditions (Lisi et al. 2013), and receive highly variable numbers of adult sockeye salmon each year. We asked 1) how juvenile coho salmon in different thermal environments and receiving different subsidy magnitudes varied in body size at the end of the summer growth season, and 2) how individual consumers within these populations differed in their physiological responses to resource subsidies, as measured by their body condition and fatty acid composition.

To address the first question, we compared mean end-of-summer size of age-0 and age-1 coho salmon in 7 study streams across multiple years to test the effects of variation in the density

of spawning sockeye salmon and water temperature on growth. We expected that coho salmon would be larger in streams and years with higher sockeye spawner densities, in response to higher egg abundance. We also predicted that higher stream temperatures would result in larger coho salmon body size, as mean temperatures at our study sites are low relative to their thermal optima (Stewart and Ibarra 1991). We expected that the effects of sockeye salmon spawner abundance (i.e. egg abundance) on growth would be temperature-dependent, with coho salmon achieving larger body size in warm streams where energy-rich eggs were present. In cold streams, on the other hand, we expected coho salmon would be limited in their ability to assimilate eggs, and thus would not grow as large despite the presence of energy-rich food resources.

To address our second question, we tested whether individual variation in egg consumption was associated with differences in body size, condition, and fatty acid composition. We compared body size, relative body condition, and fatty acid composition of age-1 coho salmon collected in late summer in 2010 and 2011 from the same 7 study streams and used muscle tissue $\delta^{15}\text{N}$ to estimate their assimilation of salmon resources. We predicted that juvenile coho salmon showing high egg predation would grow larger and have better relative body condition than individuals who assimilated fewer marine resources. We also expected that egg-consumption would shift the fatty acid composition of lipid stores within coho salmon muscle tissue by elevating concentrations of omega-3 fatty acids such as DHA (22:6n3) and EPA (20:5n3), which are crucial to salmonid development (Heintz et al. 2010).

Methods:

Field sampling

Juvenile coho salmon were sampled from seven streams in the Wood River watershed in the Bristol Bay region of southwest Alaska (59°20' N, 158°40'W). Annual sockeye salmon (*O. nerka*) escapement to this system has averaged 1.1 million over the last 50 years (Baker et al. 2006). Three of the streams (Bear, Yako, Whitefish) are tributaries of Lake Aleknagik, two (Fifer, Silver Salmon) are tributaries of the lower Wood River, one (Squaw) flows into Nushagak Bay, and one (Lynx Creek) is a tributary of Lake Nerka. Sampling sites within all streams are low gradient (0.5-1%), low elevation (<100 m above sea level), and range in bank-full width from 4 to 15 m (Marriott 1964). Four of these streams (Bear, Yako, Whitefish, Lynx) are habitat for spawning sockeye salmon, while three are not (Squaw, Fifer, Silver Salmon). The streams without sockeye salmon spawning lack suitable nursery lake habitat for juvenile sockeye salmon, and receive an occasional small number of spawning pink salmon, but are otherwise similar to sockeye spawning streams.

Between ten and thirty juvenile coho salmon were collected for stable isotope and fatty acid analyses with a stick seine on one sampling date per stream (late August through early September in 2010 or 2011). Sockeye streams were sampled concurrently or after the active sockeye salmon spawning period. Fork length and wet mass were measured on site (Table S1), with fork length ranging from 70 to 140 mm, large enough to prey on sockeye eggs (Armstrong et al. 2010). Fish were frozen at -20 °C until further analysis. Aquatic insect taxa previously detected in juvenile coho salmon diets (Trichoptera, Ephemeroptera, Plecoptera, Diptera; Armstrong et al. 2010, Armstrong and Schindler 2013) were collected by Surber sampling from

at least three reaches in each stream except for Fifer Creek. Insect samples were sorted by order and frozen at -20 °C until analysis for carbon and nitrogen stable isotope ratios.

The effects of stream temperature and sockeye salmon spawner abundance on late summer size distributions of juvenile coho populations were assessed using multi-year data collected in Bear (2007-2012), Whitefish (2007-2012), Yako (2007-2012), Lynx (2008-2013), Silver Salmon (2007-2012), Fifer (2009-2011), and Squaw (2012-2013) creeks. Juvenile coho salmon were collected in each stream by stick seining in the last week of August or first week of September. Fish were then anaesthetized with MS-222 and measured for fork length. A subset of the fish were weighed on an electronic scale.

In streams that support sockeye salmon spawning (Bear, Whitefish, Yako, Lynx), live and dead spawners were counted at least three times per season, by walking upstream and recording numbers in 200 m stream reaches until at least three consecutive reaches without salmon were observed. Peak spawner density (spawners*m⁻²) was calculated by dividing peak spawner count by the distance surveyed and mean stream width.

In each of the sampling years, I-button temperature recorders (Maxim Integrated Products, Sunnyvale, CA) were placed in stream mouths, suspended 3-5 cm above the streambed, to record temperatures at 90-min intervals with 0.125 to 0.5 °C resolution from June 30 to September 1. Mean summer temperature for each stream was calculated from these data (Lisi et al. 2013).

Stable isotope analysis

Because sockeye salmon put on the majority of their mass in the ocean where they occupy a relatively high trophic position, and rarely feed upon re-entry to freshwater, their

tissues, including eggs, are enriched in heavier isotopes of carbon and nitrogen (Kline et al. 1990), allowing the tracing of these resources through aquatic food webs. We used carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios of coho dorsal muscle tissue as measures of diet composition and trophic level. Reichert et al. (2008) measured seasonal change in muscle tissue stable isotope signatures of juvenile coho salmon in the Skagit River, WA, and found elevated $\delta^{15}\text{N}$ in coho salmon in spring after over-winter feeding on salmon carcasses. Our samples were collected in late August or early September, allowing juvenile coho salmon at least four weeks of access to sockeye salmon resources, and thus muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ should reflect this diet source if it was assimilated. Samples were analyzed at the Isolab at University of Washington on a Thermally-Coupled Elemental Analyzer (TC-EA) coupled to a Thermo-Finnigan MAT253 Mass Spectrometer to determine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Results are reported as deviations from international standards (‰; Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$, atmospheric N for $\delta^{15}\text{N}$). Because the coho muscle samples had high C:N ratios (mean = 3.53), $\delta^{13}\text{C}$ values were adjusted for lipid content based on empirical corrections provided in Post et al. (2007).

Fatty acid analysis

Fatty acid extraction and analysis of coho salmon muscle tissue was performed as described in Strandberg et al. (2014). Samples were weighed (1-2 mg dry weight), then extracted with chloroform/methanol/water (2:1:0.8, by volume). Lipids were dissolved in toluene and trans-methylated at 50 C for 16 h, using an acidic catalyst (1 % H_2SO_4 in methanol). The resulting fatty acid methyl esters (FAME) were analyzed at the University of Washington, with a HP6890 gas chromatograph (GC), equipped with flame ionization detection (FID), using a DB-23 capillary column (length 30 m, ID 0.25 mm, film thickness 0.25 mm, Agilent) with helium as

carrier gas (1 mL min⁻¹). FAME were tentatively identified by comparison of retention times with known standards (37-component FAME mix, Supelco).

For final determination of peak identities, a subset of samples was analyzed by gas chromatography/mass spectrometry (Shimadzu GCMS QP2010 plus; Agilent DB-23 column) with splitless injection. Double-bond configuration of C16 and C18 mono-unsaturated fatty acids (MUFA) was determined by analysis of their dimethyl disulphide adducts (Nichols et al. 1986). In all, 40 fatty acids were identified, and all data were mass corrected as well as converted to proportion of total fatty acids ([g FA methyl ester/g total FA methyl ester]).

We used the following shorthand notation for referring to fatty acids: A:BnX, where ‘A’ is the number of carbon atoms, ‘B’ is the number of double bonds, and ‘X’ is the position of the first double bond relative to the methyl end. Saturated fatty acids (SAFA) have no double bonds, mono-unsaturated fatty acids (MUFA) have one double bond, and poly-unsaturated fatty acids (PUFA) have 2 or more double bonds.

The fatty acid composition of an animal’s storage lipids should reflect a mixture of the FA compositions of its prey, and ultimately the FA produced at the base of the food web by plants, algae, and bacteria (Dalsgaard et al. 2003). Certain fatty acids are produced in higher concentrations by marine organisms—for example 20:1n9 and 20:1n11 are most likely derived from marine calanoid copepods and are found in elevated concentrations in adult salmon tissue (Heintz et al. 2010). Adult salmon returning from the ocean also have substantially higher proportions of omega-3 fatty acids such as EPA and DHA than do freshwater organisms such as aquatic insects or juvenile coho salmon. As a result, freshwater consumers that assimilate salmon carcasses or eggs can accumulate marine-derived lipids in their own fat stores (Heintz et al.

2010). Therefore, elevated concentrations of these biomarkers in freshwater organisms can indicate consumption of marine-derived resources such as salmon tissue.

Effect of temperature and subsidy magnitude on body size in juvenile coho salmon

Because juvenile coho salmon in Alaskan streams typically rear in freshwater for two years (Quinn 2005), stream populations are mixtures of two age classes with potentially different responses to temperature and sockeye egg abundance. For example, previous work shows that coho salmon are gape-limited in their ability to consume water-hardened salmon eggs until they grow to approximately 70 mm in length, thus limiting the benefit of this resource subsidy for all but the largest age-0 fish (Armstrong et al. 2010). Late summer size distributions of juvenile coho salmon in all 7 study streams were roughly bimodal (Figures S1-S7): size thresholds for the two age classes present (age 0 and age 1) were determined from these distributions. Coho salmon in a given stream and year were assigned an age class based on the size threshold for that stream-year combination.

We tested the effects of temperature, sockeye spawning presence/absence, sockeye spawner density, and any interactions on mean late summer body size of age-0 and age-1 coho salmon using multiple linear regression in R (R Core Development Team 2013). To account for non-independence of data collected from the same stream, we followed the model selection protocol outlined in Zuur et al. (2009). We first compared random model structures using Akaike's information criterion, corrected for small sample sizes (AICc; Burnham and Anderson 2002). We compared the following model structures: no random effects, a random intercept, and random intercept and slope, and found that the model without random effects fit the data best ($\Delta\text{AICc} > 2$ for models that included random effects of stream). Fixed effects only models were

then fit using maximum likelihood and compared using AICc. AICc model weights were calculated as described in Burnham and Anderson (2002).

Individual variation in physiological responses to salmon resource subsidies

We examined differences in late summer energetic status and fatty acid composition of age-1 juvenile coho salmon collected in 2010 and 2011. Variation in fatty acid composition among coho salmon from different streams (and therefore different access to marine-derived resources) was first assessed with principal component analysis (PCA), using the vegan package in R (Oksanen et al. 2012). For ease of interpretation, proportions of structurally similar FA's were summed, resulting in 22 FA variables used in subsequent analyses (results were similar using all 40 variables). Prior to statistical analyses, FA data were log-transformed to adjust for right-skew. Significance of the resulting eigenvalues was tested using Monte Carlo randomization (1000 permutations). To test whether coho salmon differed significantly in overall FA composition among streams, we used analysis of similarity (ANOSIM; Clarke 1993), a non-parametric multivariate procedure analogous to an ANOVA. The test statistic, R, if greater than zero, denotes that between-group dissimilarities are significantly larger than within-group dissimilarity. In addition, we tested for differences in proportions of specific FAs (22:6n3, DHA; C₂₀+C₂₂ MUFA; 20:5n3, EPA; 18:2n6, LIN; 18:3n3, ALA) between 'sockeye' versus 'non-sockeye' groups, using mixed effects regression with the lme4 package in R (Bates et al. 2015).

We tested whether the contribution of sockeye salmon resources to age-1 coho diets (n=90) affected measures of body size, condition, and FA composition using mixed effects linear regression models in the lme4 package in R (Bates et al. 2015), following the model selection protocol described in Zuur et al. (2009).

Coho diet proportions were estimated by treating an individual's $\delta^{15}\text{N}$ as a mixture of two sources (sockeye eggs and aquatic invertebrates; Figure 1). Aquatic invertebrates from each stream except Fifer creek were analyzed for $\delta^{15}\text{N}$, thus we were able to use stream-specific $\delta^{15}\text{N}$ values in diet mixture calculations. For Fifer creek we used Squaw creek insect $\delta^{15}\text{N}$ values, because Squaw is the closest study stream and is similar in habitat characteristics. We used an average $\delta^{15}\text{N}$ value for sockeye eggs ($11.97\text{‰} \pm 0.20$, mean, standard deviation, $n = 13$) in calculations, from samples collected in the Wood River watershed in 2013. Invertebrate and sockeye egg $\delta^{15}\text{N}$ values were corrected for trophic discrimination before calculating diet contributions ($+ 3.4\text{‰}$; Post 2002). We used the following equations to calculate the fraction of coho salmon diet made up by eggs (f_{egg}):

$$\delta^{15}N_{\text{coho}} = f_{\text{insect}}\delta^{15}N_{\text{insect}} + f_{\text{egg}}\delta^{15}N_{\text{egg}}$$

$$f_{\text{insect}} + f_{\text{egg}} = 1$$

f_{egg} , hereafter referred to as 'egg consumption', was subsequently used as predictor variable in regression models.

We calculated the relative body condition (e.g. wet mass residual) of each coho salmon and used this as a response variable in our regression models. Individuals with a positive relative body condition are heavier given their length than the population average. We defined relative body condition as an individual's residual from the linear relationship between log-mass and log-length of the entire population. Data from juvenile coho salmon measured between 2007 and 2012 in all seven study streams were included in the length-weight regression ($n=7927$). Relative body condition of individual coho salmon was calculated using the regression coefficients output

from this model. Yako creek fish used in FA analyses lacked wet weight measurements and were thus excluded from this analysis.

Results

Effect of temperature and subsidy magnitude on body size in juvenile coho salmon

Juvenile coho salmon in both age classes grew largest in warm streams (average $>10^{\circ}\text{C}$) where sockeye salmon spawned (Whitefish, Lynx; Figure 2a and 2c). Increased subsidy magnitude (spawner density) did not result in larger average body size for either age class at the end of the growing season (Figure 2b and 2d).

The best model for late summer body size attained by age 0 coho salmon included a significant positive interaction between sockeye spawning presence and stream temperature (AIC_c weight = 0.95; see Table 1 for model comparisons). Models including sockeye spawning density as a predictor variable fit the data significantly worse than alternative models ($\Delta\text{AIC}_c > 17$).

Similar to age 0 coho salmon, the best model for age 1 body size included a significant positive interaction between temperature and sockeye spawning presence (AIC_c weight = 0.70; Table 1), whereas a model including sockeye spawner density had significantly less support ($\Delta\text{AIC}_c > 20$).

Effects of sockeye egg consumption on individual size, condition and FA composition

The first two axes of the PCA comparing fatty acid compositions of age 1 coho salmon were significant and explained 28% and 21% respectively of the variation among individuals ($n=90$; $p < 0.001$, Figure S8). All 22 FA variables loaded onto both axes, though PC axis 2

roughly characterized a gradient in marine-derived/associated fatty acids (C20 + 22 MUFA, EPA, and DHA versus LIN, ALA; Table S2). While there was substantial overlap in FA composition between coho salmon from sockeye and non-sockeye streams, the two groups separated weakly along PC axis 2, and the ANOSIM indicated that they differed significantly in overall FA composition ($R = 0.24$, $p < 0.001$). Stream populations also had significantly different FA compositions ($R = 0.36$, $p < 0.001$).

Coho salmon in sockeye spawning streams had higher proportions of marine derived or associated FA such as DHA ($n = 55$, mean = 0.27 ± 0.049 , $p = 0.24$) and C₂₀ + C₂₂ MUFA (0.01 ± 0.0061 , $p = 0.10$) than those in non-sockeye streams ($n = 35$, DHA 0.23 ± 0.07 , C₂₀+C₂₂ MUFA 0.0057 ± 0.0049), but differences were not statistically significant when random effects (stream) were included in models. Coho salmon in non-sockeye streams had higher proportions of LIN (0.051 ± 0.017 , $p = 0.10$) and ALA (0.043 ± 0.014 , $p = 0.51$) than coho salmon in sockeye streams (LIN: 0.037 ± 0.009 , ALA: 0.028 ± 0.008) but differences were not statistically significant; these FA are abundant in freshwater invertebrates (Torres-Ruiz et al. 2007, Smits et al. 2015). Coho salmon did not differ significantly in their proportion of EPA (overall mean 0.09 ± 0.017). Coho salmon in sockeye spawning streams had higher total FA concentration in their muscle tissue (38.14 ± 20.65 $\mu\text{g}/\text{mg}$ dry weight, $p = 0.34$) than those in non-sockeye streams (30.97 ± 17.27 $\mu\text{g}/\text{mg}$).

Body size of age 1 coho salmon was positively related both to stream temperature and to egg consumption (Figure 3). The best model fit the data significantly better than alternative models and included both egg consumption as well as its positive interaction with stream temperature as significant predictors of individual body size (AIC_c weight = 0.96; Table 2).

Relative body condition, which has been correlated with the recent growth rate in other fish species within our study watershed (Bentley and Schindler 2013), was positively but weakly related to egg consumption and to stream temperature. The best model was an intercept only model, including random effect of stream (Table 2), but there was little statistical support for any one model (AIC_c weight < 0.5 for all models). Within individual stream sites, higher egg fraction in coho salmon diets did not result in higher relative body condition (Figure 4), but stream populations differed from one another, with the highest condition fish occurring in warm, sockeye spawning streams (Whitefish and Lynx creeks).

Consumption of sockeye salmon eggs was associated with altered FA composition of age 1 coho salmon (Figure 5), though it did not affect the total FA concentration within their muscle tissue ($p = 0.25$; Figure 5a). As expected, individuals who consumed more sockeye eggs had elevated proportions of $C_{20} + C_{22}$ MUFA, reflecting a marine-derived food source (Figure 5b). The best model included a random effect of stream on the intercept, as well as egg consumption as a direct effect: models including stream temperature as a predictor fit the data significantly worse ($\Delta AIC_c > 2$, Table 2). Coho salmon that ate more eggs had higher omega 3: omega 6 FA ratios (Figure 5c): the best model included a random effect of stream on the intercept, as well as egg consumption as a predictor variable (AIC_c weight = 0.60; Table 2). Models that included stream temperature as a predictor fit the data significantly worse than alternative models ($\Delta AIC_c > 2$).

Discussion

Multiple years of juvenile coho salmon size data showed that temperature strongly controls consumer growth responses to a marine resource subsidy. The presence of sockeye

salmon eggs as a food resource substantially increased the mean body size of juvenile coho salmon in warm streams ($> 10^{\circ}\text{C}$): coho salmon in Whitefish and Lynx creeks were on average 20 mm larger in late August than those in Silver Salmon Creek, a stream with comparable summer temperatures (Figure 2). On the other hand, the presence of sockeye eggs did not enhance growth in cold streams: coho salmon were no larger on average in Bear or Yako creeks than in Fifer or Squaw creeks. These divergent size distributions in cold and warm sockeye spawning streams are consistent with previous findings that warm temperatures allow age 0 coho salmon to outgrow gape limitation and consume sockeye eggs, which then further accelerates their growth (Armstrong et al. 2010). While juveniles in warm streams such as Silver Salmon Creek have higher growth potential than those in cold streams (Armstrong et al. 2010), this potential remains unrealized in non-sockeye streams, presumably because these sites lack the energy-dense resources fish need to overcome increased metabolic costs.

Contrary to our initial hypotheses, juvenile coho salmon did not grow larger in streams or years with higher subsidy magnitudes (sockeye spawner density). While the presence of sockeye salmon spawning, and thus eggs, significantly increased coho salmon growth in warm streams, and egg consumption by individuals was associated with larger body size, growth was not affected by sockeye salmon abundance in these streams. This was somewhat surprising because small resident fishes must prey on eggs ejected from the gravel during spawning or nest-digging: in high return years, redd superimposition greatly increases egg availability to consumers in the stream channel (Moore et al. 2008). Our findings contrast with studies conducted in south central Alaska and the Pacific Northwest; $\delta^{15}\text{N}$ enrichment and condition in sculpins was positively correlated with salmon spawning density in British Columbia streams (Swain et al. 2014), and juvenile coho salmon were more $\delta^{15}\text{N}$ -enriched and had higher growth rates in south central

Alaska streams with higher salmon spawner biomass (Rinella et al. 2011). Growth responses by other resident fish species (grayling, rainbow trout) to egg subsidies within the Wood River system corresponded with sockeye salmon run size as well as underlying stream productivity, though the growth responses saturated at relatively low spawner densities (Bentley et al. 2012). However, similar studies in the Copper River Delta, Alaska, did not detect strong growth responses by juvenile coho salmon with access to spawning salmon resources (Lang et al. 2006), despite $\delta^{15}\text{N}$ enrichment at multiple trophic levels (Hicks et al. 2005).

There are several potential reasons why sockeye density (i.e. egg abundance) is uncorrelated with juvenile coho salmon growth in Wood River watersheds. First, competition among juvenile coho salmon for eggs is likely weak due to a food-saturated environment in sockeye spawning streams. Juvenile coho salmon density is low, whereas sockeye salmon density varies between years but can be relatively high for 1st – 3rd order streams (>1 spawner $\cdot\text{m}^{-2}$). In lower latitude streams with reduced salmon spawning populations, on the other hand, egg abundance may be low enough to constrain consumer growth. Second, stream temperature controls assimilative capacity in juvenile coho salmon: a tagging study in Bear Creek showed that individuals who migrated to warm microhabitats after consuming eggs grew substantially larger than individuals that did not (Armstrong et al. 2013). Further, even in warm habitats closer to the physiological optimum for coho salmon ($\sim 15^\circ\text{C}$; Stewart and Ibarra 1990), individuals were strongly digestively constrained (i.e. digestion rates were 200 - 400 % slower than maximum foraging rates) due to their large meal size and the long gut retention time for eggs (Armstrong et al. 2013). Most streams within the Wood River watershed are colder than thermally optimal for coho salmon, therefore the distribution of favorable thermal habitat may present a greater constraint on digestive capacity and growth than egg abundance.

Consistent with previous experimental and observational studies (Heintz et al. 2004, 2010), egg consumption shifted the FA composition of juvenile coho salmon towards higher proportions of marine-associated biomarkers (20:1n9, 20:1n11, DHA). However, contrary to the rapid fat accumulation observed in other studies, wild individuals in Wood River streams that consumed more salmon resources did not accumulate higher total concentrations of FA in their muscle tissue (Figure 5A). Further, while we observed differences in relative body condition among six stream populations, with the heaviest fish occurring in warm sockeye spawning streams (Whitefish, Lynx), within individual sockeye spawning streams, relative body condition was unrelated to egg consumption. Long winters at northern latitudes present a substantial period of resource scarcity for consumers, and fishes with higher lipid levels in autumn survive winter at higher rates (Post and Parkinson 2001b, Biro et al. 2004). Therefore, we expected juvenile coho salmon with access to abundant, high quality resources to allocate excess energy towards fat stores. Instead, there was a high degree of variation in the allocation of energy to FA storage and growth among individuals living in the same environment, and consuming similar diets (as inferred from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). The lack of clear responses (FA accumulation, body condition) to egg consumption by fish in this study, which contrasts with previous findings (Heintz et al. 2004; Rinella et al. 2011), may stem from ontogenetic shifts in lipid storage and metabolism. We analyzed only age 1 coho salmon for FA composition and body condition, whereas other studies showing responses in lipid accumulation analyzed mainly age 0 coho salmon (Heintz et al. 2004; Rinella et al. 2011). Because we did not analyze any age 0 fish, we cannot test for different responses among age classes, but this presents an important gap in our understanding of the effects of salmon egg subsidies on juvenile salmonids.

Tradeoffs between fat storage and somatic growth in temperate and high latitude fishes may occur for several reasons: large fish are less vulnerable to predation, while mass-specific metabolic rate decreases with larger body size (lower starvation risk; Post and Parkinson 2001, but see Connolly and Petersen 2003). Egg consumption was most directly related to increased body size rather than FA content or body condition—it may be more advantageous for consumers in these streams to grow larger during the summer than to allocate energy to lipid reserves. Armstrong et al. (2013) observed highly variable foraging strategies among juvenile coho salmon within a single sockeye-spawning stream (Bear Creek); our results show similar diversity in energy allocation among individuals. Extreme inter-annual variation in sockeye salmon abundance (Rogers and Schindler 2008), coupled with spatial heterogeneity in flow and temperature (Armstrong and Schindler 2013), likely support multiple evolutionarily stable strategies for resource use and energy allocation by juvenile coho salmon.

The individual variation in FA composition we observed in juvenile coho salmon, while largely related to differences in diet, may also reflect differential retention of essential FAs versus non-essential FAs. There is some evidence that fish can preferentially retain or metabolize FAs depending on environmental and physiological conditions: Bendiksen and Jobling (2003) found that Atlantic salmon parr strongly retained omega-3 essential FA, but not omega-6 FA, relative to the proportions in diets, and that retention increased at lower temperatures and with low-lipid diets. While most studies of FA metabolism involve laboratory feeding experiments rather than natural populations, it is likely that FA composition in wild individuals varies for reasons besides diet. For example, age 1 coho salmon in Squaw creek, a non-sockeye stream, had DHA proportions (mean = 0.29 ± 0.07) as high as juvenile coho salmon in Whitefish creek, a sockeye stream (mean = 0.26 ± 0.03), despite lacking DHA-rich food resources such as salmon

eggs (stream insects contain only trace levels of DHA; Smits et al. 2015). Squaw creek coho salmon had the lowest relative body condition of all individuals sampled (Figure 4), thus high DHA retention (and preferential metabolism of non-essential FA) may reflect physiological responses to caloric deficits. High proportions of DHA, or conversely, low proportions of other marine biomarkers such as $C_{20} + C_{22}$ MUFA in consumer tissue, should not necessarily be interpreted as an individual's degree of reliance on marine resources.

Geomorphology, hydrology, and climate interact to generate complexity in habitats and resources for freshwater consumers. Consumer responses to resource subsidies should reflect this complexity. Much of the literature on marine subsidies provided by spawning Pacific salmon ignore the mediating effects of local environment on consumer responses. While it is now recognized that incorporation of salmon-derived nitrogen by freshwater and riparian primary producers depends on the presence of alternative nitrogen sources within watersheds (i.e. N-fixing plants such as alder; Helfield and Naiman 2002, Hocking and Reynolds 2011), similar interactions at higher trophic levels remain less well characterized. Our results show that the benefits of salmon subsidies to consumers often depend as strongly on environmental conditions as on the magnitude of resource pulses.

As boreal and arctic regions warm due to climate change, production and growth of freshwater organisms may improve as temperatures approach thermal optima for certain species. However, resultant increases in metabolic costs for consumers must be offset by adequate food resources to sustain higher production. A forty year time series of juvenile sockeye salmon size data in SW Alaska lakes showed that while earlier spring ice breakup and higher zooplankton abundance led to higher summer growth, the negative effects of con-specific density were on average twice as large, demonstrating the complexity of ecological responses to climate change

(Schindler et al. 2005). Our results show that warm temperatures must be coupled with an abundant food resource subsidy to enhance body size in juvenile coho salmon. As temperatures continue to warm, releasing freshwater consumers from thermal constraints, resource abundance may become an increasingly important control on production in high latitude systems. Managing populations in the future may be improved by understanding the interactions between the physical and chemical attributes of landscapes and resource availability for consumers. Maintaining habitat heterogeneity may be an effective management approach where future climate impacts on species and landscapes remain uncertain.

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Tables

Table 1. Linear models considered for mean late summer body size of age 0 and age 1 coho salmon (2007-2014) in Bear, Yako, Whitefish, Lynx, Silver Salmon, Fifer, and Squaw Creek. K is the number of parameters estimated in each model. The optimal models for age 0 and age 1 coho mean body size are highlighted in bold font. No random effects were included in models.

	Predictors	Sample Size	K	AICc	ΔAICc	AICc Weight	Adjusted R ²
Age 0	Temperature; Spawner presence; Interaction	39	5	215.0	0.0	0.95	0.74
	Temperature; Spawner presence	39	4	221.0	5.7	0.05	0.6785
	Temperature; Spawner density; Interaction	39	5	233.0	17.9	0	0.558
	Temperature; Spawner density	39	4	234.0	18.5	0	0.527
	Temperature	39	3	234.0	18.7	0	0.501
	Spawner presence	39	3	253.0	37.5	0	0.1192
	Spawner density	39	3	257.0	42.4	0	-0.021
Age 1	Temperature; Spawner presence; Interaction	33	5	218.7	0.0	0.70	0.672
	Temperature; Spawner presence	33	4	220.4	1.6	0.30	0.637
	Spawner presence	33	3	240.5	21.7	0	0.3
	Temperature; Spawner density	33	4	240.8	22.0	0	0.326
	Temperature	33	3	241.7	22.9	0	0.274
	Temperature; Spawner density; Interaction	33	5	242.7	24.0	0	0.32
	Spawner density	33	3	253.3	34.6	0	-0.03

Table 2. Mixed effects linear regression models considered for body size (fork length; mm), relative body condition, and fatty acid composition (proportion of total) of individual age 1 coho collected in 2010 and 2011 from Bear, Yako, Whitefish, Lynx, Silver Salmon, Fifer, and Squaw Creek. F_egg refers to the proportion of coho salmon diet made up by sockeye eggs (i.e. egg consumption). The optimal models are highlighted in bold font.

Response	Random effects	Predictors	Sample Size	K	AICc	Δ AICc	AICc weight
Fork Length (mm)	None	f_egg; Temperature; Interaction	76	5	578.0	0.0	0.96
		f_egg; Temperature	76	4	584.4	6.4	0.04
		f_egg	76	3	593.5	15.5	0
		Temperature	76	3	594.3	16.3	0
		Intercept only	76	1	602.6	24.6	0
Relative Body Condition	Random effect of stream on intercept	Intercept only	65	3	-134.7	0.0	0.46
		f_egg	65	4	-133.2	1.1	0.26
		Temperature	65	4	-132.3	2.0	0.17
		f_egg; Temperature	65	5	-130.9	3.3	0.09
		f_egg; Temperature; Interaction	65	6	-128.6	5.6	0.03
C20 + 22 MUFA	Random effect of stream on intercept	f_egg	76	4	-598.5	0.0	0.64
		f_egg; Temperature	76	5	-596.2	2.3	0.20
		f_egg; Temperature; Interaction	76	6	-595.5	2.9	0.15
		Intercept only	76	3	-588.7	9.7	0
		Temperature	76	4	-586.6	11.8	0
Omega 3: Omega 6 FA ratio	Random effect of stream on intercept	f_egg	76	4	300.6	0.0	0.61
		f_egg; Temperature	76	5	302.6	2.0	0.22
		f_egg; Temperature; Interaction	76	6	304.7	4.0	0.08
		Intercept only	76	3	305.1	4.5	0.06
		Temperature	76	4	307.2	6.6	0.02

Figures

Figure 1. The left panel shows isotopic signatures of all age 1 coho salmon collected from 7 study streams in 2010 and 2011, as well as their potential food sources (sockeye eggs, stream invertebrates). Black dots represent individual coho salmon from non-sockeye streams, while pink dots are individuals collected in sockeye spawning streams. Isotopic values for sockeye eggs and stream invertebrates were corrected for trophic discrimination (Post 2002). Small right-hand panels show examples of data from two of the study streams: proportional egg consumption by individual coho salmon was calculated using stream-specific invertebrate $\delta^{15}\text{N}$. All axes share the same units and scale.

Figure 2. Effects of stream temperature and sockeye spawner density on mean late summer body size of age 0 (panels a and b) and age 1 (panels c and d) juvenile coho salmon in seven streams between 2007 and 2014. Unique symbols correspond to data from the same stream in different years. Data from sockeye spawning streams are denoted by pink colored symbols. Dashed lines show linear relationships between mean coho body size and stream temperature in sockeye spawning streams (pink) and non-spawning streams (black).

650

Figure 3. Fork length (mm; y-axis) and egg consumption (proportion; x-axis) of individual age 1 coho salmon collected in 2010 and 2011. Colored dots are coho salmon collected from sockeye spawning streams (Whitefish, Lynx, Bear, Yako), and black dots are coho salmon from non-sockeye streams (Silver Salmon, Fifer, Squaw). Average summer stream temperature (June–August; ° C) during the year sampled is included below stream name in each panel.

Figure 4. Marine resource (i.e. egg) consumption (proportion; x-axis) versus relative body condition (y-axis) of age 1 coho salmon ($n = 76$). Each panel shows individuals collected in one stream in 2010 or 2011. Colored dots represent coho salmon collected in sockeye salmon spawning streams. We did not calculate the relative body condition of Yako Creek coho salmon because they lacked wet weight measurements. Average summer stream temperature (June–August; °C) during the year sampled is included below stream name in each panel.

Figure 5: Marine resource consumption (proportion; x-axis) of age 1 coho salmon versus a) total FA concentration ($\mu\text{g}/\text{mg}$ dry mass), b) proportion of marine-origin FA ($\text{C}_{20} + \text{C}_{22}$ MUFA) and c) omega-3 to omega-6 FA ratio of muscle tissue. Black dots represent individuals collected from non-sockeye spawning streams, while colored dots represent individuals collected from streams where sockeye salmon spawn.

$\delta^{15}\text{N}$ (‰)

Relative Body Condition

Supplementary Information

Figure S1. Size distributions of juvenile coho salmon seined in late summer in Bear Creek (2007-2012)

Figure S2. Size distributions of juvenile coho salmon seined in late summer in Lynx Creek (2008-2013)

Figure S3. Size distributions of juvenile coho salmon seined in late summer in Yako Creek (2007-2012)

Figure S4. Size distributions of juvenile coho salmon seined in late summer in Whitefish Creek (2007-2012). Note that scale of y-axis is different for 2008 than for other years.

Figure S5. Size distributions of juvenile coho salmon seined in late summer in Silver Salmon Creek (2007-2012)

Figure S6. Size distributions of juvenile coho salmon seined in late summer in Squaw Creek (2012-2013)

Figure S7. Size distributions of juvenile coho salmon seined in late summer in Fifer Creek (2009-2011)

Figure S8. Biplot showing the first two axes of a principal components analysis using 22 FA variables. Principal components 1 and 2 explain 28% and 21.4% of the variation in FA composition among juvenile coho salmon, respectively. Dots represent the mean score for juvenile coho salmon from each study stream (WF = Whitefish, B = Bear, Y = Yako, L = Lynx, F = Fifer, Sq = Squaw, SS = Silver Salmon). Error bars represent one standard deviation.

Table S1. Fork length and wet mass of age 1 juvenile coho salmon analyzed for fatty acid composition and stable isotope ratios. Means plus or minus one standard deviation are reported. Wet mass was not measured for Yako Creek fish.

Stream	Sample size	Fork length (mm)	Wet mass (g)
Bear	18	101.55 ± 12.18	13.22 ± 4.76
Whitefish	8	110.00 ± 17.26	20.97 ± 8.16
Yako	11	93.18 ± 9.31	NA
Lynx	10	110.1 ± 15.73	19.14 ± 6.91
Silver Salmon	11	101.64 ± 7.16	13.31 ± 3.32
Squaw	10	100.00 ± 9.65	10.73 ± 3.74
Fifer	8	98.75 ± 8.48	12.76 ± 3.07

Table S2. Correlations between FA variables and the first two principal components axes (PC1 and PC2), which together explain half the variation in FA composition among coho salmon muscle samples (n = 90). FA variables are sums of structurally similar FA's, which are listed below.

Variable name	FA	PC1	PC2
C ₁₄ MUFA	14:1n7	0.044	-0.465
C ₁₆ MUFA	16:1n5; 16:1n7; 16:1n9	-0.76	-0.316
MOB	16:1n6; 16:1n8	0.335	-0.223
C ₁₆ PUFA	16:2n7	-0.514	-0.25
C ₁₇ MUFA	17:1n8	-0.786	-0.085
C ₁₈ MUFA	18:1n5; 18:1n7; 18:1n9	-0.829	0.135
gLA	18:3n6	-0.328	-0.441
LIN	18:2n6	-0.149	-0.883
C ₁₉ MUFA	19:1n9	0.568	0.111
C ₂₀ + C ₂₂ MUFA	20:1n7; 20:1n9; 20:1n11; 22:1n11	-0.594	0.582
C ₂₀ n6 PUFA	20:2n6; 20:3n6	0.162	-0.624
C ₂₀ n3 PUFA	20:3n3; 20:4n3	-0.345	0.501
ALA	18:3n3	-0.217	-0.663
DHA	22:6n3	0.722	0.602
C ₂₄ MUFA	24:1n9	0.149	0.538
SDA	18:4n3	-0.56	0.061
C ₁₄ _C ₁₇ SAFA	C14:0; C15:0; C16:0; C17:0	0.414	-0.632
C18:0	C18:0	0.605	-0.519
C ₂₀ _C ₂₂ SAFA	C20:0; C22:0	-0.509	-0.391
Branched	i15:0; i16:0; i17:0; a17:0	-0.815	-0.18
ARA	20:4n6	0.738	-0.402
EPA	20:5n3	-0.105	0.427