Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy

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Abstract. Pulsed resource subsidies generate ephemeral fluxes of nutrients and energy among ecosystems. The effects of pulsed subsidies should depend on the magnitude of the pulse, the in situ productivity of the recipient system, and the ability of consumers to capitalize on the resources, yet empirical data on these relationships are limited. We assessed the ecological consequences of variation in resource pulse magnitude, as represented by anadromous salmon returns, for the foraging and growth responses of two species of stream-dwelling salmonids in two streams that vary in productivity in southwestern Alaska. Over 11 years and across a greater than 10-fold variation in sockeye salmon (Oncorhynchus nerka) density, both rainbow trout (O. mykiss) and Arctic grayling (Thymallus arcticus) exhibited a relatively similar, but mechanistically different, non-linear saturating growth response to increasing salmon density. This growth response was driven by both an increase in consumption of salmon eggs and also a decrease in dietary overlap between the two species. However, the relative change in growth from low to high salmon densities was different between streams and depended in situ stream productivity. In low salmon density years the growth of resident consumers fell 46–68% relative to high years in the low productivity stream, but only by 26–34% in the high productivity stream. Our study provides strong evidence that understanding of both the foraging ecology of consumers and the in situ productivity of recipient ecosystems, which together regulate the ecological consequences of variation in resource subsidies, is required for successful implementation of ecosystem-based management in systems dependent on pulsed resource subsidies.

Key words: Arctic grayling; Bristol Bay, Alaska, USA; functional response; habitat productivity; marine-derived resources; rainbow trout; resource pulse magnitude; salmon; stream fishes.

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INTRODUCTION

It has long been recognized that resource availability shapes consumer and food web dynamics (Holling 1973, Persson et al. 1992). However, there is increasing appreciation that resource abundance can be highly heterogeneous across space and time, and that rare, high magnitude events can have disproportionate ecological effects (Ostfeld and Keesing 2000, Holt 2008, Yang et al. 2008). For example, in many systems a single pulse can account for the
majority of all annual resource availability (e.g., Noy-Meir 1973, Bergeron et al. 2011), thus exerting enormous influence on energy acquisition, reproductive success, and survival of consumers (Yang et al. 2010). Although the occurrence of resource pulses are often predictable (e.g., seasonally), the magnitude of pulses can be extremely variable among events (Yang et al. 2008). This variation in resource availability is important as it may have substantial impacts on individual growth and fitness, which can shape population dynamics, species interactions, and ultimately community structure and composition (e.g., Schmidt and Ostfeld 2008). Therefore, knowing the ecological responses of consumers to varying magnitudes of pulsed resources is critical for understanding the importance of these events to food webs and communities.

While larger resource pulses should lead to larger consumer responses, the realized response will be mediated by the characteristics of the resource pulse, the focal consumer, and the ecosystem (Yang et al. 2010). Specifically, the overall impact of resource pulses on consumer fitness will be not only controlled by the magnitude of the event, but also by the ratio of pulse resources relative to ambient resources (Marczak et al. 2007, Yang et al. 2010) and the ability of consumers to capitalize on short-term superabundance of pulsed resources (Armstrong et al. 2010). This is of particular importance as the background productivity may determine the capacity of a system to support individuals during long, inter-pulse periods or when the magnitude of resource pulses is relatively low (but see Noy-Meir 1973).

Over the last decade, there has been a considerable advancement in our understanding of how pulsed resource events can directly and indirectly affect ecological interactions in a wide range of systems (Yang et al. 2010), but at present there remains little understanding of how the fitness of interacting consumers is effected by the variation in the magnitude of resource pulses and background productivity of an ecosystem. In this study, we evaluated the foraging and growth response of two competing salmonids to a >10-fold variation in the magnitude of a high quality resource pulse in two streams with varying in situ productivity. In the absence of the resource pulse these species have a high degree of dietary and spatial overlap (Scheuerell et al. 2007), leading to the expectation that they may have similar foraging and growth responses to high quality resource pulses. Here we show that both species benefit from high magnitude pulsed resource subsidies, but that the mechanistic response differed and that the relative impact was driven by the background productivity of each stream.

Pacific salmon (*Oncorhynchus* spp.) have long been valued as an annual source of renewable food for humans (Lichatowich 2001), returning to freshwater ecosystems throughout the Northern Pacific Rim by the millions to spawn after accumulating >95% of their body mass at sea (Quinn 2005). More recently, research has highlighted the importance of salmon as a pulsed resource subsidy (sensu Polis et al. 1997), linking marine, estuarine, freshwater, and riparian ecosystems (Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003). Salmon spawning migrations generate massive resource fluxes into freshwater and terrestrial ecosystems, producing a pulse of nutrients and energy to inland food webs that often surpass background levels of in situ productivity (Gende et al. 2002). These pulsed subsidies are utilized by a wide range of taxa, including everything from periphyton, macroinvertebrates and fishes (Kline et al. 1993, Holtgrieve et al. 2010) to terrestrial mammals and birds (Willson and Halupka 1995, Hilderbrand et al. 1999). Yet, there remains a distinct lack of quantitative understanding of how the growth and survival of freshwater and terrestrial consumers respond to variation in the magnitude of salmon spawning runs.

It has become clear that stream-dwelling freshwater fishes directly benefit from spawning salmon through the consumption of salmon tissues (particularly eggs; Bilby et al. 1996, Scheuerell et al. 2007, Denton et al. 2009). Although the duration of this seasonal pulse of food is relatively brief, salmon eggs are 2–3 times as energy dense as benthic and terrestrial invertebrates (Cummins and Wuycheck 1971, Armstrong 2010) and can be available when other sources of food are low in abundance (Moore and Schindler 2010). Additionally, spawning behavior of salmon can indirectly benefit resident fishes by dislodging otherwise relatively inaccessible benthic invertebrates dur-
ing their nest construction (Scheuerell et al. 2007). While it is clear that stream-dwelling fishes benefit from the increased resources salmon provide, there remains little empirical description of the relationship between consumer fitness and changes in the magnitude of salmon resource pulses. Such relationships are necessary for understanding the roles salmon play in an ecosystem context and are critical for developing ecosystem-based management strategies that balance the conflict between allocating salmon to commercial fisheries versus freshwater and terrestrial ecosystems that support sport fisheries for resident species (Moore et al. 2008) as well as charismatic megafauna, such as grizzly bears (Levi et al. 2012).

Rainbow trout (O. mykiss) and Arctic grayling (Thymallus arcticus) commonly co-occur in freshwater streams and rivers supporting anadromous sockeye salmon (O. nerka) in southwestern Alaska. Previous studies have shown these two species to have strong, but varying foraging responses with the seasonal arrival of spawning salmon (Scheuerell et al. 2007, Moore et al. 2008). In these systems, sockeye salmon spawn timing is relatively consistent from year-to-year (Moore and Schindler 2010), and at the scale of an entire watershed the overall annual abundance of spawners is relatively constant due to fisheries management that sets an overall escapement goal to maximize yield (Baker et al. 2009). However, the number of salmon returning to an individual spawning location can be extremely variable among years as a result of natural population dynamics (Fig. 1; Rogers and Schindler 2008, 2011). Thus, salmon subsidies should have varying effects on the foraging and growth response of resident fish species among years and streams with varying pulse magnitudes and differing levels of background in situ productivity of alternative, non-salmon prey.

Using 11 years of field survey data from two streams located in Bristol Bay, southwest Alaska, we evaluated the foraging and growth response of individual rainbow trout and Arctic grayling among years with sockeye salmon densities ranging from 0.04 to 1.04 m$^{-2}$. The objectives of this study were to quantify the relationship between growth and the magnitude of the salmon resource pulse, determine if the two species respond differently, and evaluate how these responses were mediated by varying levels of underlying in situ stream productivity in the two streams.

Fig. 1. Peak sockeye salmon abundance in Hidden Creek (solid-black) and Lynx Creek (dashed-white) over the 11 years summer growth rates were evaluated. The inset highlights the variability in the inter-annual peak salmon abundance from 1956–2012.
METHODS

Study system

This study was conducted in the Wood River watershed (59°34’37” N, 158°48’25” W) which drains into Bristol Bay in southwestern Alaska. The Wood River system covers an area of 3590 km² and consists of five large, deep, oligotrophic lakes, which are fed by numerous tributaries and connected by small rivers. Adult sockeye salmon are the dominant anadromous species, spawning in streams, rivers, and beaches throughout the system. Although present from mid-July through late October, individual populations of sockeye salmon are typically active on individual spawning grounds, and vulnerable to aquatic and terrestrial predators, for two to four weeks (Rogers and Rogers 1998, Schindler et al. 2010). Over the last 50 years, sockeye salmon escape (run size after commercial fishing) to the Wood River system has averaged 1.2 million (Baker et al. 2009).

Data were collected in Hidden and Lynx creeks, which are two third-order tributaries of Lake Nerka, each fed by small (<100 hectare) headwater lakes and smaller tributaries (see Ruff et al. 2011). While summer stream temperatures (July 1–August 31) are similar in the two sites, phosphorus and chlorophyll a concentrations are on average 22.5% and 37.5% higher in Hidden Creek (Moore et al. 2007, Holtgrieve et al. 2010; Bentley et al., unpublished data), respectively, likely leading to the >200% higher average benthic invertebrate densities in Hidden Creek (Table 1; Moore and Schindler 2008).

Rainbow trout and Arctic grayling comprise >95% of the resident stream fish biomass within Lynx and Hidden creeks, but are part of a larger stream community consisting of Arctic char (Salvelinus alpinus), three-spined stickleback (Gasterosteus aculeatus), juvenile coho (O. kisutch) and sockeye salmon, coastrange (Cottus cognatus) and slimy (C. aleuticus) sculpin, and rainbow smelt (Osmerus mordax). Biweekly snorkel surveys, conducted from mid-June through early September in 2010–2012, revealed that densities of rainbow trout and Arctic grayling were similar in Lynx and Hidden creeks both within and among years during the time of year when salmon are spawning (Bentley et al., unpublished data; Appendix A: Table A1). Since 1946, the average annual return of sockeye salmon to Lynx and Hidden creeks has been 3252 (1226 salmon/km) and 2774 (1881 salmon/km), respectively. However, the annual return of sockeye spawners to Lynx and Hidden creeks is quite variable among years, ranging from a few hundred to over 17000 individuals (Fig. 1; Rogers and Schindler 2008).

Data collection

Rainbow trout and Arctic grayling were sampled in Lynx and Hidden creeks in late August from 2002 to 2012, coinciding with the end of sockeye salmon spawning. Beginning in 2007, these two streams were sampled every 10 to 20 days from mid-July through early-September to correspond with the entire salmon spawn timing. Fish were collected using a fine mesh stick seine. All captured individuals were transferred to holding containers, anesthetized using a 50-ppm solution of MS-222 (tricaine methane sulphonate), weighed (g) and measured (fork length; mm). A random subset of individuals that spanned the size range of fish in the catch was sampled for diet composition via gastric lavage (Scheuerell et al. 2007). Diet samples were identified into coarse taxonomic groups (typically Order; Appendix B: Table B1) and enumerated in the field or laboratory after preservation in

Table 1. Temperature and instream productivity characteristics for Hidden and Lynx creeks, Alaska.

| Characteristic      | Hidden Creek | Lynx Creek |
|---------------------|--------------|------------|
| Temperature (°C)    | 11.8 ± 1.1   | 11.7 ± 0.6 |
| Total phosphorus (µg/L) | 14.7 ± 4.4 | 12.0 ± 2.6 |
| Total nitrogen (µg/L)  | 393.8 ± 99.8 | 573.0 ± 100.7 |
| Algal biomass (µg chl a/cm²) | 0.33 ± 0.17 | 0.24 ± 0.14 |
| Invertebrate biomass (mg/m²) | 18.7 ± 8.5  | 6.2 ± 2.8  |

Note: Values are averages ± 1 SD calculated from data collected from 2002–2005 (nitrogen, phosphorus, invertebrates), 2002, 2006–2012 (temperature), and 2006, 2007, 2009, 2010 (algae).
EtOH. In subsequent analyses, only fish ≥125 mm were used because at this size both species were capable of eating sockeye eggs and were large enough to tag.

A subsample of rainbow trout and Arctic grayling was also monitored over the 11 years of our study using uniquely identifiable tags to estimate individual growth rates (2002–2006: VI-Alpha tags, Northwest Marine Technology, Inc.; 2007–2012: passive integrated transponder (PIT) tags, full duplex, 134.2 kHz, 11.5 mm length, 2.1 mm diameter, Allflex-USA, Dallas-Fort Worth Airport, Texas). During each sampling event, individually captured fish large enough to have received a tag (≥125 mm) were scanned using a hand-held PIT-tag detector (Destron Fearing, St. Paul, Minnesota) for potential recaptures.

Sockeye salmon were enumerated visually by wading the entire main stem of each stream at approximately the same time each year during the peak of spawning activities from 1956–2012 (Rogers and Rogers 1998, Rogers and Schindler 2011). Although our study region has experienced substantial warming over the last half century (Schindler et al. 2005), there has been little change in the peak spawn date. These counts were standardized by the total area of each stream to estimate spawner density (salm-on/m²).

Summer water temperatures were monitored in Hidden (years: 2002, 2007–2012) and Lynx creeks (years: 2002, 2006–2012) from July 1st through August 31st using iButton temperature recorders (Maxim Integrated Products, Sunnyvale, CA). Temperature loggers were placed within 0.5 km of the mouth of the two streams, in the same location each year, and recorded temperature at 90 minute intervals with 0.125 to 0.5°C resolution. All loggers were cross-calibrated before the start and at the end of the study and found to be within ±0.5°C of each other. Because we did not have stream temperature data for all 11 years of the study to use in the growth analysis, we correlated average summer stream temperature and average July and August point lake surface temperature measurements taken from Hidden and Lynx lakes. These lakes provide the majority of the summer stream flow and we found stream and lake surface temperatures to be highly correlated for both Hidden (r² = 0.70) and Lynx (r² = 0.67) creeks.

Foraging analyses

The goal of the foraging analysis was to evaluate the foraging response (diet composition and relative feeding rate) of rainbow trout and Arctic grayling to inter-annual variation in salmon density to determine whether species responded differently to salmon-derived resource pulses. For each diet, dry masses of individual prey items were estimated using a length-weight relationship for each prey taxon, developed either from preserved diet items or from the literature (Johnston and Cunjak 1999, Sabo et al. 2002). Diets were standardized by both the mass of the fish to allow for comparison among different sized individuals and converted to percent composition to account for the absolute dietary intake differences among species. Based on our growth results, we pooled the diets of individuals for each species and stream combination into either high (0.75–1.04) or low (0–0.10) salmon density (salm-on/m²). We only used diet data from years in which we had more than one sampling event in each stream during the time of salmon spawning so that we had reasonable sample sizes (n > 30 in all but one sample). Therefore, over four years (2007, 2008, 2010, 2011) we enumerated the diets of 315 Arctic grayling and 726 rainbow trout across 31 sampling events.

For our first analysis, we compared the relative dietary mass (mg dry prey/g of wet fish) of both salmon-derived and non-salmon-derived prey items for both consumer species (see Appendix B: Table B1). While mass specific consumption rates decline exponentially with fish size, this allometric effect is strongest in small fish (<10 g; Hanson et al. 1997). The median size of all of our samples was >63 g making our analysis robust to size related difference among samples. Because ration sizes were not normally distributed, we used the non-parametric two-way Mann-Whitney U test to compare consumption rates. Here, we were interested in comparisons within species among the two streams which had varying levels of in situ productivity for both diet categories at the two salmon density levels. An alpha value of 0.05 was used for all comparisons to test the significance of the relationship.

For our second analysis, diet compositions were compared among individual rainbow trout
and Arctic grayling in both Lynx and Hidden creeks at the two different salmon levels using multiple one-way analysis of similarity (ANOSIM) tests paired with nonmetric multidimensional scaling (NMDS) ordinations based on a Bray-Curtis distance similarity matrix (Clarke 1993, Legendre and Gallagher 2001). ANOSIM tests return an R-statistic for the corresponding pair-wise group comparisons, which ranges from −1 to 1, along with a level of significance. A value of 1 meant that all objects within groups were more similar to one another than all objects in other groups while a value of 0 indicated that all objects within groups were as similar to one another as those in the other group. NMDS uses an iterative approach to arrange the samples in ordination space to minimize the disagreement (referred to as stress) between ranked ordinations and multivariate space distances. The spacing of points on NMDS plots relative to one another is meaningful, but the locations along the axes are arbitrary. Because the results from a single NMDS run may not be globally optimized, a maximum of 1000 random starts were used to best assure a stable solution. Vector loadings were used to access which diet taxon influenced the specific ordination of individual fish. A permutation test \( n = 1000 \) was used to test the significance of each loading on the first two ordination dimensions. All analyses were performed using the vegan (Oksanen et al. 2007) and biostats (McGarigal 2011) packages in the program R (R Development Core Team 2011).

**Inter-annual growth comparison**

To evaluate the growth response of rainbow trout and Arctic grayling to among year differences in salmon density, we first had to calculate growth rates for our individually captured fish. Therefore, we developed an empirical model of summer instantaneous individual growth rates \( \text{day}^{-1} \) as a function of fish body condition (Bentley and Schindler unpublished manuscript). The full linear mixed-effects model was:

\[
\text{Growth}_i = \beta_0 + \beta_1 \times \text{BCI}_i + \beta_2 \times W_i + \beta_3 \times \text{BCI}_i \times W_i + n_i + \epsilon_i
\]  

(1)

where \( \text{BCI}_i \) is the body condition index of individual \( i \), \( W_i \) is the mass \((g)\), \( \beta_i \)'s are the model coefficients, \( n_i \) is the random effect of individual used to account for fish recaptured more than once, and \( \epsilon \) is the normally distributed residual error. Our final model for both rainbow trout and Arctic grayling only included a normally distributed random-intercept term. This growth model is powerful as we were able to estimate instantaneous summer growth rates for each rainbow trout and Arctic grayling we had body length and mass measurements on to calculate a BCI. Additionally, this model allowed us to account for the variable size distributions among sampling events by standardizing the growth estimate for one size \((100\, g)\) of fish, which was necessary due to the allometric effects of size on growth (Peters 1986).

Although we did sample these two streams multiple times per year (from 2007–2012), in order to make the growth rate estimates comparable among years, we only used sampled fish from our end of summer survey (typically August 29–31st) coinciding with the end of the salmon resource subsidy. Over the 11 years, we sampled a total of 1512 rainbow trout and 568 Arctic grayling during this annual survey in both streams. Samples sizes for individual rainbow trout growth rates varied between 7 and 163, with an average of 68.7 individuals per stream per year. Arctic grayling were sampled every year in Hidden Creek, but only sampled in 9 of the 11 years in Lynx Creek (not sampled in 2003 or 2005), with samples sizes ranging from 2 to 88 and an average of 28.4 individuals per stream per year.

Using the individually calculated instantaneous growth rates, we evaluated the functional response in growth of rainbow trout and Arctic grayling to the observed range of sockeye salmon spawner densities in Lynx and Hidden creeks over the past 11 years using linear and non-linear mixed effects models (Zuur et al. 2009). Mixed effects models were used to account for the lack of independence among individuals captured in the same stream and in the same year. Each stream and species combination \((2 \times 2\) streams\) were modeled separately because the two species had markedly different growth rates and it also allowed for each species in each stream to be described by a potentially different relationship. In our mixed effects models, we allowed both the slope and intercept to vary as random effects among years; however, only the random intercept term was significant in all
model comparisons. The main fixed effect we were interested in was salmon density. However, because temperature can have large effects on the serial process comprising energy intake (i.e., foraging [Englund et al. 2011] and assimilation [Elliott 1976]), which ultimately results in growth, we also included temperature as a candidate fixed effect to account for differences in stream temperature among years.

Because we were interested in the relationship between resident fish growth rates and sockeye salmon density, we fit three candidate mixed effects models that represented biologically plausible models: a linear model (Eq. 2) and two non-linear models that had a saturation point but varying shapes (Eqs. 3 and 4). We chose to use a modified non-zero intercept Hill’s sigmoid equation (Eq. 4) because it can effectively be collapsed to fit our other two models (Eqs. 2 and 3). Each of our four datasets was used to fit each of the following nested equations:

Linear (Type I):
\[ \hat{Y}_{ijk} = y_o + a \times x + T + T^2 \]  
(2)

Power (Type II):
\[ \hat{Y}_{ijk} = y_o + a \frac{x}{s_o + x} + T + T^2 \]  
(3)

Sigmoid (Type III):
\[ \hat{Y}_{ijk} = y_o + a \frac{x^b}{s_o^b + x^b} + T + T^2 \]  
(4)

where \( \hat{Y}_{ijk} \) is the predicted instantaneous growth rate (day\(^{-1}\)) for individual \( k \) captured in year (salmon density) \( j \), and in stream \( i \). In all three equations \( y_o \) is the y-intercept, i.e., the estimated growth rate when salmon density = 0, \( x \) is salmon density (m\(^{-2}\)), and \( T \) is temperature. In Eq. 2, \( a \) is the estimated slope parameter, while in the non-linear equations \( a \) is the estimated height of the overall response to salmon at a saturating salmon density, i.e., \( a + y_o \) is where the response saturates. In Eq. 3 and Eq. 4, \( s_o \) is the inflection point and can be thought of the salmon density that produces growth rates at 50% of \( a \). In Eq. 4, \( b \) controls the strength of the sigmoidal relationship, with larger values leading to a steeper slope at \( s_o \). (Note: \( b \) is effectively set to 1 in Eq. 3.)

In each of the above models, individual growth rates were predicted using a two-level approach. The first level is used to predict growth rates for individual fish using:

\[ \hat{Y}_{ijk} = \mu_{ij} + \epsilon_{ijk} \]  
(5)

where \( \epsilon_{ijk} \sim N(0, \sigma^2) \) and \( \mu_{ij} \) is the mean and equal to the second level (year effect):

\[ \mu_{ij} = f(x_i, \beta) + \epsilon_{ij} \]  
(6)

where \( f(x_i, \beta) \) is the function in Eq. 2, Eq. 3, and Eq. 4 and \( \epsilon_{ij} \sim N(0, \tau^2) \).

To select the best model for each species and stream combination, we used Akaike’s information criteria (AIC; Burnham and Anderson 2002) using restricted maximum likelihood (REML) parameter estimation. The models that fit the data the best had the lowest AIC value and the highest Akaike weight (\( w_i \)). All mixed effects models were fit and evaluated using the nlme package (Pinheiro et al. 2009) in the program R.

**Results**

**Feeding rates and diet composition**

From 2002 to 2012, we observed peak salmon abundances in the two study streams ranging from 375 to 14018 individuals, translating to salmon densities spanning 0.04–1.04 m\(^{-2}\) (Fig. 1). We observed an increase in the total average ration size of rainbow trout and Arctic grayling coinciding with an increase in salmon density in both Lynx and Hidden creeks (Fig. 2). While the ration sizes were not significantly different between the two streams in high salmon density years for each species (Appendix C), we did detect significantly higher rations in Hidden Creek in low salmon density years for both rainbow trout and Arctic grayling (Fig. 2). While the ration sizes were not significantly different between the two streams in high salmon density years for each species (Appendix C), we did detect significantly higher rations in Hidden Creek in low salmon density years for both rainbow trout (\( U_{158,270} = 25373, p = 0.0011 \)) and Arctic grayling (\( U_{88,139} = 8897, p < 0.0001 \)) owing to the higher consumption of in situ derived, non-salmon prey (mostly aquatic insect larvae and nymphs). Thus, total average ration sizes in Lynx Creek increased by 200% and 491% as salmon densities went from low to high for rainbow trout and Arctic grayling, respectively, whereas ration sizes only increased by 86% and 76% in Hidden Creek. However, due to low sample sizes and large among-individual variation at high salmon densities, the increase in consumption for Arctic grayling was not statistically significant in either Hidden (\( U_{41,88} = 1047, p = 0.144 \)) or Lynx Creek (\( U_{12,139} = 1866, p = 0.756 \)).

Rainbow trout and Arctic grayling showed...
markedly different patterns in dietary overlap among individuals in the population in low versus high salmon density years (Fig. 3). The average diet composition of the two species was much more similar in low salmon years (Hidden: $R = 0.2074$, $p = 0.001$; Lynx: $R = 0.01434$, $p = 0.15$) compared to high (Hidden: $R = 0.4558$, $p = 0.001$; Lynx: $R = 0.6291$, $p = 0.001$). NMDS ordinations showed that while some individual rainbow trout in low salmon years had diets comprised of almost entirely salmon derived resources, there were a high percentage of individuals in the population whose diets primarily consisted of non-salmon prey items. In high salmon years, nearly all rainbow trout switched to an entirely salmon based diet, while Arctic grayling continued to display a wide range of individual variation, with some switching to salmon derived resources while others consumed mainly in situ derived prey.

**Growth**

Over the period of study during which salmon density varied by more than 10-fold, we observed significant, non-linear increases in both rainbow trout and Arctic grayling growth rates as a function of increasing salmon densities in both Lynx and Hidden creeks (Fig. 4). Although stream temperatures showed modest variation among years, the best-fit models for both species and both streams only included a salmon density effect; temperature effects were not significant. The non-linear, sigmoid (type III) models fit the growth rate data best for three of our four analyses, with the $\Delta AIC$ of the second best candidate models being $> 2$ (Appendix D: Table D1). Rainbow trout in Lynx Creek was the only analysis where growth rates as function of salmon density were best described by the power (type II) model.

Predicted average growth rates increased by 35 and 209% for rainbow trout, and 52 and 85% for Arctic grayling as salmon densities increased from 0 to $1 \text{ m}^{-2}$ in Hidden and Lynx creeks, respectively. The difference in the percent change in growth rates between the two streams was due to the fact that predicted average growth rates were significantly higher in Hidden Creek than Lynx Creek when salmon density was zero for both rainbow trout ($p < 0.0001$) and Arctic grayling ($p < 0.0001$; Appendix E: Table E1). However, average growth rates of both species saturated at comparable levels once a salmon density of 0.25–0.30 $\text{ m}^{-2}$ was reached in each of the streams.

**DISCUSSION**

Over the last decade, we observed extreme variation in the densities of two populations of spawning sockeye salmon (Fig. 1). Although the salmon resource subsidy occurred every year, the...
magnitude of the pulse affected the consumption rates (Fig. 2) and foraging patterns (Fig. 3) of both rainbow trout and Arctic grayling, ultimately impacting the average growth rates of these two species (Fig. 4). While prior studies have shown that salmon subsidies can positively impact the nutritional status of stream-dwelling salmonids (e.g., Bilby et al. 1996, Wipfli et al. 2003, Rinella et al. 2012), we uniquely (1) demonstrated that the foraging and growth response of resident fishes can substantially vary across a wide naturally occurring range of salmon densities, (2) documented how varying levels of background in situ productivity can affect the relative impacts of the subsidy, and (3) showed that the magnitude of resource pulses can affect competing species differently.

As salmon densities increased we observed a saturating growth response in both species of resident fishes. This result demonstrates that resource pulses can saturate the growth responses of consumers to short-term, high quality episodes of feeding. In three of the four comparisons, we observed a sigmoid-shaped growth

Fig. 3. NMDS ordinations of the diet composition of individual rainbow trout (white) and Arctic grayling (black) at both low (A = Hidden Creek, B = Lynx Creek) and high (C = Hidden Creek, D = Lynx Creek) salmon spawning densities. Dashed (grayling) and solid (rainbow) ellipses depict one standard deviation of the pair-wise dissimilarity scores per grouping. Statistically significant (p ≤ 0.05) vector loadings added to plots to aid with interpretation. Samples sizes are listed for both species in each comparison. Stress was 0.16 (points based on a single NMDS but sub-plotted to aid with visual interpretation). Note that in panels (C) and (D), many of the data points for rainbow trout are obscured because the data are densely clustered within the ellipse.
response (Fig. 4). This pattern is likely a result of salmon spawning behavior, the physical characteristics of the spawning sites, and the physiological limitations of resident consumers. Female salmon bury their eggs in the gravel of streams, rivers, and beaches by digging nests (redds) that protect their embryos from predators and scour (Quinn 2005). Streams have a limited number of suitable nest-sites based on in-stream characteristics, such as the distribution of substrate sizes, amount of structure, slope, and hyporheic flow (Essington et al. 2000). Although some eggs are spilled during the burial process and thus available to resident consumers independent of spawner density (J. B. Armstrong and K. T. Bentley, personal observations), egg availability remains relatively low until spawning habitat saturates (Moore et al. 2008). Once this threshold density is reached, females begin to spawn on top of previously dug nests, dislodging buried eggs, resulting in a non-linear increase in salmon egg availability.

While ideal free distribution (sensu Fretwell and Lucas 1969) predicts that both territorial spawning behavior and negative density dependence in progeny survival in salmon should minimize redd superimposition until spawning habitat becomes limiting (Essington et al. 2000), it is possible that a distinct threshold could be weakened or non-existent. For example, our best-fit model for growth rates of rainbow trout in Lynx Creek as a function of sockeye salmon density was characterized by a more gradual increase with no clear break point (Fig. 4A). Bilby et al. (2001) found a similar pattern in the isotopic enrichment of salmon derived resources ($\delta^{15}$N) in the tissues of juvenile coho salmon across 26 western Washington streams. A potential explanation for this alternative pattern could be that habitat availability alone does not lead to higher rates of superimposition as females may preferentially spawn on previously constructed reddss (Essington et al. 1998), particularly in systems where there is considerable variation in redd site quality. Thus, egg availability is not only driven by the intrinsic habitat characteristics of a system, but also the specific behavior of individual spawning salmon. Nonetheless, we observed that a relatively small increase in spawner density can have disproportionately large effect on both resource abundance and consumer

![Graph](image.jpg)

Fig. 4. Mean individual ($\pm$ 2 SE) growth rates (day$^{-1}$) of (A) rainbow trout and (B) Arctic grayling as a function of salmon density (salmon/m$^2$) in Hidden Creek (black) and Lynx Creek (white). Lines (solid = Hidden, dashed = Lynx) represent the best-fit mixed effects models (see Appendix C: Table C1; Appendix D: Table D1). Growth rates were standardized for 100-g individuals. Note the different y-axis scales between panels. Confidence intervals for Arctic grayling in Lynx Creek sampled in four of the nine years were substantially higher than the confidence bounds for the rest of the data points due to low sample sizes (n = 2–5).
fitness as a result of the non-linear response.

Given that over-winter survival of individual fish is positively correlated with end of summer body size and lipid accumulation (Quinn and Peterson 1996, Post and Parkinson 2001), salmon abundance likely has strong impacts on the productivity of resident fish populations. However, our data suggest that the benefits of additional spawning salmon on resident fishes do not continue to increase indefinitely. Matching previous studies on stream-dwelling fishes (Wipfli et al. 2003, Heintz et al. 2004; but see Rinella et al. 2012) we observed a saturating functional response in growth rates with increasing salmon density. While we were unable to directly evaluate the mechanisms behind this pattern, one explanation is that although fish have a remarkable ability to capitalize on foraging opportunities (Armstrong and Schindler 2011), feeding rates can saturate an individual’s digestive capacity (Armstrong et al., unpublished manuscript). Therefore, individuals may be limited by their assimilation rates even though food availability may continue to increase. Another explanation for the saturating response is a numerical response from competitors. Although we did survey resident fish densities in three years and observed little among year variation (Appendix A), these years happened to coincide with lower than average salmon densities in both streams. Thus, it is possible that densities of resident fish were higher in Lynx and Hidden creeks when salmon densities were higher leading to density-dependent growth, a phenomenon widely reported in stream-dwelling salmonid populations (Bohlin et al. 2002, Grant and Imre 2005). Unfortunately, due to high variation in growth rates among individual fish captured at the same salmon density and the limited number of data from years around the inflection point, we were unable to predict the exact density where superimposition occurred with high confidence (Appendix D: Table D1). However, it is clear for both rainbow trout and Arctic grayling, sockeye salmon densities between 0.2 and 0.6 m⁻² saturated their growth responses in each of the streams.

In low salmon years, both rainbow trout and Arctic grayling had significantly lower growth rates as a result of not only decreased ration sizes, but also a decrease in the proportion of diets represented by salmon-derived prey (Fig. 2). However, the relative effects were different between the two streams. We found that rainbow trout and Arctic grayling had significantly higher ration sizes and growth rates in Hidden Creek, relative to Lynx Creek, during low salmon years, likely due to higher rates of in situ production of non-salmon prey (i.e., aquatic insects). An alternative explanation for our results is that variation in growth was driven not by variation in food abundance, but by variation in consumer performance, due to variation in temperature. Temperature affects the ability of poikilotherms to capture and process prey, so it has the potential to influence the levels of surplus energy available for growth. In the Wood River system, stream temperatures range from 5 to 15°C. Armstrong et al. (2010) demonstrated thermal constraints on the ability of juvenile fish to capitalize on salmon subsidies in cool habitat (5–9°C). However, rainbow trout and Arctic grayling in the Wood River system are absent from the coldest streams, but rather inhabit streams that range in summer temperature from 10 to 15°C; empirically derived physiological models of rainbow trout growth (Hanson et al. 1997) suggest that this thermal variation would have relatively small effects on growth relative to variation in consumption rate. Indeed, other authors have found that rainbow trout growth is insensitive to the variation in temperatures that we documented (Railsback and Rose 1999), and including annual stream temperatures in our analysis did not improve our ability to model growth. Therefore, the most parsimonious explanation for our results is that differences in salmon abundance and productivity lead to the growth and consumption differences both among years and streams.

Interestingly, we observed similar overall growth responses in the two species in both streams across the full range of resource pulse magnitudes, but due to slightly different mechanisms. Regardless of salmon density, rainbow trout were superior at consuming the energetically dense salmon eggs, where even in low salmon density years, eggs were found in >65% of rainbow trout diets but were almost absent from grayling diets. Although consumption rates of salmon-derived prey decreased by >50% in low salmon density years, rainbow trout were
able to partially compensate by increasing their consumption in situ derived prey. By supplementing their diets with benthic and terrestrial invertebrates in low salmon years, dietary overlap among the two species significantly increased. This result is important because previous bioenergetics models predicted that Arctic grayling would be less sensitive to low salmon densities due to their relative reliance on non-salmon prey (Scheuerell et al. 2007). However, we found that Arctic grayling growth rates were equally affected as rainbow trout by low salmon densities, likely due to rainbow trout monopolizing salmon eggs and increasing competition for non-salmon prey. These results emphasize the importance of evaluating both direct and indirect impacts of pulsed resource subsidies on consumers across the full range of potential magnitudes within the context of the natural system.

While it has been widely accepted that declines of spawning salmon have adverse effects on freshwater ecosystems (Gresh et al. 2000, Naiman et al. 2002), our results highlight two previously unacknowledged implications for the maintenance and rehabilitation of salmon watersheds and the consumers who rely on these resources. First, though it is not surprising that a decrease in salmon resources significantly depressed the ration sizes and growth rates of resident fishes, streams with higher in situ productivity are less dependent on salmon-derived resources for supporting growth of consumers. Because the abundance of salmon at the scale of an individual stream is highly variable among years even in relatively pristine ecosystems (Schindler et al. 2010, Rogers and Schindler 2011), the availability of alternative resources will determine the relative effects of low resource pulse magnitudes on resident consumers. Therefore, maintaining access to diverse foraging opportunities through multiple food web pathways (e.g., Nakano and Murakami 2001, Wipfli and Baxter 2010) will buffer consumers from the substantial fluctuation in the magnitude of resource pulses that are an inherent characteristic of natural populations. Second, there is a point of diminishing returns as higher densities of salmon eventually saturate the growth rates of resident fishes. Thus, from the standpoint of managing salmon escapement levels to benefit resident fishes, it is likely that maintaining variation in spawn timing among populations to ensure longer seasonal access to salmon eggs for resident fishes (Ruff et al. 2011) may be more important than managing simply for higher total salmon escapements. This conclusion assumes a negligible numerical response in stream fishes to increases in salmon densities, an assumption that needs to be tested in further research.

In a more general sense, the spatial and temporal characteristics of pulsed resource subsidies largely influence the strength of the patterns and processes we observe (Polis et al. 2004). Supporting the results of Yang et al. (2010), our study demonstrates that the relative impact of resource pulses will ultimately be mediated by the magnitude of the subsidy, the ability of consumers to directly and indirectly capitalize on the resource, and the relative in situ productivity of an ecosystem. Our results illustrate the importance of understanding the ecological response of consumers to varying levels of resource availability through appropriately scaled research to assist in developing strategies for achieving ecosystem-based management that aims to balance the contributions of salmon to fisheries versus to ecosystem processes.

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SUPPLEMENTAL MATERIAL

APPENDIX A

ESTIMATIONS OF RESIDENT FISH DENSITIES

Densities of Arctic grayling and rainbow trout were visually estimated via snorkel surveys conducted in Hidden and Lynx creeks. Sample units (Hidden: n = 44; Lynx: n = 55–67) were demarcated in each stream in early-June 2010 and subsequently surveyed every 10–21 days from mid-June through mid-September in 2010–2012. The cumulative length of the sample units comprised ~35–50% of the total length of each stream. However, the sample units consisted of almost all of the pools in each stream, which is the preferred habitat for both rainbow trout and Arctic grayling, along with a sub-sample of runs and riffles. Thus, a large majority of the realized habitat was surveyed during each sample event. During a survey, a single snorkeler moved upstream through each unit, enumerating the fish by species, and estimating fork lengths of each individual to the nearest 50 mm size class.

For each year, abundance densities were

| Year | Arctic grayling | | Rainbow trout | |
|------|----------------|--------|----------------|--------|
|      | Biomass Hidden | Abundance Hidden | Biomass Hidden | Abundance Hidden |
| 2010 | 1.39          | 0.0008 | 2.36           | 0.0030 |
| 2011 | 1.44          | 0.0007 | 3.41           | 0.0032 |
| 2012 | 2.86          | 0.0014 | 1.74           | 0.0034 |
| Average | 1.90 | 0.0009 | 2.50           | 0.0032 |

Note: Estimates are from surveys conducted in late August in all years to correspond with the peak of the salmon run.

Table A1. Biomass (kg/m²) and abundance (no./m²) densities estimates for Arctic grayling and rainbow trout in Hidden and Lynx creeks from 2010–2012.
estimated by dividing the total number of each species enumerated throughout all sample units by the total length of stream surveyed (i.e., number of fish/m²). Biomass densities (kg/m²) were estimated by calculating the average mass for each individual fish, based on the length-mass relationship developed for each species (Bentley and Schindler, unpublished manuscript), and then summing the total mass across the total length of stream surveyed. In each year, densities of both rainbow trout and Arctic grayling increased from mid-June through late-July, but then remained fairly similar during August, the time of year when salmon are spawning in both streams (Bentley, unpublished data). Therefore, only snorkel surveys conducted in mid- to late-August, which also correspond to the peak of the salmon spawning runs, were included in this analysis.

**APPENDIX B**

Table B1. Dietary items used in diet analyses.

| Diet item      | Taxon                          | Source      |
|----------------|-------------------------------|-------------|
| Blackflies     | Simuliidae                     | non-salmon  |
| Caddisflies    | Tricoptera                     | non-salmon  |
| Eggs           | Oncorhynchus nerka             | salmon      |
| Fish           | Various spp.                   | non-salmon  |
| Maggots        | Diptera: Calliphoridae         | salmon      |
| Mayflies       | Ephemeroptera                  | non-salmon  |
| Midge          | Diptera (terrestrial)          | non-salmon  |
| Terrestrial    | Various spp.                   | non-salmon  |
| Parasitic wasp | Hymenoptera                   | non-salmon  |
| Stoneflies     | Plecoptera                     | non-salmon  |
| Worm           | Phylum: Annelid                | non-salmon  |

**APPENDIX C**

**Comparison of Ration Sizes Among Streams, Species, and Pulsed-Magnitudes**

We found significant increases in the total average ration sizes of rainbow trout coinciding with an increase in salmon densities in both Lynx and Hidden Creek (Fig. 2). At low salmon densities, salmon derived resources (Appendix A: Table A1) constituted 65–72% of the average rainbow trout diet, with total average ration sizes of 1.78 and 2.70 mg g⁻¹ in Lynx and Hidden creeks, respectively. Although rainbow trout did consume significantly more salmon-derived prey in Hidden Creek (2.00 mg g⁻¹) than in Lynx Creek (1.39 mg g⁻¹; U₁₅₈,₂⁷₀ = 25469, p = 0.00028), they also consumed significantly more in situ derived non-salmon items in Hidden Creek (0.694 mg g⁻¹) than Lynx Creek (0.387 mg g⁻¹; U₁₅₈,₂⁷₀ = 25373, p = 0.0011) supporting the higher growth rates we observed in Hidden Creek. In high salmon density years, rainbow trout diets consisted of 96–97% salmon derived resources. While non-salmon diet rations were slightly higher in Hidden than Lynx Creek (U₉₅,₁₈₅ = 9986, p = 0.041), total average ration sizes were 5.01 and 5.33 mg g⁻¹ for Hidden and Lynx Creek, respectively, and were not significantly different (U₉₅,₁₈₅ = 9106, p = 0.62).

Average ration size for Arctic grayling was substantially lower than rainbow trout, and at low salmon densities 79% and 89% of the total average ration was derived from non-salmon prey items for Lynx and Hidden Creek, respectively. When salmon densities were low, the average ration size of non-salmon prey items was statistically higher in Hidden Creek (0.708 mg g⁻¹) than in Lynx Creek (0.269 mg g⁻¹; U₈₈,₁₃₉ = 8897, p < 0.0001), while the small ration of salmon derived prey items was not (t₈₈,₁₃₉ = 6251, p = 0.530). In high salmon years, the salmon derived resources constituted 63 and 94% of the average ration of an Arctic grayling in Hidden and Lynx Creek, respectively; however, the ration sizes were highly variable. While Lynx Creek did have a higher total average ration (2.01 mg g⁻¹) compared to Hidden (1.41 mg g⁻¹), they were not significantly different (U₄₁,₁₂ = 252, p = 0.908), nor were the rations of salmon (U₂₄,₁₂ = 248, p = 0.974) and non-salmon prey (U₄₁,₁₂ = 261, p = 0.758).
## Appendix D

Table D1. AIC model results for growth as a function of salmon density. Model selection metrics for mixed effects models fit to Arctic grayling and rainbow trout growth data as a function of sockeye salmon density (SD) and temperature (T) in Lynx and Hidden Creeks, Bristol Bay, Alaska.

| Model                                      | K  | –2\(\ell\) | AIC    | ΔAIC  | \(w_i\) |
|--------------------------------------------|----|------------|--------|-------|---------|
| Arctic grayling, Hidden Creek              |    |            |        |       |         |
| Sigmoid: SD + T + T^2                      | 8  | –1882.30   | –3748.60 | 4.46  | 0.0628  |
| Sigmoid: SD + T                           | 7  | –1882.28   | –3745.56 | 2.50  | 0.1673  |
| Sigmoid: SD                               | 6  | –1882.53   | –3753.06 | 0.00  | 0.5839  |
| Power: SD + T + T^2                       | 7  | –1879.17   | –3744.33 | 8.73  | 0.0074  |
| Power: SD + T                             | 6  | –1879.45   | –3746.89 | 6.17  | 0.0267  |
| Power: SD                                 | 5  | –1879.79   | –3749.57 | 3.49  | 0.1020  |
| Linear: SD + T + T^2                      | 6  | –1877.51   | –3743.01 | 10.05 | 0.0038  |
| Linear: SD + T                            | 5  | –1877.61   | –3745.22 | 7.84  | 0.0116  |
| Linear: SD                                | 4  | –1877.70   | –3747.40 | 5.66  | 0.0545  |
| Arctic grayling, Lynx Creek               |    |            |        |       |         |
| Sigmoid: SD + T + T^2                     | 8  | –771.22    | –1526.44 | 4.55  | 0.0689  |
| Sigmoid: SD + T                           | 7  | –771.34    | –1528.68 | 2.31  | 0.2111  |
| Sigmoid: SD                               | 6  | –771.50    | –1530.99 | 0.00  | 0.6700  |
| Power: SD + T + T^2                       | 7  | –766.57    | –1519.13 | 11.86 | 0.0018  |
| Power: SD + T                             | 6  | –767.22    | –1522.44 | 8.55  | 0.0093  |
| Power: SD                                 | 5  | –767.55    | –1525.09 | 5.90  | 0.0351  |
| Linear: SD + T + T^2                      | 6  | –763.00    | –1513.99 | 17.00 | 0.0001  |
| Linear: SD + T                            | 5  | –763.95    | –1517.89 | 13.10 | 0.0010  |
| Linear: SD                                | 4  | –764.02    | –1520.03 | 10.96 | 0.0028  |
| Rainbow trout, Hidden Creek               |    |            |        |       |         |
| Sigmoid: SD + T + T^2                     | 8  | –3125.01   | –6234.01 | 4.17  | 0.0819  |
| Sigmoid: SD + T                           | 7  | –3125.01   | –6236.02 | 2.16  | 0.2237  |
| Sigmoid: SD                               | 6  | –3125.09   | –6238.18 | 0.00  | 0.6586  |
| Power: SD + T + T^2                       | 7  | –3118.89   | –6227.77 | 14.41 | 0.0005  |
| Power: SD + T                             | 6  | –3119.72   | –6227.43 | 10.75 | 0.0031  |
| Power: SD                                 | 5  | –3120.43   | –6236.86 | 7.32  | 0.0169  |
| Linear: SD + T + T^2                      | 6  | –3118.49   | –6224.97 | 13.21 | 0.0009  |
| Linear: SD + T                            | 5  | –3119.21   | –6225.02 | 13.16 | 0.0015  |
| Linear: SD                                | 4  | –3119.21   | –6230.41 | 7.77  | 0.0135  |
| Rainbow trout, Lynx Creek                 |    |            |        |       |         |
| Sigmoid: SD + T + T^2                     | 8  | –3007.19   | –6000.37 | 12.69 | 0.0012  |
| Sigmoid: SD + T                           | 7  | –3007.73   | –6003.45 | 9.61  | 0.0057  |
| Sigmoid: SD                               | 6  | –3009.84   | –6009.68 | 3.38  | 0.1274  |
| Power: SD + T + T^2                       | 7  | –3009.52   | –6007.04 | 6.02  | 0.0340  |
| Power: SD + T                             | 6  | –3009.58   | –6009.15 | 3.91  | 0.0977  |
| **Power: SD**                             | 5  | –3010.53   | –6013.06 | 0.00  | 0.6902  |
| Linear: SD + T + T^2                      | 6  | –3000.44   | –6000.87 | 12.19 | 0.0016  |
| Linear: SD + T                            | 5  | –3003.21   | –6003.21 | 9.85  | 0.0059  |
| Linear: SD                                | 4  | –3010.61   | –6007.22 | 5.84  | 0.0372  |

Note: For each model, K is the number of estimated parameters, ΔAIC is the difference in AIC relative to the best model, –2\(\ell\) is twice the negative log-likelihood, and \(w_i\) is the AIC weight.

## Appendix E

Table E1. Parameter estimations (±2 SE) of the best-fit models for resident fish growth as a function of salmon density in Lynx and Hidden Creek, Bristol Bay, Alaska (see Appendix D: Table D1 for candidate model structure).

| Species and stream | \(\gamma_c\) | \(a\) | \(s_c\) | \(b\) |
|--------------------|------------|------|--------|------|
| Arctic grayling    |            |      |        |      |
| Hidden             | 0.0050     | 0.0026 | 0.2551 | 15.54|
| Lynx               | 0.0039     | 0.0033 | 0.2708 | 22.87|
| Rainbow trout      |            |      |        |      |
| Hidden             | 0.0171     | 0.0060 | 0.2436 | 92.87|
| Lynx               | 0.0104     | 0.0217 | 0.4896 | 880.03|

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