Ecology of stream-dwelling fishes in response to inter-annual variation in the abundance of spawning sockeye salmon

Kale T. Bentley

A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2014

Committee:
Daniel E. Schindler, chair
Timothy E. Essington
Phil Roni

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington

Abstract

Ecology of stream-dwelling fishes in response to inter-annual variation in the abundance of spawning sockeye salmon

Kale T. Bentley

Chair of the Supervisory Committee:
Professor Daniel E. Schindler
School of Aquatic and Fishery Sciences

Each year, millions of salmon enter the final stage of their life-cycle and migrate back towards their natal watersheds to reproduce. After accumulating >95% of their adult body mass in marine environments, salmon spawning migrations generate massive fluxes of nutrients and energy to inland food webs that can exceed background levels of *in situ* productivity, and these resources are utilized by a wide range of taxa (Naiman et al. 2002, Gende et al. 2002, Schindler et al. 2003). However, one-half to three-fourths of all returning salmon are harvested by commercial fisheries in coastal oceans prior to reproducing, as salmon fisheries in Alaska are currently managed to maximize the long-term sustainable yield of salmon (Baker et al. 2009). Although this practice is widely touted as a fisheries management success story (Hilborn 2006), people are beginning to ask, what effect does removing the biomass of salmon prior to spawning have on freshwater and terrestrial ecosystems. Thus, there has been a call to shift the paradigm of fisheries management from one that focuses solely on maximizing the yield of single target

species to a more holistic approach that accounts for other ecosystem processes (Pikitch et al. 2004, Crowder et al. 2008, Piccolo et al. 2009).

In order to develop an ecosystem-based management approach, salmon managers need to be able to assess the trade-offs of different management scenarios that affect how many salmon are harvested versus released to the watershed (known as "escapement") to spawn and benefit inland ecosystems. Currently, assessing these trade-offs is difficult; while there is a well-established theory of how to optimize commercial catch based on stock-recruit relationships (Ricker 1954, Hilborn and Walters 1992, Quinn and Deriso 1999), we lack a quantitative understanding of how the number of salmon returning to spawn influences freshwater and terrestrial ecosystems. The focus of my thesis was to evaluate of the ecological response of Arctic grayling (*Thymallus arcticus*) and rainbow trout (*Oncorhynchus mykiss*), two species of resident fish that rely heavily on consumption of salmon resource subsidies (Scheuerell et al. 2007, Moore et al. 2008), to variation in the abundance of adult sockeye salmon (*Oncorhynchus nerka*) in the Wood River watershed, Bristol Bay, Alaska.

The first chapter of my thesis assessed the ability of a body condition index to serve as a proxy for estimating individual instantaneous growth rates as obtaining direct measurements of growth can be time consuming, costly, and logistically impractical. We found that relative body condition of grayling and rainbow trout, as measured by the residuals around a length-mass regression, was strongly correlated with direct measures of individual instantaneous growth from recaptured tagged fish. Using the derived relationship between body condition and growth, we developed a model to estimate growth rates of individual fish based on their observed body condition.

Chapter two evaluated the foraging and growth responses of grayling and rainbow trout in two streams that vary in *in situ* productivity to changes in the abundances of spawning sockeye salmon. Over 11 years, and across a greater than 10-fold variation in density of spawning sockeye salmon, both species of resident fish exhibited a relatively similar, but mechanistically different, 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 on *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. Growth rates of both consumer species saturated in years when densities of sockeye salmon exceeded about 0.3 – 0.4 m^2 on the spawning grounds.

Chapter three evaluated the movement patterns of Arctic grayling and rainbow trout within and among streams, which offer patchily distributed foraging opportunities during the summer months. Across both years, approximately 50% of individual grayling and rainbow trout exhibited kilometer-scale movements among two or more streams across the river network within a single summer. Movements were concentrated in June and July, and subsided by early August, coincident with the arrival of spawning sockeye salmon (*O. nerka*). These inter-stream movements may represent prospecting behavior as individuals seek out the most profitable foraging opportunities. Thus, resident fishes in the Wood River system appear to use the broad network of habitat available to them across the riverscape, rather than depend on individual tributaries for achieving growth.

Together the results of this thesis improve our understanding of how inland ecosystem respond to changes in salmon abundance. These results will be of use for resource managers interested in directly evaluating the socio-economic trade-offs of allocating salmon resources among user groups. The results of this work also highlight the importance of maintaining connectivity to enable movements of resident fish across river basins, the ecological consequences of which remain poorly understood.

Acknowledgements

First and foremost, I want to thank my advisor Daniel E. Schindler. Over the past four years, Daniel and I literally spent thousands of hours in the field together, slogging up streams, netting fish, and even pouring concrete footings. Through this time, I benefitted not only from Daniel's extensive research knowledge, but also from his passion for science. I feel extremely fortunate to have had an advisor who supported me financially, pushed me intellectually, and who I know will be one of my biggest advocates moving forward.

I would also like to express my sincere gratitude the Schindler Lab, both past and present, who I have got to know so well over the years. I have benefitted from each and every individual through exchanges of ideas, collaboration on projects, and feedback on manuscripts and presentations. Over the years, these individuals have provided invaluable emotional support and become some of my closest friends.

The field work for this thesis was conducted by the Alaska Salmon Program (ASP), which is comprised of countless individuals but included: Daniel Schindler, Peter Lisi, Casey Ruff, Jonny Armstrong, Mackenzie Consoer, Tim Cline, Adrianne Smits, KathiJo Jankowski, Anne Hilborn, Laura Payne, Hannah Stapleton, Kristen Omori, Teresa Edwards, Julio Lanceloti, Emily Davis, Mark Scheuerell, Jon Moore, Tessa Francis, Sue Johnson, and Gordon Holtgrieve. Additionally, Gabriel Brooks from NOAA provided technical assistance on PIT-tag antennas that I could not have done without. I would also like to thank Jackie Carter and Chris Boatright for coordinating the ASP field operations and Daniel Schindler, Ray Hilborn, and Tom Quinn for writing successful grants that make our field program possible.

Financial support for the work described here, as well as my education, was provided through a scholarship from the National Science Foundation's (NSF) Graduate Research Fellowship Program in addition to grants from: NSF Biocomplexity and Dynamics of Coupled Natural and Human Systems Programs and the Gordon and Betty Moore Foundation.

Lastly, I would like to thank my friends and family, and in particular Allan Fish, Mallory Kimble, and Stephanie Clark, for their unconditional love, encouragement, and support. Although none of their names appear on my chapters and manuscripts, their involvement and influence was immeasurable.

Tables of Contents

List of Tables and Figures

Chapter 1: Body condition correlates with instantaneous growth in stream-dwelling rainbow trout and Arctic grayling

Introduction

Body condition indices are a common metric used to evaluate biotic and abiotic effects on populations and communities by indirectly assessing the physiological state of individual fish (Anderson and Neumann 1996, Blackwell et al. 2000). For example, body condition factors have been used to assess everything from overwinter survival (Reimers 1963) and density-dependent growth (Kebus et al. 1992) to habitat condition (De Raedemaecker et al. 2012) and water quality (Bervoets and Blust 2003). Although many different condition indices exist (Bulow 1970, Cone 1989, Couture et al. 1998, Pope and Kruse 2007), the widespread use of length-mass based measures is possible because the data are collected routinely from wild populations, while also imposing minimal mortality (Fechhelm et al. 1995). Over time, many different length-mass indices have been developed and refined such as Fulton's condition factor (*K*), relative weight (Wr), and residual analysis of length-mass regressions (see Pope and Kruse 2007). All length-mass condition indices operate under the same assumption; that the heavier a fish is for given length the better its physiological condition. While this assumption has obvious caveats, such as the potential effect of sex, maturation, morphology, diet, and body composition on the relative size of an individual (Bolger and Connolly 1989), the plumper an individual fish is the more likely it has capitalized on foraging opportunities and recently grown.

Fish, like most species, not only need to grow to reach sexual maturity and reduce predation risk (Weatherley et al. 1987), but must accumulate energy reserves to survive periods of prey scarcity (Biro et al. 2004). Because fish have evolved a remarkable ability to rapidly respond to drastic fluctuations in resource availability (Armstrong and Schindler 2011), somatic growth represents an individual's response to a given set of biological and environmental conditions. Therefore, body growth, which influences mortality and recruitment, is an important parameter to measure when evaluating the ecology of populations as it pertains to the assessment and management of fisheries (Summerfelt and Hall 1987).

Numerous techniques are used to evaluate individual and population level growth rates in fish. Growth rates can be directly calculated through the examination of annual, and even daily, growth rings sequestered in calcified tissues, such as spines (Tyus and Nikirk 1990), cleithra (Venturelli and Tonn 2006), scales (Thompson et al. 1997), and otoliths (DeVries and Frie 1996, Bestgen and Bundy 1998) as well as the use of uniquely identifiable tags to record body measurements at two separate points in time (Guy et al. 1996, Ruff et al. 2011). Growth can also be estimated indirectly by assessing the concentrations of different hormones (Beckman 2011), nucleic acids (Bulow 1970, Rinella et al. 2012) or radioactive amino acids in a fish (Adelman 1987). While each of these methods have advantages and disadvantages depending on the specific objectives of a study and the species of interest, each are similar in that they are typically time consuming and costly relative to length-mass condition indices, and can be impractical due to scale of the study system or restrictions on protected species. Thus, the use of a condition index as a surrogate for recent growth would be useful if it provided a robust proxy of growth performance (Anderson and Neumann 1996).

Numerous studies have been conducted to evaluate the utility of condition indices to estimate both body composition and growth rates of fishes (see Blackwell et al. 2000). While some investigators have found strong correlations between the body condition and the growth and nutritional status of fish (Willis 1989, Brown and Murphy 1991, Gabelhouse Jr 1991), others have cautioned using condition indices as surrogates for growth rates (Liao et al. 1995, Simpkins et al. 2003, Hartman and Margraf 2006). One potential reason previous studies have found mixed results is due to the time scale over which body condition and growth were compared; with most studies correlating instantaneous body condition with annual growth. Because growth can display strong seasonal patterns (Railsback and Rose 1999), the ability of a body condition index to serve as a surrogate for growth would be more appropriately evaluated using instantaneous growth rates. Therefore, we investigated the association between individual instantaneous growth rates measured on marked-and-recaptured fish, evaluated at a scale of weeks to greater than one year, and a relative body condition index, as measured by the residuals around a length-mass regression.

Using individual marked-and-recaptured rainbow trout *Oncorhynchus mykiss* and Arctic grayling *Thymallus arcticus* in southwest Alaska sampled over a 10 year period, we developed an empirical model of summer instantaneous individual growth rates (day^{-1}) as a function of fish body condition, and assessed the time frame over which body condition reflected previous growth. While direct measurements of growth may be more desirable, our results demonstrate that a simple body condition index provides a reasonable metric of summer growth performance for these two stream-dwelling salmonids.

Methods

Study system and data collection

Rainbow trout and Arctic grayling were sampled from 2002 - 2011 in 2nd and 3rd order tributaries of Lake Nerka, which is located in the Wood River watershed (59° 34’37”N, 158°

48’25”W), Bristol Bay, southwest Alaska. Within these tributaries, rainbow trout and Arctic grayling comprise roughly 40 - 100% of the resident stream fish biomass, 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 (*O. nerka*), coastrange (*Cottus cognatus)* and slimy (*C. aleuticus)* sculpin, and rainbow smelt (*Osmerus mordax*). Fish were collected using a fine mesh stick seine or hook-and-line from mid-June through early-September, with an average of 13.2 (SD, 6.5) sample events per year and an average inter-sample interval of 15.5 (SD, 11.5) days.

During stream surveys, all captured individuals were transferred to 53-liter holding containers, anesthetized using a 50-ppm solution of MS-222 (tricaine methane sulphonate), and weighed (g) and measured (fork length, mm; Scheuerell et al. 2007). A subsample of rainbow trout and grayling was also tagged to estimate individual growth rates. From 2002 - 2006, fish were tagged in the transparent adipose tissue just posterior of the left eyelid using VI-Alpha tags (Northwest Marine Technology, Inc.). From 2007- 2011 resident fish were surgically implanted with a passive integrated transponder (PIT) tag in their visceral cavity, mid-way between the pectoral and pelvic fins (PIT tags; full duplex, 134.2 kHz, 11.5 mm length, 2.1 mm diameter; Allflex-USA, Dallas-Fort Worth Airport, Texas). During each sample 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. Although no comparative study of VI-Alpha versus PIT tags exists to our knowledge, both have been shown to have negligible effects on fish growth and survival (Zerrenner et al. 1997, Ombredane et al. 1998). Nonetheless, >96% of the recaptured individuals were from 2007-2011, with 442 and 456 being recaptured within the same year they were tagged, and 69 and 79 being recaptured in different years, for rainbow trout and Arctic grayling, respectively. Of these individuals, 305 Arctic grayling and 85 rainbow trout were recaptured multiple times (i.e., handled three or more times), either within or among years. The average individual was recaptured 1.52 (SD, 0.88) and 1.27 (SD, 0.62) times for Arctic grayling and rainbow trout, respectively.

One potential issue of using length-mass based body condition indices to infer the physiological status of individuals occurs when evaluating abrupt seasonal changes in body size, specifically pre- and post-spawning periods. Fish can allocate a large proportion of their total energy to reproductive tissues, which is subsequently expelled (e.g., Le Cren 1951, Craig 1977, Huntington et al. 2001), affecting the relative body condition of a fish (Neumann and Murphy 1991). Additionally, the relative investment in reproductive tissues can vary between males and females (Le Cren 1951, Craig 1977). While we were unable to accurately assess the sex of our sampled fish, we were able to minimized these potential issues. First, the majority of the fish in our model were likely sub-adults. Post-spawning rainbow trout were sampled in two tributaries of Lake Nerka in early-June 2012. Eighty-six percent of the fish used in our model were smaller than the smallest spawning rainbow trout (311 mm) and 98% were smaller than the modal spawner (450 mm). We do not have similar data for Arctic grayling for our study system, but using age-at-maturity (Northcote 1995) and size-at-age (DeCicco and Brown 2006) data from other Alaskan grayling populations, 91% of our sampled fish were smaller than 300 mm; the size at which a quarter of grayling are typically sexually mature (Northcote 1995). Second, rainbow trout and Arctic grayling typically spawn in late-April to late-May in our study system while 95% of our samples were collected from July 8th to September 11th.

Calculating body condition and growth

Body Condition Index - We developed a simple body condition index using residual analysis of the length-mass relationship (Pope and Kruse 2007) for both rainbow trout and Arctic grayling. We chose to use the residual analysis as our condition index as it overcomes length- and species-related biases that have been show to plague the commonly used Fulton's condition factor (LeCren 1951, Cone 1989, He et al. 2008) and relative weight (Wr; Cone 1989, Gerow et al. 2004, Cade et al. 2008). This condition index is ideal for evaluation of temporal trends within a population (Cone et al. 1989), but is important to note that inferences derived from this index are only applicable to individuals used in developing the length-mass regression model (Pope and Kruse 2007).

First, the lengths (FL; mm) and weights (W; g) were logarithmically transformed and a linearized version of the power function $W_i = aFL_i^b + \varepsilon_i$ was fit to the data for each species. Second, using the fitted equations, ordinary least square residual errors (ε) were calculated for individual fish and used as the index of body condition (BCI), or

$$BCI_i = \log_e(W_i) - \log_e(a) - b \cdot \log_e(FL_i);$$

where BCI_i is the body condition of individual fish i with a live mass of W_i and fork length of FL_i, and a and b are the coefficients from the regression model, developed separately for both rainbow trout and Arctic grayling. Therefore, a fish with a positive residual is in better than average condition and a fish with a negative residual is in worse than average condition, and the magnitude of the values can be compared among individuals. This method produced a body condition index that was consistent across all fish lengths. For example, a 100 mm fish that has a mass 10% higher than the average 100 mm fish will have the same BCI value as a 500 mm fish that has a mass 10% higher than the average 500 mm fish.

Growth rates – Individual instantaneous growth rates (day^{-1}) were calculated for all marked-and-recaptured fish using

$$Growth_i = \frac{\log_e(W_{i,final}) - \log_e(W_{i,initial})}{\Delta t};$$

where $W_{i,\,final}$ is the mass at final capture, $W_{i,\,initial}$ is the mass at initial capture, and Δt is the duration of time (days) between captures.

Relationship between body condition and growth rates

We developed candidate mixed-effects regression models to evaluate the relationship between instantaneous growth rates and the body condition of an individual fish using

$$Growth_i = \beta_o + \beta_1 X_{1i} + \beta_2 X_{2i} + \cdots + \beta_n X_{ni} + n_i + \tau_i$$

where X_i represents the different fixed-effects predictors for individual i, β's are the model coefficients, n_i is the random effect of individual used to account for fish recaptured more than once, and τ are the normally distributed residual errors. The main predictor we were interested in was the body condition index (BCI), but also included the final mass (i.e., mass at recapture), year of capture, and their potential interactions (Table 1.1 and 1.2). Although each fish's body condition index is size-independent, we included final mass as a possible predictor in the growth model as our fish samples ranged in size from 23-990 g and 24-1879 g for Arctic grayling and rainbow trout, respectively; thus allowing the model to account for the inherent allometric effects on growth (Peters 1986). Previous studies have shown that energy allocation (i.e., skeletal vs. fat reserves) can be influenced by the interaction of water temperature and food availability (Hewett and Kraft 1993, Jacobs et al. 2011), both of which can vary among years. Therefore, year was included as a potential predictor to examine whether the BCI-growth relationship varied across years.

Species-specific models were developed for both rainbow trout and Arctic grayling. Mixed-effects models were used to account for the lack of independence among individual fish which were captured multiple times both within and among years. We used an iterative process to select the best model for each species as outlined by Zuur et al. (2009). First, different random-effects structures were evaluated with all possible fixed-effects using Akaike's information criteria (AIC; Burnham and Anderson 2002) with restricted maximum likelihood (REML) parameter estimation. The models that fit the data best had the lowest AIC value and the highest Akaike weight (w_i). Once the random-effects structure was selected, all candidate models with varying fixed-effects were compared using AIC with maximum likelihood (ML) parameter estimation. With the most parsimonious fixed-effects structure, we reevaluated the random-effects structure. Our final model for both rainbow trout and Arctic grayling only included a normally distributed random-intercept term. All mixed-effects models were fit and evaluated using the *nlme* package (Pinheiro et al. 2009) in the program R (R Development Core Team 2011).

To evaluate the ability of growth rates to be estimated from our body condition index, we regressed the estimated growth rates calculated from the model above against the observed growth rates. Because the duration of time between captures of known individuals varied from 2 - 768 days, we were interested in the quality of the relationship between BCI and instantaneous growth as measured across different time length intervals. Therefore, we evaluated the fit of the growth model using 10 - 15 day duration bins for individuals recaptured within the same year (duration <75 days), and then by pooling all individuals with a duration of <300 days, and >300 days (recaptured in different years). Correlation coefficients (r) were used to evaluate the strength and direction of the relationship between modeled and observed growth rates. A Student’s t-test was used to test whether the slope the of the relationship differed from 1 and whether the y-intercept differed from 0 (Zar 1999). Residual plots were visually evaluated to assure each model met the assumptions of normality and homoscadasticity.

Results

Body condition was calculated using the residual errors of the log-transformed length-mass data for 3,003 Arctic grayling (Figure 1.1a) and 6,254 rainbow trout (Figure 1.1b). The best mixed-effects regression models used to estimate instantaneous growth for both species included the body condition index (BCI) of a fish, an allometric effect of body mass on growth (final mass), and the interaction of mass and BCI. Although the BCI of each individual fish was independent of its length, instantaneous growth rates are not. Because our models included such a wide range of fish sizes (23-990 g and 24-1879 g for Arctic grayling and rainbow trout, respectively) simpler models that did not include the allometric effects of growth performed substantially poorer (ΔAIC>15, Tables 1.1 and 1.2). By including the final mass in the model, we were able to account for allometric effects on growth and directly compare the correlation between body condition and instantaneous growth rates.

We evaluated the correlation between body condition and individual growth rates over varying time periods between the initial capture and the recapture using the best-fit multiple regression models (i.e., Model 4 for both species; Table 1.3). The correlation (r) between body condition and growth using 10 - 15 duration intervals spanning 2 - 75 days ranged from 0.68 - 0.90 for rainbow trout and 0.39 - 0.72 for Arctic grayling (Figure 1.2). Correlations between growth and body conditions were quite stable over this entire interval, demonstrating that body condition reflected growth rates of fish for up to 10 weeks prior to sampling. The only duration intervals with correlation coefficient less than 0.68 were for Arctic grayling recaptured 19 days or less from their original capture. The ability of the models to estimate growth for fish whose recaptures occurred in different years than the original tagging event (>300 days) was weaker for both rainbows (r = 0.51) and graylings (r = 0.58). Overall, body condition of individual fish was most strongly correlated with instantaneous growth rates over durations of roughly 2 - 10 weeks for both Arctic grayling (Figure 1.3a) and rainbow trout (Figure 1.3b).

Discussion

Obtaining direct growth measurements from individually tagged fish in large wild populations is notoriously labor intensive, and thus costly, relative to collecting just body measurements from a single sample of individuals from a population. To assess the performance for detecting variation in growth rates from a metric that is easier to derive in the field, we evaluated the correlation between growth and a body condition index based on length-mass measurements. We found that instantaneous growth rates were highly correlated with the body condition of individually marked-and-recaptured rainbow trout and Arctic grayling. The overall correlation between body condition and growth was slightly higher for rainbow trout than for

Arctic grayling, as a result of relatively poor correlations between growth and condition for Arctic grayling when this relationship was evaluated with individuals recaptured less than 20 days from their previous capture. This difference is likely a result of the slower growth rates of Arctic grayling (about one third as fast as rainbow trout) which produced a weaker growth signal relative to observation errors in our data. Additionally, handling fish can lead to short-term physiological stress (Pickering et al. 1982, Cooke et al. 2002), and perhaps Arctic grayling are more sensitive to sampling than rainbow trout. Thus, in our study system, body condition reflected growth rates best for time intervals of at least 10 days long.

Other indices have been used to indirectly assess growth of individual fish. By measuring the activity or concentration of biochemical markers in the tissue or blood of fish, growth rates can be inferred without the difficulties associated with tagging and the mortality involved with direct measurements of body composition. One advantage of these physiological indictors over our index is that growth can theoretically be assessed even during abrupt seasonal changes in body size, such as early spring growth and pre- and post-spawning events. Two such growth indices include RNA-DNA ratio (Chícharo and Chícharo 2008) and insulin growth factor-1 (IGF-1; Duan 1997). Beckman (2011) accessed the utility of IGF-1 as a growth index by reviewing 25 studies and found the correlation (r) between IGF-1 and growth varied between non-significant and 0.96. Similarly, RNA-DNA ratios have been shown to be an effective indicator of recent feeding and growth in some fish (e.g., Grant 1996), but few comparisons exist and correlations are also highly variable (Bulow 1987, Buckley et al. 1999). Therefore, while these indices will always be more time intensive and costly than length-mass based indices, it is not clear that they will produce a substantially different perspective of the growth performance of fish than the method we show here.

The use of a body condition index as an indicator of recent growth can be complicated by many factors, such as sex (Henderson et al. 2003), maturation (Morgan 2004), morphology (Brönmark and Miner 1992), diet (Milner et al. 2003), and body composition (Breck 2008). Despite these potential limitations, we found that that residual body condition is a strong indicator of growth within an individual river basin. While body condition and growth are not necessarily linked to body composition (Sutton et al. 2000), this limitation can be minimized by comparing time periods when energy allocation among individuals is similar (e.g., end of summer or autumn for spring-spawning species; Brown and Murphy 2004). Here, we sampled the body condition and growth rates of two species collected from a single watershed during the peak of the growing season. Additionally, the majority of the fish we sampled were sub-adults and collected months after the peak spawning period, minimizing the confounding effects of sex and maturation on body condition. Thus, the physiological status of an individual fish was likely correlated with the calculated body condition (Fechhelm et al. 1995).

The use of condition indices as a metric of recent growth performance, as well as how well growth reflects the nutritional status of individuals, has been debated for decades (Bolger and Connolly 1989, Cone 1989, Jakob et al. 1996, Green 2001, Schulte-Hostedde et al. 2005, Peig and Green 2010). Many of these inconsistencies are likely methodological, in addition to the biological complexity associated with linking trophic ecology and physiological condition. While standard length-mass condition indices continue to be refined (Lleonart et al. 2000, Peig and Green 2009), it is important that these methods remain usable for a wide range of ecologists and free of size- and species-related biases. Our results suggest that a simple regression based body condition is strongly correlated with recent individual growth rates over time scales of weeks to months if length-mass data are collected during a time of year when confounding physiological and morphological effects are minimized. While direct measurements of growth may be preferred when logistically possible, our data demonstrate that body condition indices provide a reliable, individual based proxy of recent growth performance. The development of other non-invasive indices to evaluate body condition and growth hold substantial promise for rapid assessment of growth performance of fishes in the wild (e.g., bioelectrical impedance analysis; Cox and Hartman 2005, Rasmussen et al. 2012). Until these methods are refined and tested across a wide range of species and conditions, variation through time in standard length-mass condition indices can provide supporting evidence for how natural and anthropogenic changes impact the physiological state of individuals, which ultimately shapes population dynamics and community structure (Stevenson and Woods 2006).

Table 1.1: Candidate linear mixed effects models to estimate growth of Arctic grayling. The predictors were: body condition index (BCI), final $\log_e$(mass), and year of observation. An intercept (βo), error (τ), and random effect of individual (n) were three additional parameters included in each model. Model 4 had the lowest AIC score (ΔAIC=0) indicating the best candidate model with the conventional r2. K represents the number of parameters in each model and AIC model weight is denoted by wi. Data includes capture-recapture durations of 2-742 days.

Model	K	AIC	ΔAIC	r^2	w_i	Predictors
1	8	-4471.96	29.50	0.30	0.0	BCI, W_{final}, Year, BCI*W_{final}, BCI*Year
2	7	-4483.26	18.20	0.30	0.0	BCI, W_{final}, Year, BCI*W_{final}
3	6	-4470.66	30.80	0.27	0.0	BCI, W_{final}, Year
4	6	-4501.46	0.00	0.30	1.0	BCI, W_{final}, BCI*W_{final}
5	5	-4485.81	15.65	0.26	0.0	BCI, W_{final}
6	4	-4409.79	91.68	0.11	0.0	BCI
7	4	-4382.18	119.29	0.08	0.0	W_{final}

Table 1.2: Candidate linear mixed effects models to estimate growth of rainbow trout. The predictors were: body condition index (BCI), final $\log_e$(mass), and year of observation. An intercept (β_o), error (τ), and random effect of individual (n) were three additional parameters included in each model. Model 4 had the lowest AIC score (ΔAIC=0) indicating the best candidate model with the conventional r^2. K represents the number of parameters in each model and AIC model weight is denoted by w_i. Data includes capture-recapture durations of 2-768 days.

Model	K	AIC	ΔAIC	r^2	w_i	Predictors
1	8	-3594.41	25.76	0.50	0.0	BCI, W_{final}, Year, BCI*W_{final}, BCI*Year
2	7	-3604.18	15.99	0.50	0.0	BCI, W_{final}, Year, BCI*W_{final}
3	6	-3533.78	86.39	0.41	0.0	BCI, W_{final}, Year
4	6	-3620.17	0.00	0.50	1.0	BCI, W_{final}, BCI*W_{final}
5	5	-3557.09	63.08	0.41	0.0	BCI, W_{final}
6	4	-3474.94	145.23	0.27	0.0	BCI
7	4	-3258.41	361.76	0.03	0.0	W_{final}

Table 1.3: Fitted parameters (± 1 SE) for the best-fit mixed effects model (Model 4). These were used to estimate instantaneous growth rates for Arctic grayling and rainbow trout (see Table 1.1 and 1.2).

Species	β_o	BCI	W_{final}	BCI*W_{final}
Arctic grayling	0.018 ± 0.001	0.094 ± 0.013	-0.003 ± 0.001	-0.014 ± 0.003
Rainbow trout	0.031 ± 0.002	0.156 ± 0.011	-0.004 ± 0.001	-0.021 ± 0.002

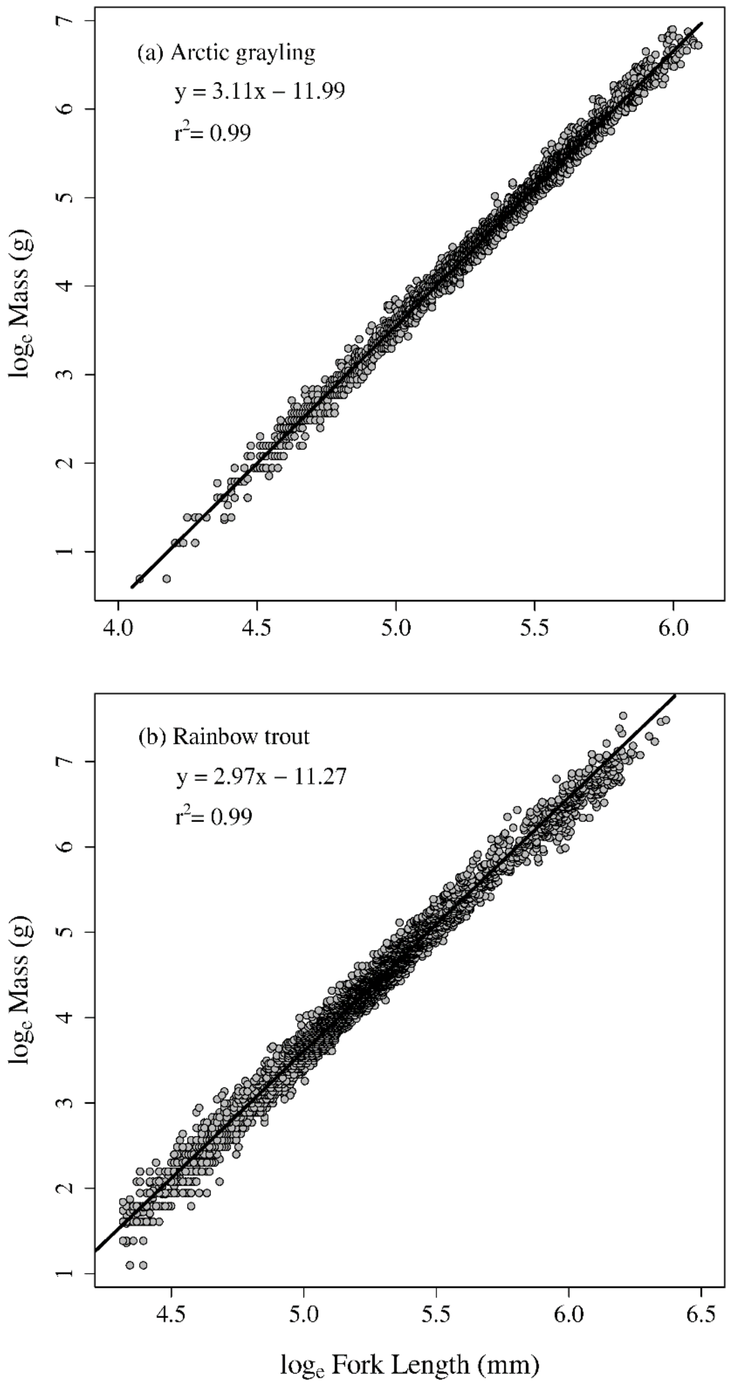

Figure 1.1: Log-transformed length-mass relationship for (a) Arctic grayling and (b) rainbow trout. The black line represents the least squares regression of the $\log_e$(mass; g) of a fish for a given $\log_e$(fork length; mm); individuals above the line are in better than average condition and those below the line in below average condition.

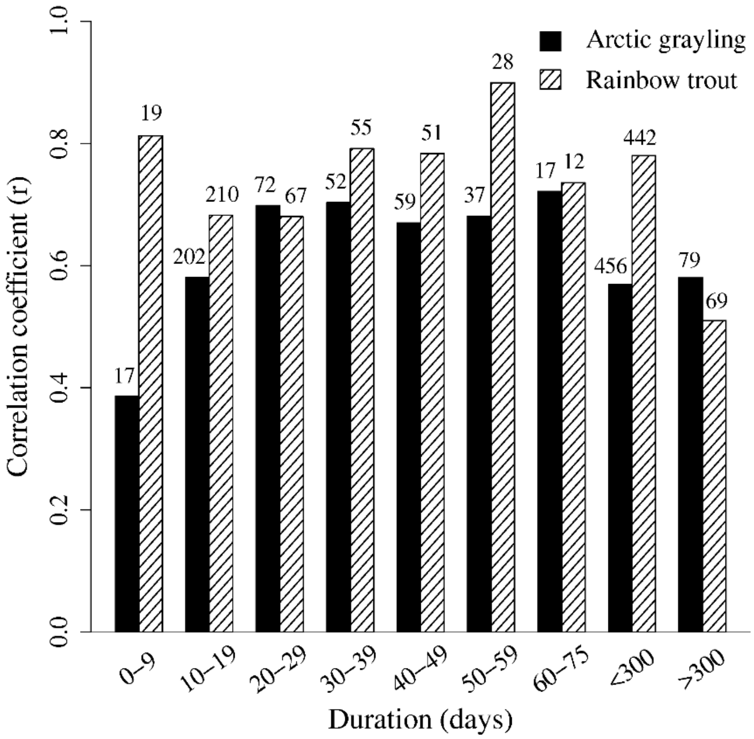

Figure 1.2: Correlation (r) between the observed and predicted instantaneous growth rates (day^{-1}) as a function of the number of days between the initial marking event and recapture (i.e., duration) used to estimate growth rates for Arctic grayling (black) and rainbow trout (hatched). Predicted growth rates were estimated using Model 4 for both species (see Table 1.1 and 1.2). The numbers above each bar correspond to the sample size. The slope and y-intercept of the relationship between observed and predicted growth were not significantly different from 1 and 0, respectively, for all comparisons.

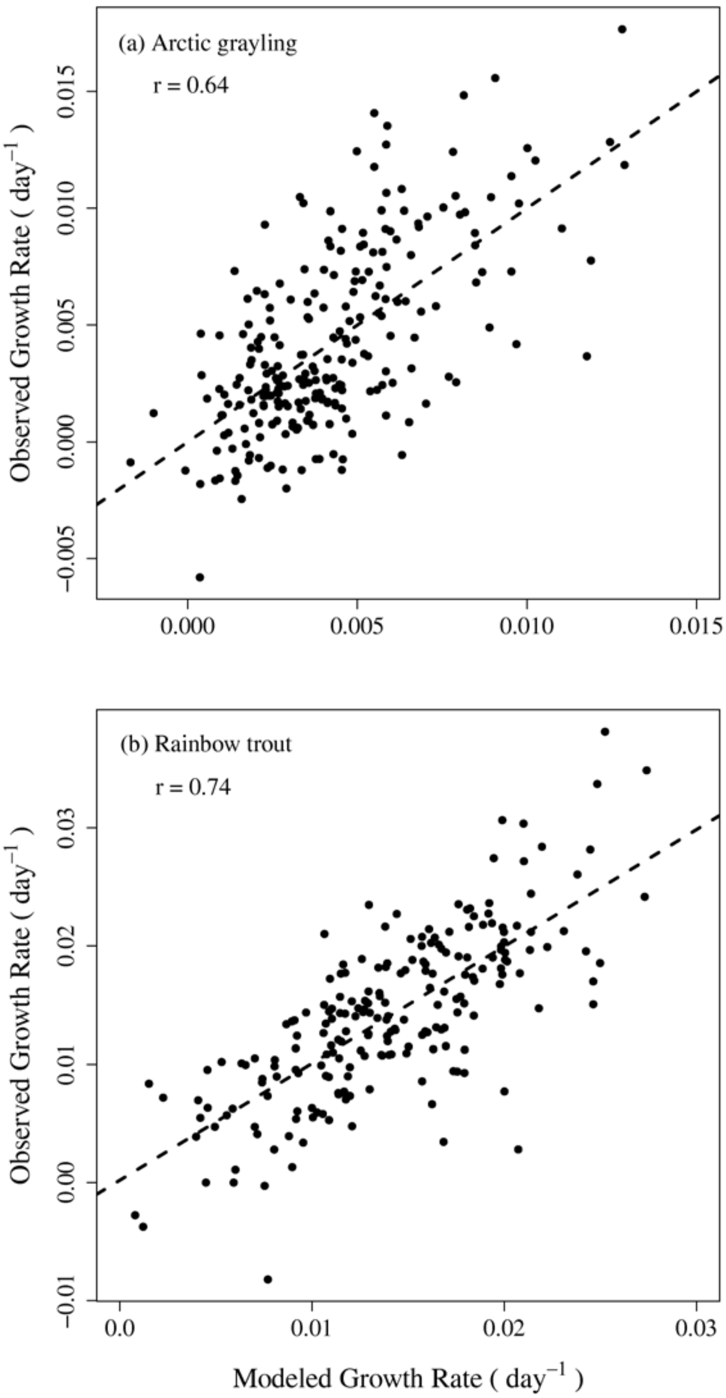

Figure 1.3: Observed versus predicted instantaneous growth rates (day^{-1}) for (a) Arctic grayling and (b) rainbow trout using individuals captured-and-recaptured between 20 to 75 days apart. Predicted growth rates were estimated using Model 4 for both species (see Table 1.1 and 1.2). Residual plots displayed no underlying structure, producing an unbiased relationship between the predicted and the observed growth rates for both species. Dashed line represents the 1:1 relationship between the observed and predicted growth rates.

Chapter 2: Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy

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 (Naiman et al. 2002, Gende 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 during 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 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 (Figure 2.1; 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 - 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.

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 km^2 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 escapement (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 2.1; 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 (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 17,000 individuals (Figure 2.1; Rogers and Schindler 2008).

Data Collection

Rainbow trout and Arctic grayling were sampled in Lynx and Hidden creeks in late August from 2002-2012, 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 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 (salmon /m^2).

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 Lake. 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 ($r^2 = 0.70$) and Lynx ($r^2 = 0.67$) 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 (salmon/m^2). 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; Hansen 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 to 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 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 an individual fish's specific ordination. 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 2008) 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 (day^{-1}) as a function of fish body condition (Bentley and Schindler 2013). The full linear mixed-effects model was:

$$Growth_i = \beta_o + \beta_1 * BCI_i + \beta_2 * W_i + \beta_3 * BCI_i * W_i + n_i + \varepsilon_i \tag{1}$$

where BCI_i is the body condition index of individual *i*, W_i is the mass (g), β's are the model coefficients, n_i is the random effect of individual used to account for fish recaptured more than once, and ε are the normally distributed residual errors. 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 (i.e., year effect). Each stream and species combination (2 species X 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 (Eq. 3 and Eq. 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 (Eq. 2 and Eq. 3). Each of our four datasets was used to fit each of the following nested equations:

$$\textit{Linear (Type I)} \qquad \hat{Y}_{ijk} = y_o + a \cdot x + T + T^2 \tag{2}$$

$$\textit{Power (Type II)} \qquad \hat{Y}_{ijk} = y_o + \frac{a \cdot x}{s_o + x} + T + T^2 \tag{3}$$

$$\textit{Sigmoid (Type III)} \qquad \hat{Y}_{ijk} = y_o + \frac{a \cdot x^b}{s_o{}^b + x^b} + T + T^2 \tag{4}$$

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:

$$\hat{Y}_{ijk} = \mu_{ij} + \varepsilon_{ijk} \tag{5}$$

Where $\varepsilon_{ijk} \sim N(0, \sigma^2)$ and μ_{ij} is the mean and equal to the second level (year effect):

$$\mu_{ij} = f(x_i, \beta) + e_{ij} \tag{6}$$

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

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 2002-2012, we observed peak salmon abundances in the two study streams ranging from 375 – 14018 individuals, translating to salmon densities spanning 0.04 – 1.04 m^{-2} (Figure 2.1). We observed an increase in the total average ration size of rainbow trout and Arctic grayling coinciding with an increase in salmon densities in both Lynx and Hidden creeks (Figure 2.2). While the ration sizes were not significantly different between the two streams in high salmon densities years for each species (Appendix C), we did detect significantly higher rations in Hidden Creek in low salmon densities 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 (Figure 2.3). 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 clearly 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 production.

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 (Figure 2.4). 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 ΔAIC 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 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 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 (Figure 2.1). Although the salmon resource subsidy occurred every year, the magnitude of the pulse affected the consumption rates (Figure 2.2) and foraging patterns (Figure 2.3) of both rainbow trout and Arctic grayling, ultimately impacting the average growth rates of these two species (Figure 2.4). 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 response (Figure 2.4). 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 (JB Armstrong and KT Bentley *personal observation*), 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 (Figure 2.4a). 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 redds (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 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 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. *in review*). 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 (Figure 2.2). 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 that 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 5-15°C (Armstrong et al. 2010, Lisi et al. *in review*). 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 in the Wood River system are absent from the coldest streams, but rather inhabit streams that range in summer temperature from 10-15°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, Power, and Huxel 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.

Table 2.1: 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/cm^2)	0.33 ± 0.17	0.24 ± 0.14
Invertebrate Biomass (mg/m^2)	18.7 ± 8.5	6.2 ± 2.8

Note: Values are averages ± 1 standard deviation calculated from data collected from 2002-2005 (nitrogen, phosphorus, invertebrates), 2002, 2006-2012 (temperature), and 2006, 2007, 2009, 2010 (algae).

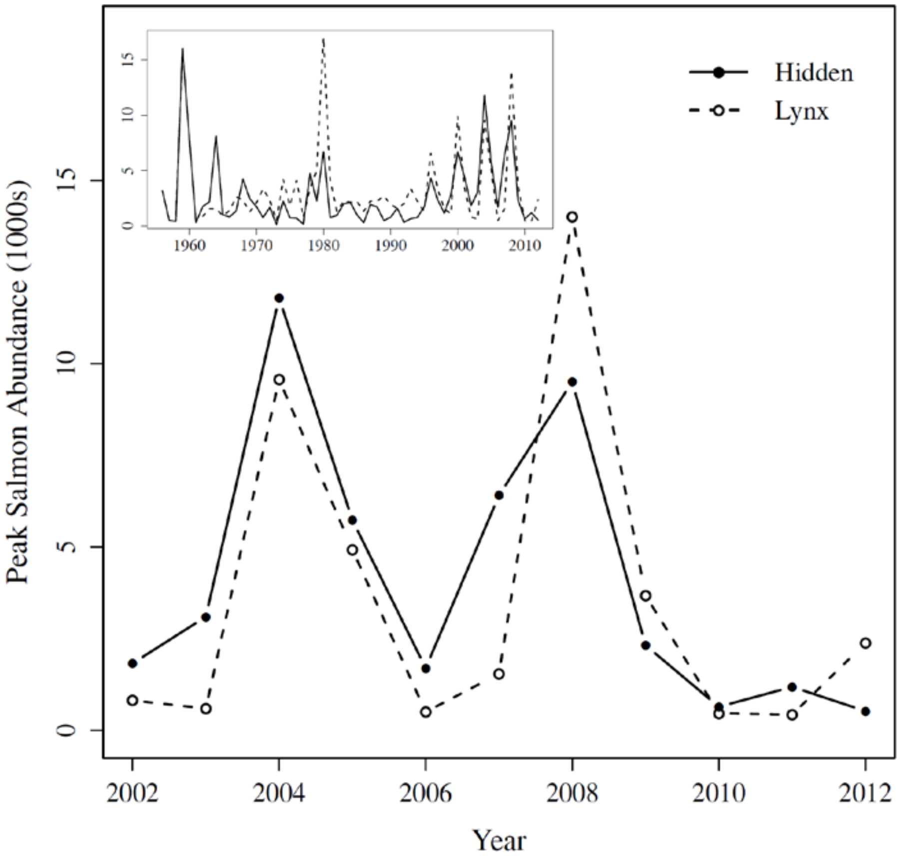

Figure 2.1: Peak sockeye salmon abundance in Hidden (solid-black) and Lynx Creek (dashed-white) over the 11 years summer growth rates were evaluated. The inset highlights the variability in the inter-annual peak salmon abundance from 1956-2012.

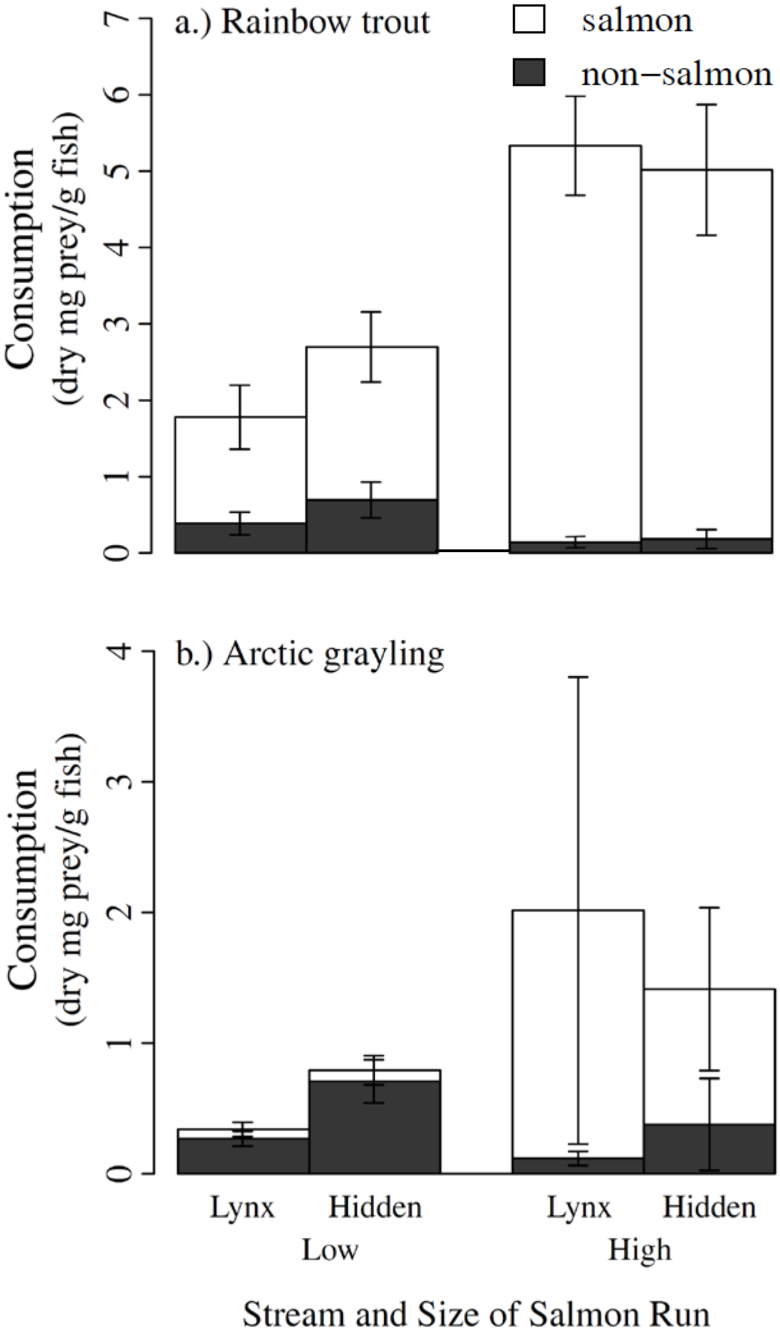

Figure 2.2: Mean individual (± 2 SE) consumption rates (dry mg prey/g fish) of non-salmon (black) and salmon (white) derived prey items (see Appendix B: Table B1) for (a) rainbow trout and (b) Arctic grayling as a function of salmon density and stream. Diets were pooled into either low (0 – 0.10) or high (0.75- 1.04) salmon density (salmon/m^2) based on our growth results. Note the different y-axis scales between panels.

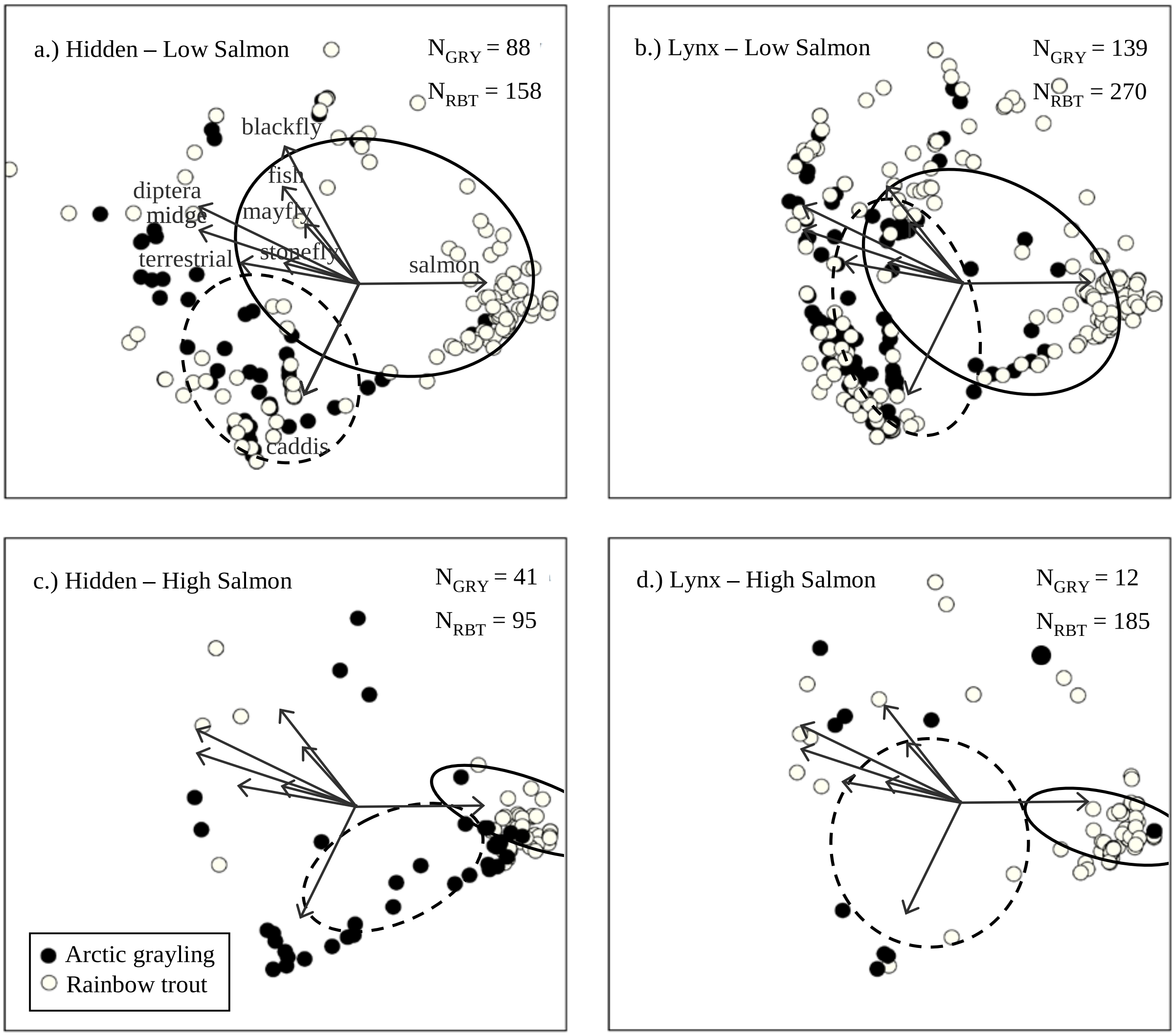

Figure 2.3: NMDS ordinations of the diet composition of individual rainbow trout (white) and Arctic grayling (black) at both low (a = Hidden, b = Lynx) and high (c = Hidden, d = Lynx) salmon spawning densities. Dashed (grayling) and solid (rainbow) ellipses depict one standard deviation of the pair-wise dissimilarity scores per grouping. Statistically significant ($p \leq 0.05$) 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.

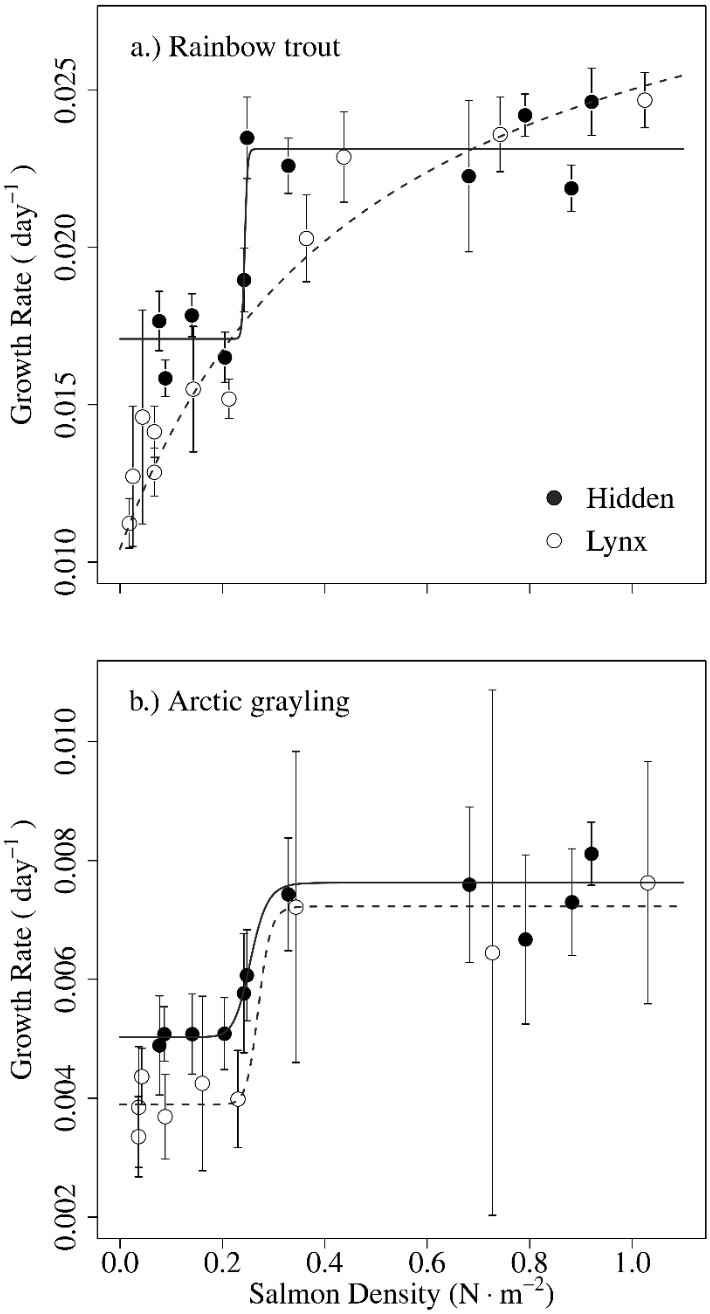

Figure 2.4: Mean individual (± 2 SE) growth rates (day^{-1}) of (a) rainbow trout and (b) Arctic grayling as a function of salmon density (salmon/m^2) in Hidden (black) and Lynx (white) Creek. Lines (black=Hidden, dashed=Lynx) represent the best-fit mixed effects models (see Appendix C: Table C1; Appendix 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).

Chapter 3: Summer movements of stream-dwelling salmonids throughout a network of lake tributaries

Introduction

River networks are hierarchically structured systems characterized by a continuum of downstream changes in biota and ecosystem processes, which generate coarse-scaled patterns of biotic and abiotic heterogeneity (Vannote et al. 1980, Rahel and Hubert 1991). However, fluvial systems also exhibit high levels of finer-scale variation within these broad-scale longitudinal patterns (Benda et al. 2004, Stanford et al. 2005, Tockner et al. 2006). For example, habitat heterogeneity across an intact floodplain, or among tributaries, may be similar in magnitude to that across the entire river continuum (Poole 2002, Stanford et al. 2005, Lisi et al. 2012). While the suitability of different environments will vary by organism, individuals often live in a patchily distributed mosaic of habitats whose resources vary across space and time (Schlosser 1991, Armstrong and Schindler 2013). Ultimately, individuals must navigate and exploit the heterogeneity of their environment to successfully grow and reproduce.

Movement among habitats is one strategy animals have evolved to track spatially and temporally variable resources. For freshwater fishes, it has been widely acknowledged that kilometer-scale movements can be of substantial importance for the long-term persistence of populations (Lapointe et al. 2013). However, the emphasis has mostly been on the need for broad-scale, inter-seasonal movements to connect complementary habitats used for reproduction, refugia, and feeding (Schlosser 1991, Schlosser and Angermeier 1995, Northcote 1997). Less attention has been paid to characterizing fish movements at the multi-kilometer, network-scale within a season that may allow individuals to exploit the heterogeneity in feeding and growth opportunities that complex riverscapes (*sensu* Fausch et al. 2002) provide to them (e.g., Ruff et al. 2011, Armstrong et al. 2013). In terrestrial ecosystems, trophic resources display substantial intra-seasonal variation across the landscape requiring animals to make broad-scale movements to achieve positive energy balance (Fryxell et al. 2005, Frair et al. 2005, Wang et al. 2006). We hypothesize that analogous to terrestrial studies, fishes may need to integrate across broad-spatial scales when foraging opportunities are patchily distributed in space and time across river-networks. Here, we investigated the summer movement characteristics of stream-dwelling salmonids throughout a network of lake tributaries whose productivity in producing prey for fishes can vary substantially among streams and years.

Arctic grayling (*Thymallus arcticus*) and rainbow trout (*Oncorhynchus mykiss*) are two species of resident (i.e., non-anadromous) salmonids that co-occur in streams and rivers throughout southwestern Alaska. Grayling and rainbow trout play a large ecological and economic role in the region, as they can often comprise the majority of resident stream biomass and are the mainstay of recreational fisheries (Duffield et al. 2007). The high productivity of these resident fish populations is supported by the annual return of spawning anadromous sockeye salmon (*O. nerka*). Specifically, the eggs of spawning salmon offer a high-quality resource pulse of food for resident fishes (Scheuerell et al. 2007, Armstrong 2010). Prior to the arrival of salmon, the diet of resident fishes primarily consists of benthic and terrestrial invertebrates (Scheuerell et al. 2007). Once spawning salmon arrive, grayling and rainbow trout begin to forage on salmon eggs, but the strength of the diet shift, and resulting growth rates, depends heavily on the abundance of salmon and the *in situ* productivity of the stream (Moore et al. 2008, Bentley et al. 2012). Interestingly, at the scale of entire watersheds, the number of salmon returning to spawn is relatively consistent among years due to fisheries management goals (Baker et al. 2009). However, the number of salmon returning to individual streams can be extremely variable as a result of natural population dynamics that produce little synchrony in salmon abundance among streams and years within the same watershed (Rogers and Schindler 2008). Thus, at the scale of a single-stream, variability in salmon run size can make food resources highly variable among years. But, at larger spatial-scales, for example across the entire watershed, population diversity greatly increases the reliability of salmon subsidies to consumers (Schindler et al. 2010, 2013), but it requires that individual fish move among tributaries. Therefore, we were interested in characterizing the movement patterns of resident fishes across a network of tributaries before and during salmon spawning to assess evidence for grayling and rainbow trout moving to exploit the shifting opportunities to forage on salmon subsidies.

We used individually tagged fish to investigate the intra-seasonal movement patterns of Arctic grayling and rainbow trout throughout a watershed in southwestern Alaska (Figure 1). Specifically, we monitored the movements of individual fish both within and among four tributaries that drained into a single lake, ranging in distance along the shoreline of 6.7 – 41 km apart, across two years. The objective of the study was to assess the functional connectivity of the four tributaries by measuring the seasonal timing and movement rates among individuals and species. This study provides one of the first-steps towards understanding not only the importance of connectivity to buffer individuals from heterogeneously distributed resources, but also their ability to potentially exploit this variation to increase demographic characteristics, such as foraging rates, growth, and survival (e.g., Ruff et al. 2011, Armstrong et al. 2013).

Methods

Study system

This study was conducted in the Wood River system (59° 34’37”N, 158° 48’25”W), which drains into Bristol Bay in southwestern Alaska. The Wood River watershed has a total drainage area of 3590 km^2 and consists of five large, deep, oligotrophic lakes that are fed by numerous tributaries and connected by small rivers. Our focal study system consisted of four tributaries (Hidden, Lynx, Teal, and Stovall creeks) that flow into Lake Nerka, which is the largest lake in the system, located midway up the river network (Figure 1). While grayling and rainbow trout inhabit dozens of tributaries across the Wood River watershed (Figure 1), our study streams were chosen based on (1) the suitability of habitat for resident fishes, (2) their geographic distribution across the lake, and (3) our ability to successfully monitor movements (specifically the width and depth of some streams were too large for our monitoring equipment). These four tributaries are 2nd- to 3rd-order streams with average wetted widths of 4.5 – 6.5 m and have approximately 1 – 5 km of total stream length used by resident fishes and sockeye salmon.

Arctic grayling and rainbow trout were chosen as our focal species because they typically comprise >95% of the resident stream fish biomass. Though dominant, grayling and rainbow trout 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, and coastrange (*Cottus cognatus)* and slimy (*C. aleuticus)* sculpin. Additionally, adult sockeye salmon spawn annually in streams and rivers that are inhabited by resident fishes. Although adult sockeye salmon are present throughout the watershed from mid-July through late-October, individual populations of salmon are typically active on individual spawning grounds for two to four weeks, and their spawning timing is tightly linked to stream temperature (Schindler et al. 2010, Lisi et al. 2012) In our four study streams, adult sockeye salmon commence spawning during the last week of July to the first week of August and by the first week in September almost all salmon have died.

Data collection

We began tagging individual grayling and rainbow trout with passive integrated transponder (PIT) tags in Hidden and Lynx creeks in 2007, Teal Creek in 2010, and Stovall Creek in 2011 (Appendix F – Table F1). Each year, the streams were sampled every 10 to 30 days from mid-June through early-September. During each sampling event, resident fish were collected in a spatially continuous manner throughout the stream using a stick seine (Bentley et al. 2012). Across the five years and four streams, we implanted a representative size range of fish (Appendix G – Figure G1) with a unique PIT-tag (full duplex, 134.2 kHz, 11.5 mm length, 2.1 mm diameter; Allflex-USA, Dallas-Fort Worth Airport, Texas). In total, we tagged 39% and 67% of all captured rainbow trout and Arctic grayling, respectively. Due to our sampling effort and the natural distribution of fish, >86% of all fish were tagged in either Hidden or Lynx creeks (Appendix F – Table F1). Tagged individuals ranged in fork length from 69 to 558 mm, but >87% of all fish were between 100-300 mm (Appendix G – Figure G1), and therefore likely sub-adults (Bentley and Schindler 2013). During these resident fish surveys, we also visually estimated the abundance of adult sockeye salmon by wading the entire main stem of the stream. We frequented these streams every 2 -3 days during late-July to get a precise estimate of when salmon began spawning.

In 2011, we installed stationary PIT-tag antenna arrays (Bond et al. 2007, Ruff et al. 2011) at Hidden, Lynx, and Teal creeks to continuously monitor the intra-seasonal movements of Arctic grayling and rainbow trout. In 2012, we added an additional antenna site at Stovall Creek (Figure 1). Each site was equipped with a pair of PIT-tag antennas, placed approximately 4 m apart, which allowed for the assessment of movement direction. Each antenna was connected to a single PIT-tag reader, which recorded fish movements by storing individual tag IDs, along with the time and date, and the antenna location. Antennas were positioned perpendicular to the stream flow (i.e., swim-through antennas) and placed approximately 100-200 m upstream of the stream mouth, at a location were the antennas spanned the entire stream channel. Antennas were installed as soon after the spring freshet as possible. In 2011, antennas were installed June 12-16 and removed September 10-12. In 2012, antenna arrays were installed June 9-10 and removed September 6-11. Antenna sites were checked every 4-8 days to swap batteries and download data. During each visit we tested the functionality of the site by passing a test PIT-tag through each antenna approximately five times. If the reader did not detect the test tag each time, the readers were adjusted until properly functioning. Read range was always greater than the height of the antennas, which were never fully inundated.

As part of our pilot study on fish movement in 2010, we visually estimated the relative intra-seasonal densities of Arctic grayling and rainbow trout using daytime snorkel surveys in Hidden and Lynx creeks. The purpose of these surveys was to characterize the change in densities over the course of the summer, determine the relative abundance of both species, and provide an independent estimate of population-level movements. Sample units were demarcated in each stream in early-June 2010 (Hidden: n = 44; Lynx: n = 67) and had an average [± SD] length and width of 16.5 ± 8.9 m and 3.5 m ± 0.9 m. 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 majority of the realized habitat was surveyed during each sample event. During each survey, a single snorkeler moved upstream through each unit, enumerating the fish by species. This was a highly effective method as stream visibility always exceeded the width and depth of the habitat units sampled. Each stream was surveyed every 10-21 days from mid-June through mid-September. In 2011, we duplicated these surveys, but did not add Teal or Stovall creeks due to low visibility in those streams due to high concentrations of dissolved organic matter. In 2012, periodic rain events increased stream flows, inhibiting several surveys, and therefore 2012 data were not included. For each year, relative densities were estimated by dividing the total number of each species enumerated throughout all sample units by the total area of stream surveyed (i.e., number of fish m^{-2}).

Data analyses

Intra-seasonal movement patterns by Arctic grayling and rainbow trout were assessed using fish that were observed in a stream, but had been tagged in a previous year of the study. By using only “returner” fish we decreased our sample size, but were able to monitor the entire intra-seasonal movements of each individual fish, and avoiding confounding our analyses with any short-term changes in behavior associated with tagging. In 2011, 59 grayling and 77 rainbow trout “returned” to one or more of our monitored streams, while in 2012, 121 grayling and 141 rainbow trout were detected returning. Of the returning fish, 71-95% were tagged in the previous year, which comprised 16-29% of all fish tagged the year prior (Appendix F – Table F1).

Based on our study design, we were able to characterize movements into (i.e., immigrations) and out of (i.e., emigrations) streams using a set of decision rules. Briefly, we first classified all movements using antenna hits that had serial detections, and used the sequence of antenna detections to define the direction of the movement (i.e., an immigration = detection on the downstream antenna, followed by a detection on the upstream antenna). Serial detections were defined as a sequence of hits on a two antennas within a span of 15 minutes. We chose this threshold because it was the maximum amount of time it took an individual to move through both antennas based on visual examination of the data. The remaining "single" antenna hits were classified as either an immigration or emigration using information based on where the fish was initially tagged, where the fish was previously detected, and if the single hit was between two serial hits of the same direction (e.g., a single hit between two serial immigrations was assumed to be an emigration). Over the two years, brown bears (*Ursus arctos*), inclement weather, and electronic issues resulted in some equipment failure and lost data. However, these failures were relatively rare. Across all sites and years, at least one antenna was functioning >96% of the time and both were working >83% of the time. Based on two independent methods, our antenna detection efficiency averaged 83% and 90% (Appendix H). Nonetheless, because our antenna detection efficiency was not perfect, our estimates of movement provide a conservative measure of the realized movement tendencies of these fishes.

Based on the categorized movements of rainbow trout and Arctic grayling, we analyzed the data both at individual sites as well as among streams. We began by calculating the elapsed time between consecutive movements, and thus, could determine the amount of time individuals spent either in the stream before emigrating or spent outside of a given stream before immigrating back. While we could classify the known location of a fish if it was detected immigrating into one of our four monitored sites, if a fish emigrated from a monitored site it resulted in one of three types of movements. First, if a fish left a particular site and was detected at another stream some time later, this emigration was defined as an inter-(among) stream movement. We calculated the total distance swam by each fish by enumerating the number of inter-stream movements within a given year and multiplying it by the respective distances between each of the sites. Hypothetically, if given sufficient time, a fish could have visited other streams where we did not have PIT-tag antennas between leaving its initial site and arriving at the next monitored stream. Therefore, the total number of sites visited, and total cumulative distance travelled, by each fish was a minimum estimate. Second, a fish could have emigrated from a stream and then immigrated back into the same stream some time later. We only defined that movement as an emigration if the fish left the stream for more than 24 hours. We based this threshold on the approximate minimum amount of time it took a fish to swim between two of our monitored sites (see results). Thus, if a fish did not leave a stream for >24 hours, it was assumed to have remained at that same site. Last, a fish could have left one of our monitored sites and was never detected again. It is possible that some of these fish died in the lake. However, we feel it is more likely that these fish travelled to a stream(s) where we did not have a PIT-tag monitoring setup as Lake Nerka harbors few predators capable of eating fish the sized we tagged and fish populations in temperate systems often accrue the majority of their mortality during winter-periods (Garvey et al. 2004). Therefore, we classified these emigrations as a fish's final movement to an "unknown" stream and said it visited a "+" number of sites. Movement data were summarized by species, stream, and year. If there were no significant difference among groupings or sample sizes were small ($n < 30$), data were lumped. Program R was used for all analyses (R Development Core Team 2013).

Results

We observed strong seasonal shifts in the densities of resident fish observed during snorkel surveys at Hidden and Lynx creeks (Figure 2). Both streams held few fishes at the onset of the growing season, during mid- to late-June, averaging (± SD) 14.2 ± 10.9 Arctic grayling and 84.1 ± 111.3 rainbow trout per stream kilometer. Over the following three to five weeks, densities quickly rose, and by late-July to early-August densities had increased 6 to 12-fold (159.6 ± 36.6 Arctic grayling and 545.2 ± 230.8 rainbow trout per stream kilometer). By late-August to early-September, densities of grayling remained at similar levels observed in late-July (130.7 ± 25.3 km^{-1}) while rainbow trout densities reached their highest levels (772.9 ± 261.9 km^{-1}).

The observed changes in stream fish densities from snorkel surveys were corroborated by individual movements of PIT-tagged fish. Using our stationary antenna arrays, we detected an overall net influx of both Arctic grayling and rainbow trout in Hidden and Lynx creeks. Individuals began entering streams in mid-June and reached their highest abundances by late-July to early-August (Figure 3 and 4 – subpanels A and B). Though, unlike the snorkel surveys, which only could detect the relative change in population level abundance, our movement data revealed high rates of immigration and emigration (i.e., turnover) by individuals at each of our monitored sites. On average, 77 ± 14% of all individual grayling and 72 ± 15% rainbow trout emigrated (see methods for definition) from a stream at least once and, overall, for every 1.11

immigrations there was 1 emigration. Fish at Teal and Stovall creeks displayed similar behaviors to fish at Lynx and Hidden creeks (Figure 3 and 4 – subpanels C and D), but sample sizes were small, and therefore overall patterns were less discernable. The one exception was grayling at Stovall Creek, where we detected a large number of individuals (n = 73), but a net efflux.

Individual movements were concentrated from mid-June through July (Figure 3 and 4). Overall, 90 ± 9% of all movements (i.e., immigrations and emigrations combined) by Arctic grayling occurred prior to the movement of spawning sockeye salmon into streams, despite this time period consisting of only 40-45% of the total monitoring period (proportion test; $\chi^2 = 416.6$, $p < 0.0001$). Similarly, 81 ± 15% of all movements by rainbow trout occurred before August 1st ($\chi^2 = 161.7$, $p < 0.0001$). While grayling and rainbow trout exhibited similar timing of their movements, they differed in their relative use of our monitored sites (Table 1; Figure 5). Combining both years, 33% of all grayling were detected at two or more of the monitored sites while only 5% of rainbow trout were detected making at least one inter-stream movement. However, of the individuals that were only detected at one of the monitored sites within a given summer, 32% of grayling and 46% of rainbow trout were last seen emigrating from a stream and were never detected again that year, and thus likely immigrated to at least one additional non-monitored site. Therefore, a minimum of 54% of grayling and 49% of rainbow trout used two or more streams across the river network during the summer foraging period in 2011 and 2012.

Over the course of a single summer, we observed a wide range of total distances swam by individual fish. We observed Arctic grayling moving as little as 6.7 km between Teal and Stovall creeks, the minimum detectable distance, to as far as 130 km (from Stovall → Lynx → Hidden → Lynx → Hidden → Stovall over a 45 day period). Overall, the total minimum cumulative distance an individual Arctic grayling moved among streams in a single summer averaged 41.3 ± 31.8 (SD) km (Figure 6a). Among stream movements by individual rainbow trout ranged from 13 to 48 km, with an overall average of 24.8 ± 8.4 km (Figure 6b). The total distances swam between species were not significantly different in either 2011 (Wilcoxon sign-ranked test; $p = 0.16$) or 2012 ($p = 0.57$).

Individual Arctic grayling and rainbow trout displayed a wide range of variation in the elapsed time between emigrations (Figure 7) and immigrations (Figure 8). For both species, the majority of emigrations (i.e., time between consecutive downstream and upstream movements) lasted <12 hours, and of these, <1% were movements among study sites (Figure 7). As the elapsed time of an emigration increased to >1 day, on average, 31% and 16% of all emigrations were detected among-stream movements for Arctic grayling and rainbow trout, respectively. Once an immigration had occurred, individuals spent anywhere between 12 minutes to 85 days in the stream before emigrating to another monitored site (Figure 8). Although there was no significant difference in the elapsed time of an immigration between species and years, we did detect a significant difference among some streams. Specifically, fish remained in Hidden Creek for a median (± SD) of 17.9 ± 20.6 days, which was statistically greater than the median time in Lynx (5.5 ± 18.6 days; Kruskal-Wallis multiple comparison, $p = 0.003$) and Teal creeks (0.74 ± 3.1 days; $p = 0.0001$), but not Stovall Creek (2.2 ± 31.5 days; $p = 0.166$) likely due to the small sample size and large individual variation at Stovall. All other pair-wise comparisons were significantly indistinguishable ($p > 0.05$). This wide range of variation in residency among sites and individuals was exemplified by a single Arctic grayling in 2012. On June 23, it immigrated to Hidden Creek and remained for ~10 days. It then emigrated, entered Lynx creek followed by Teal Creek, remaining in each stream for approximately 2 hours each, before moving to Stovall

Creek, and staying for about 2 days. On July 12 it left Stovall, returning to Lynx Creek on July 14, and remaining for approximately eight hours before emigrating, after which it was never detected again. Over the course of this three week period, the fish had moved a minimum of 60.7 km.

Discussion

Our data demonstrate that Arctic grayling and rainbow trout exhibit kilometer-scale, intra-seasonal movements between tributaries during the summer foraging period, which occur in addition to pronounced inter-seasonal changes in habitat use. In mid- to late-June, sub-adult resident fishes began immigrating into previously unoccupied streams and over the following month relative densities increased 6-12X (Figure 2). Had we only used snorkel surveys to characterize habitat use these increases in fish density would have appeared to only be a population-level shift in habitat use between overwintering and summer foraging habitats. However, by monitoring the movement of individuals, we found that while there was typically an overall net influx of grayling and rainbow trout into streams in June and July, there was simultaneously high rates of immigration and emigration, producing substantial turnover in the identity of individuals comprising the population (Figure 3-4). Additionally, by monitoring movements at several tributaries across Lake Nerka, we also detected movements among streams that occurred throughout the growing season (Figure 5-6, Table 1). Therefore, broad-scale movements may not only be necessary for individuals to complete the different stages of their life-cycle, but may be an important component of fish behavior as individuals navigate the heterogeneity of riverscapes.

Over the course of three months, we observed both Arctic grayling and rainbow trout moving among streams separated by 6.7 – 41 km. By using paired antennas at the mouth of each stream, we were able to assess the directionality of movements and determine the location (i.e., in a monitored stream or not) of all fish through time. Therefore, although an individual may have left one of our monitored streams and never detected again, we can use other knowledge of the river network to have some idea of where the fish may have immigrated. For example, while we know from radio-tracked rainbow trout adults that there is little movement among lake basins (Dye 2005), there are at least 22 other streams within the watershed of Lake Nerka, 11 of which are used by grayling and rainbow trout during the summer foraging period (Figure 1; Alaska Salmon Program, *unpublished data*). Specifically, some resident fishes are likely moving to the Agulowak and Agulukpak rivers, which connect Lake Nerka to Lake Aleknagik and Lake Beverley. These two rivers offer high quality habitat and foraging opportunities, but are difficult to sample due to their size. Additionally, we can use information on among-stream travel time to estimate whether an individual could have visited an unmonitored site between consecutive emigrations and immigrations (Figure 7). For example, we detected a high frequency of emigrations lasting <12 hours, but few produced among stream movements that we detected. While movement distance will obviously influence the time needed for an individual to travel between two streams, most inter-stream movements took >12 hours. Thus, we can postulate that if an individual left one of the monitored sites for >24 hours before returning, it had sufficient amount of time to have moved to an unmonitored site and back. One assumption we are making here is that fish are only using Lake Nerka as a movement corridor and not actually for foraging or refuge. While we cannot reject this possibility, it is unlikely given that grayling and rainbow trout are rarely caught in lake habitat of the Wood River system by either anglers or during extensive beach seine sampling for juvenile salmon. Regardless, fish were using disparate habitats separated by up to tens of kilometers over a course of days to weeks during the summer foraging period.

Fish may exhibit high rates of movement to capitalize on spatially and temporally heterogeneous early-season growing opportunities. The majority of movements by Arctic grayling and rainbow trout occurred in early summer, with few detected after August 1st.   Fish in temperate streams can be in relatively poor body condition following the long and energetically challenging winter period (Cunjak and Power 1987, Berg et al. 2011). Resident fishes feed on benthic and terrestrial invertebrates during June and July prior to the seasonal influx of high-quality salmon-derived resources (Scheuerell et al. 2007). Similar to salmon abundance, *in situ* productivity varies among streams. For example, the densities of benthic invertebrates are approximately 5-7X higher in Hidden Creek relative to Lynx Creek (Moore and Schindler 2008) and may explain why fish remained in Hidden Creek significantly longer before emigrating (Figure 8). But, resident fishes, and their associated movements, are most certainly influenced by a range of biological and environmental conditions (Heggenes 1988, Ebersole et al. 2001, Albanese et al. 2004). Specifically here, it is likely that the movements by grayling and rainbow trout were at least partially influenced by foraging opportunities afforded by spawning sockeye salmon, as has been suggested by other studies (Brink 1995, Eastman 1996, Meka et al. 2003).

The relative decrease in resident fish movement activity coincided with the occupation of streams by spawning sockeye salmon. Streams with spawning salmon offer high quality foraging opportunities for stream fishes (Armstrong 2010) and previous research has shown that ration sizes and energy intake of grayling and rainbow trout can increase 400-600% after salmon arrive (Scheuerell et al. 2007, Moore et al. 2008). However, the ration sizes and growth rates of these fishes are heavily influenced by the relative abundance of salmon, which can vary up to 10-20X among years for individual streams (Rogers and Schindler 2008, Bentley et al. 2012). Given that rainbow trout and grayling have the capacity to move among streams, we initially anticipated that there would be more resident fish movement during the peak of salmon spawning activity, especially if there were relatively few spawning salmon, such as in Hidden and Lynx in 2011 and 2012 (Bentley et al. 2012). We offer two explanations for why resident fish stop moving among streams during the salmon spawning season. First, the opportunity cost associated with leaving a stream that already has salmon, regardless of the density, may be too high to offset the potential gains of moving to a stream with an unknown amount of salmon. Second, some grayling and rainbow trout may be prospecting a range of potential foraging sites across the watershed during early summer and potentially using that information to inform current and future movement decisions (Fretwell and Lucas 1969, Charnov 1976, Delgado et al. 2014). While the mechanisms causing grayling and rainbow trout to move large distances are unclear, a large fraction of each population were documented moving among heterogeneously distributed habitat patches, and our results provide one of the first examples of individuals doing so during the summer foraging period.

While we are not the first study to document long-distance, intra-seasonal movements by stream-dwelling fish (e.g., Meka et al. 2003, Muhlfeld and Marotz 2005), it is interesting to consider why movements at these spatial scales are rarely documented. One explanation is that the range of observed movement distances will directly depend on the interplay between the finest spatial and temporal resolution studied (grain) and the size of the entire study area or duration (extent; Wiens 1989, Fausch et al. 2002). As Gowan et al. (1994) highlight, movement studies can be biased against detecting long-distance movements because of a failure to monitor over large areas. Second, perhaps the spatial and temporal heterogeneity of foraging opportunities in systems like the Wood River system is much higher than in other systems where homogenization of habitat may make the benefits of such movement strategies insignificant. Last, movement studies are routinely conducted in fragmented river systems possibly biasing our understanding of movement patterns and connectivity in intact river networks. While impassable barriers are known to directly inhibit movement (Warren and Pardew 1998, Porto et al. 1999, Schmetterling 2003), it is possible that they also indirectly affect the range of observed movement distances. Similar to studies that have shown that recreational fisheries indirectly decrease the overall growth rate of populations by harvesting the most aggressive, fast-growing individuals (Biro and Post 2008), barriers could potentially remove the most mobile individuals while the more sedentary are more likely to persist (Morita and Yamamoto 2002). Therefore, movement studies conducted in impacted watersheds may not fully represent the historic movement capacity of fish populations. One promising area of future research will be to model how individual fish movements interact with varying degrees of spatially and temporally heterogeneous resources, and various scenarios of habitat connectivity, to influence the persistence and productivity of resident fish populations.

In summary, this study showed that a high proportion of individual resident fishes used multiple streams across a river network during the summer foraging period. Although we did not directly measure the factors controlling the movement of individuals, the spatial and temporal scale at which the movements occurred provide insight to the spatial scales that heterogeneously spaced resources matter to these fishes. Previous studies have highlighted the importance of maintaining connectivity among complementary habitats for individuals to complete the different stages of their life-cycle (Schlosser 1991, Fausch et al. 2002, Lapointe et al. 2013). Our results highlight that individuals may also need to move large distances among streams and habitats to capitalize on patchily distributed foraging opportunities. Therefore habitat fragmentation and homogenization may have even farther reaching effects on the productivity and long-term persistence of stream-dwelling fish populations than previously recognized.

Table 3.1: Movement rates of individual Arctic grayling and rainbow trout among streams. Fish moving to "unknown" streams are individuals last seen leaving a site and were not detected again in that year (either re-entering the same site or emigrating to another site). Fish moving "from" and "to" the same stream (e.g., Hidden to Hidden) are individuals that were last detected entering that stream; however, these fish could have immigrated from another site or left a stream and came back, but were not detected at another site. Movement rates were similar between 2011 and 2012, and thus combined.

			To Stream				
Species	From Stream	Sample size (N)	Hidden	Lynx	Teal	Stovall	Unknown
Arctic grayling	Hidden	98	0.48	0.21	0.00	0.05	0.26
	Lynx	94	0.31	0.47	0.04	0.00	0.18
	Teal	13	0.31	0.31	0.08	0.23	0.08
	Stovall	76	0.05	0.32	0.04	0.22	0.37
Rainbow trout	Hidden	49	0.31	0.06	0.00	0.00	0.63
	Lynx	171	0.04	0.39	0.01	0.00	0.56
	Teal	6	0.00	0.17	0.17	0.17	0.50
	Stovall	5	0.00	0.00	0.00	0.00	1.00

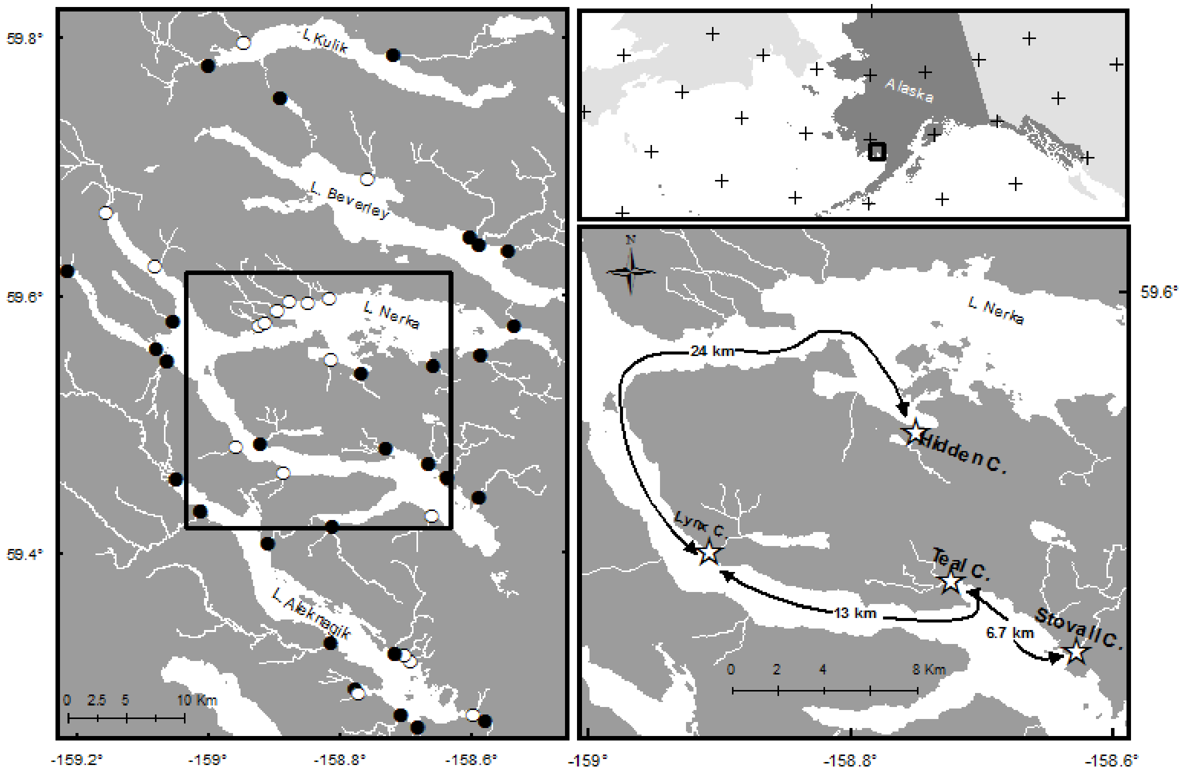

Figure 3.1: Map of the Wood River system, southwestern Alaska. Left panel denotes streams throughout the watershed where Arctic grayling and rainbow trout are either present (●) or absent (○) during summer months. Lower-right panel denotes streams equipped with stationary PIT-tag antenna arrays.

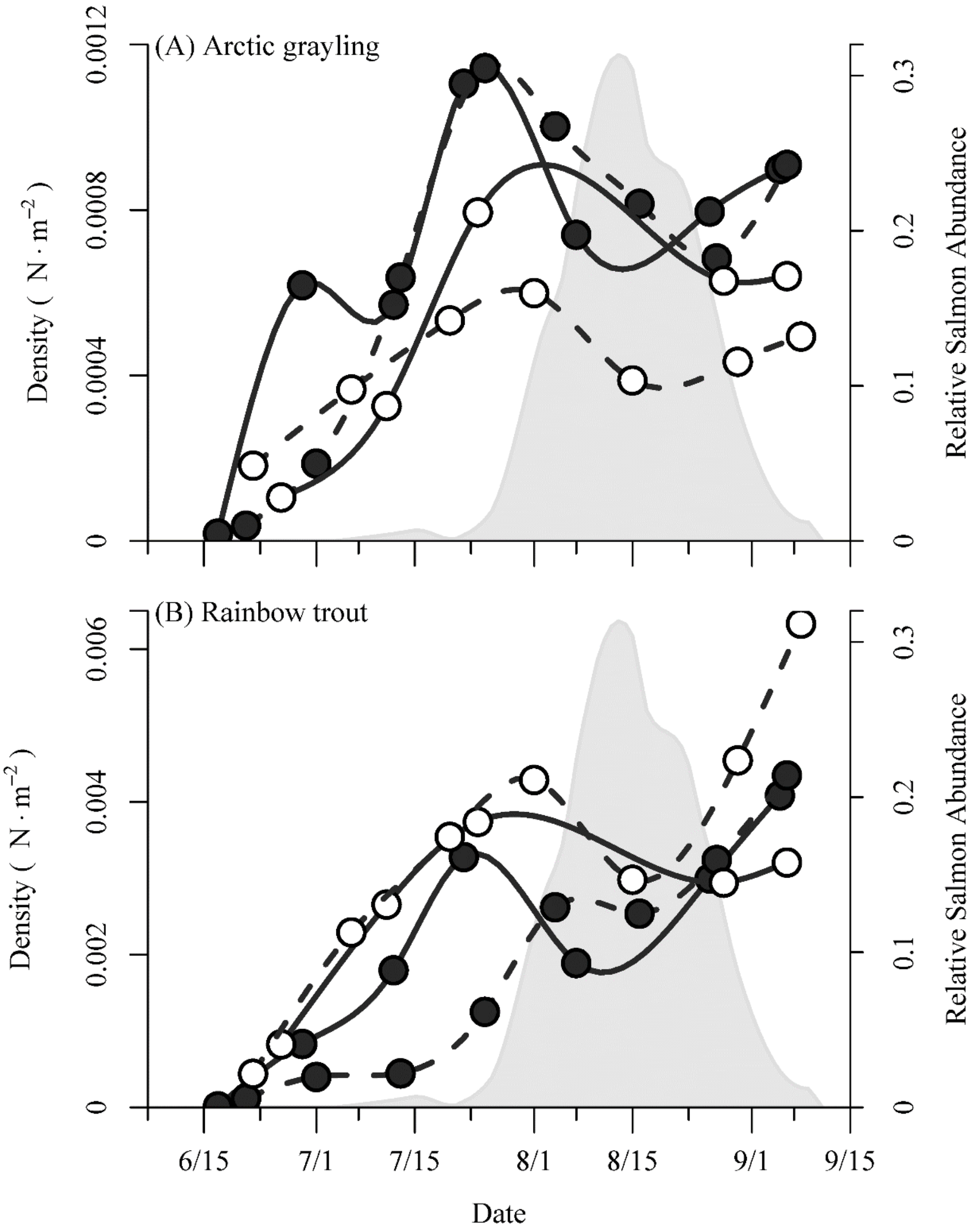

Figure 3.2: Density (N · m^{-2}) of (A) Arctic grayling and (B) rainbow trout in Hidden (●) (black circle) and Lynx (○) during 2010 (—) and 2011 (- -) estimated via snorkel surveys. The shaded area is the relative abundance of sockeye salmon averaged for both streams and years.

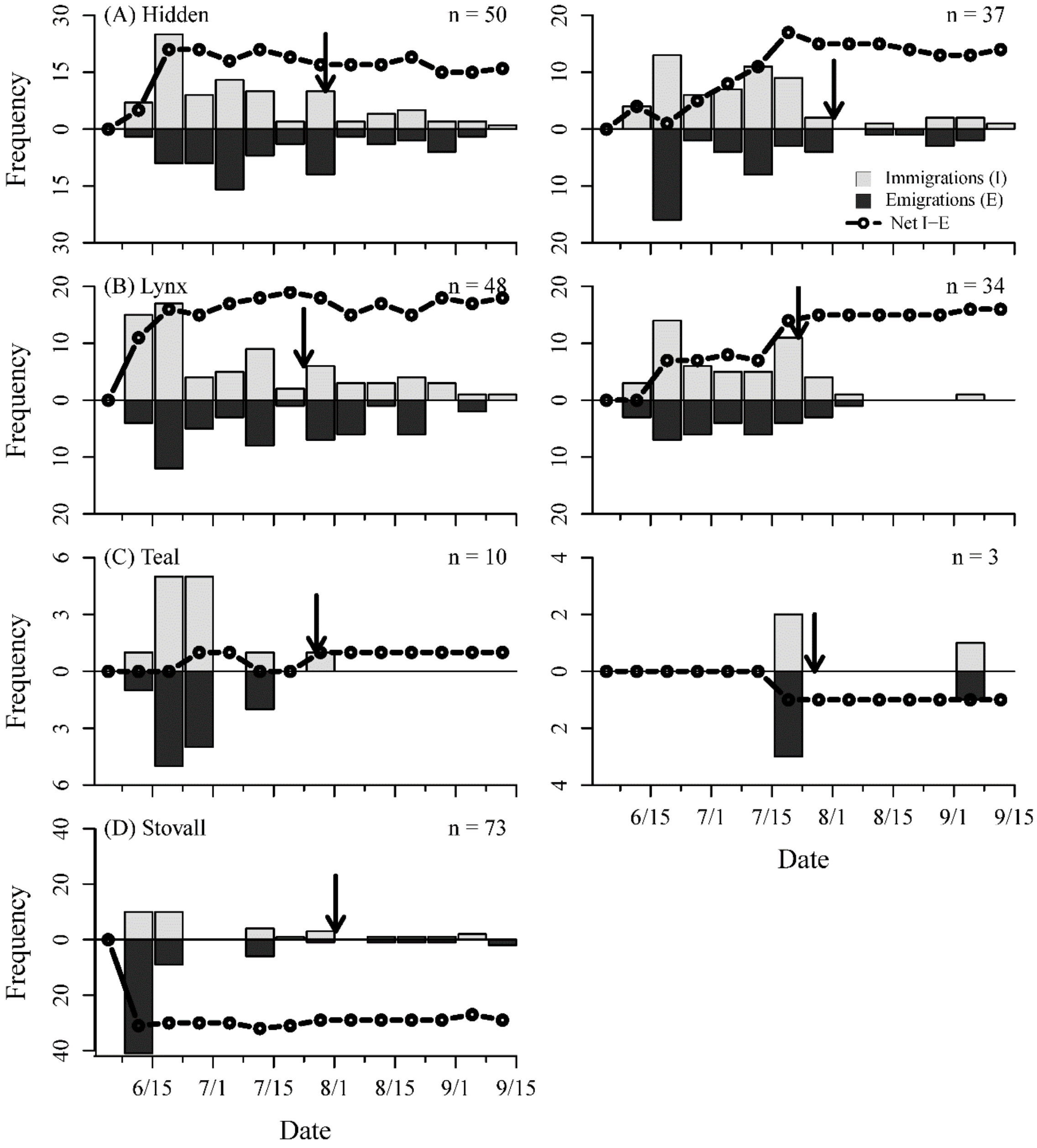

Figure 3.3: Immigrations (gray bars), emigrations (black bars), and the net immigrations and emigrations (black line) of PIT-tagged Arctic grayling during 2012 (left) and 2011 (right) in (A) Hidden, (B) Lynx, (C) Teal, and (D) Stovall creeks. The number (n) on each panel denotes the total number of individual fish and the vertical arrow is the date of sockeye salmon entry.

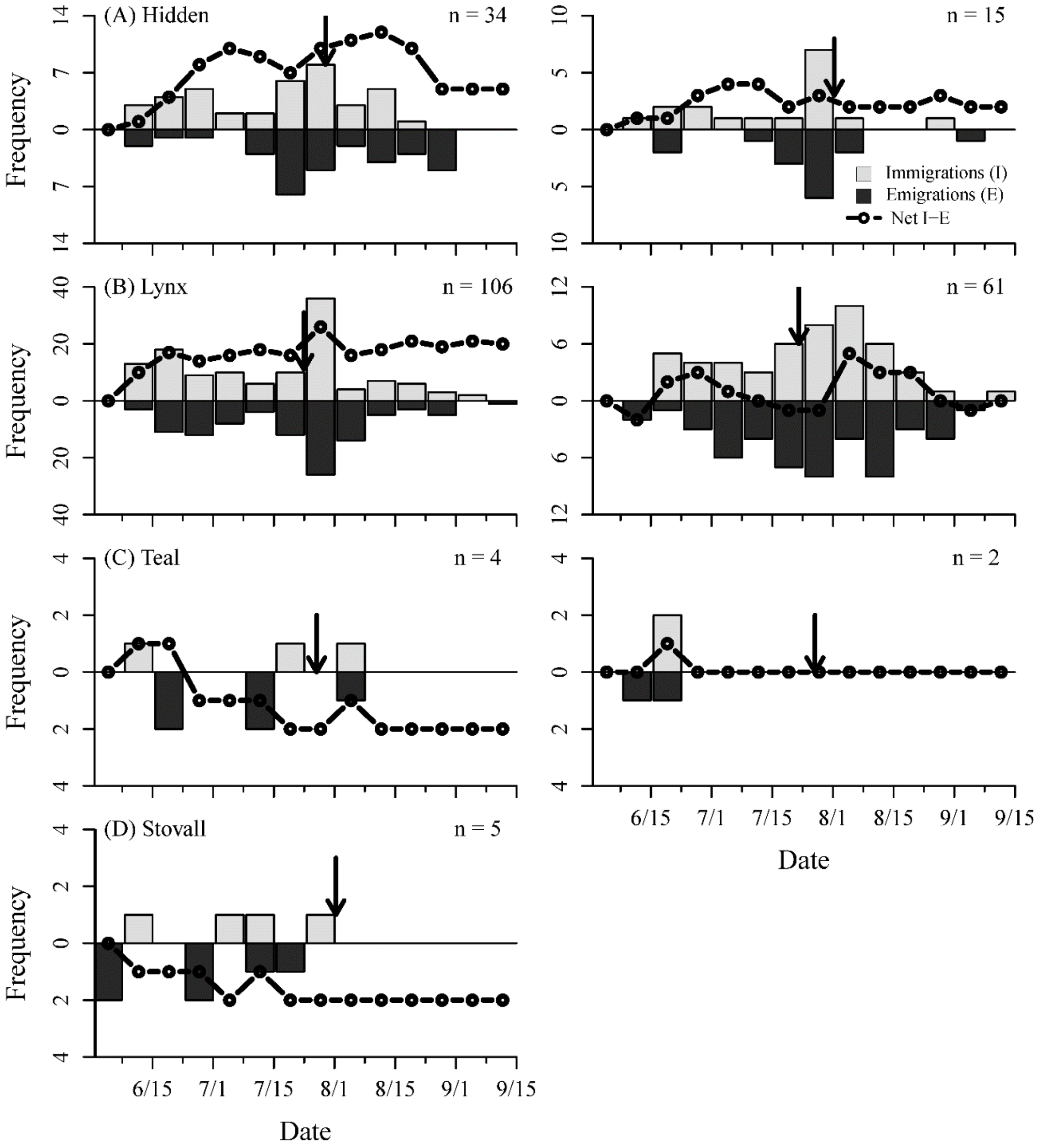

Figure 3.4: Immigrations (gray bars), emigrations (black bars), and the cumulative sum of immigrations and emigrations (black line) of PIT-tagged rainbow trout during 2012 (left) and 2011 (right) in (A) Hidden, (B) Lynx, (C) Teal, and (D) Stovall creeks. The number (n) on each panel denotes the total number of individual fish and the vertical arrow is the date of sockeye salmon entry.

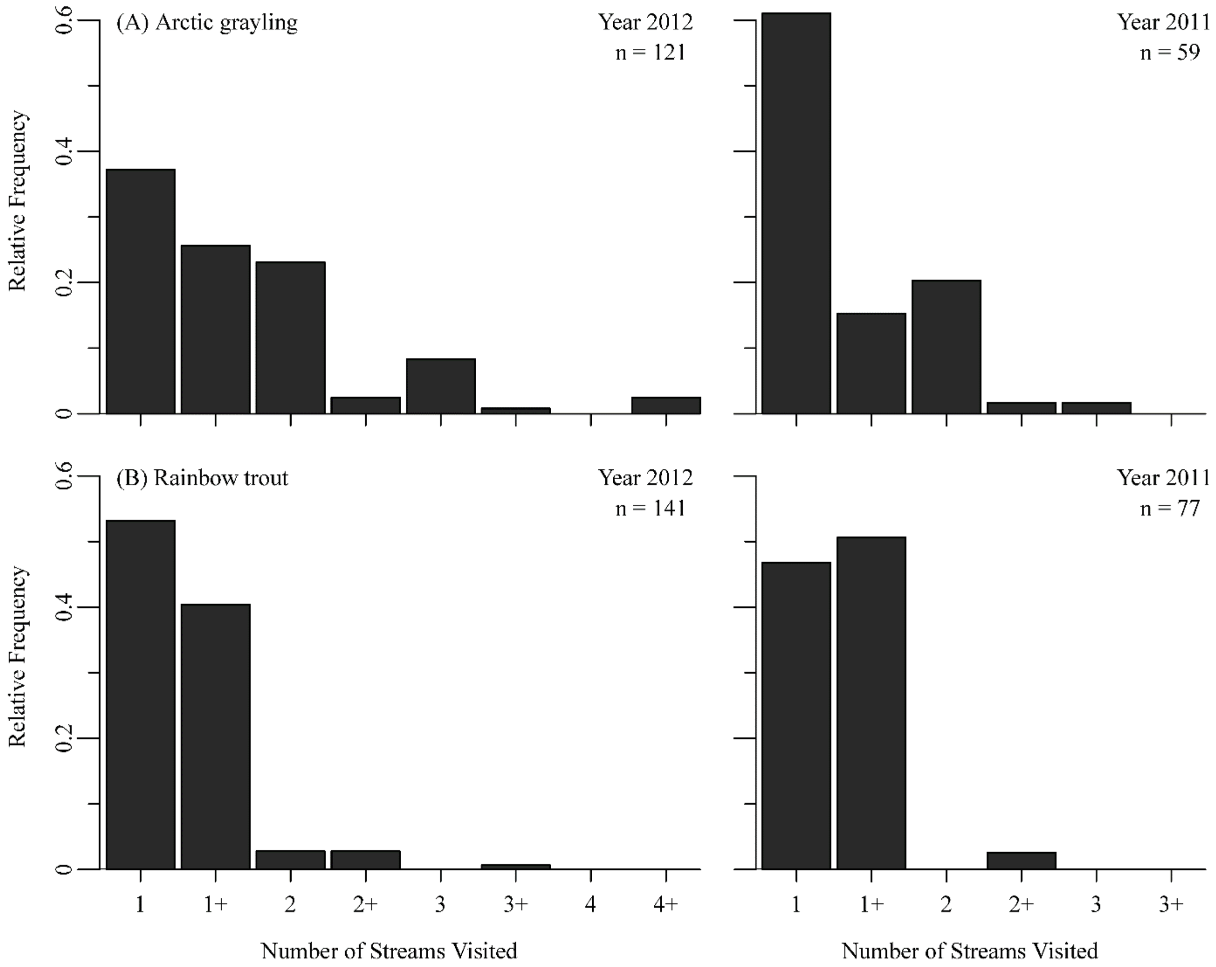

Figure 3.5: Relative number of streams visited by (A) Arctic grayling and (B) rainbow trout in 2012 (left) and 2011 (right). Fish that visited a "+" number of streams (e.g., 1+) were last seen leaving a site and were not detected again in that year. Note: fish could have visited a site more than once (e.g., Hidden->Lynx->Hidden), but only unique visits were counted.

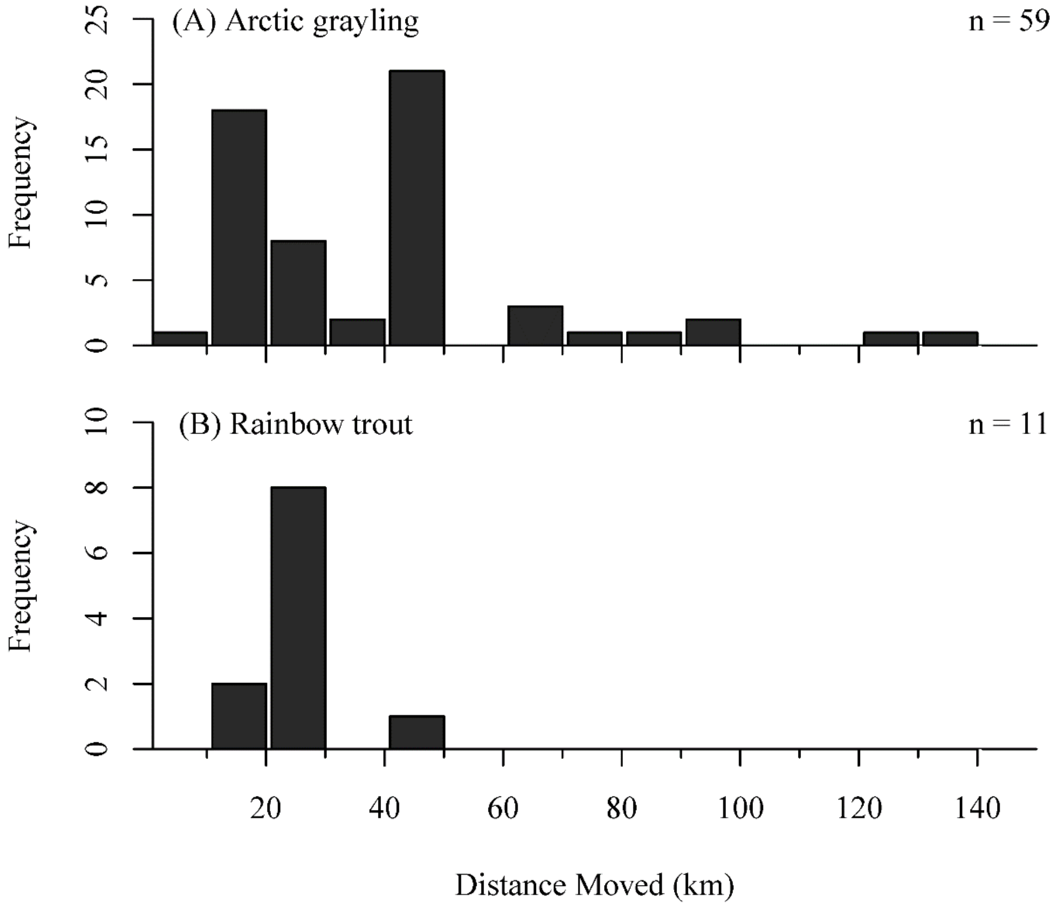

Figure 3.6: Minimum cumulative distance (km) of inter-stream movements by individual (A) Arctic grayling and (B) rainbow trout for years 2011 and 2012 combined. Note: these distance estimates only include fish moving among monitored sites.

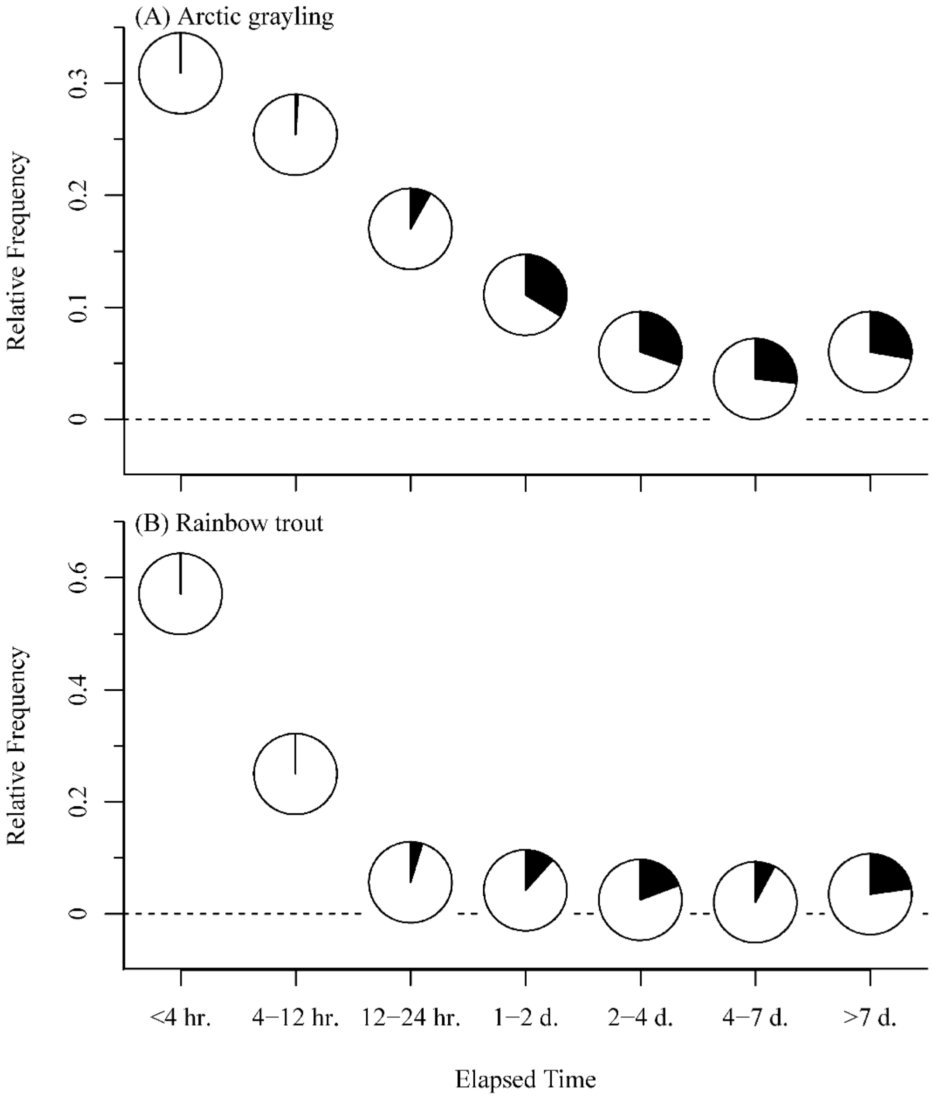

Figure 3.7: Relative frequency of transit time between movements as a function of whether the movement was to a new stream. Transit time was calculated as the time elapsed between a downstream (emigration) and upstream (immigration) movement for (A) Arctic grayling and (B) rainbow trout. The black portion of the pie represents the relative proportion that were inter-stream movements (i.e., the white portion represents fish that emigrate from a stream and then immigrated back into the same stream, but were not detected at another site between those two movements).

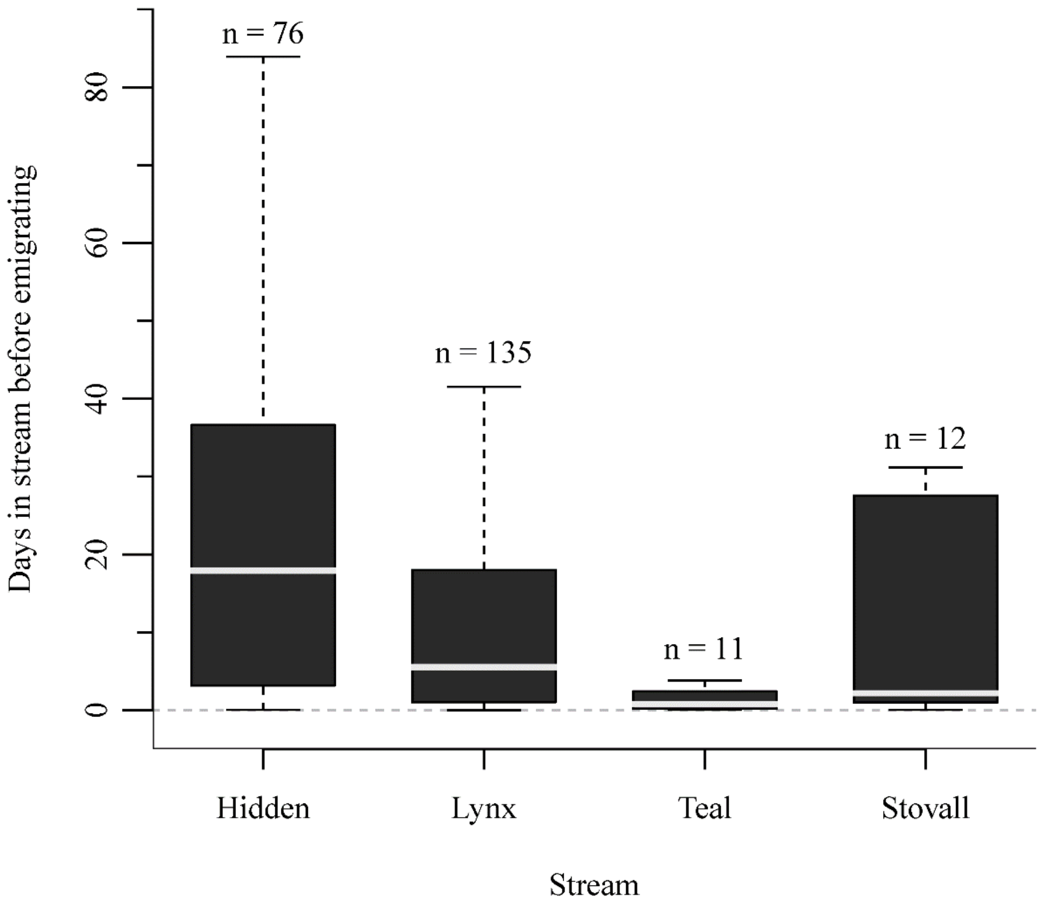

Figure 3.8: Duration of time (days) individual fishes spent in a stream prior leaving and immigrating to another stream. The light gray line in the box is the median; the lower and upper edges of the box are the lower and upper quartiles (25th and 75th percentiles, respectively; the smallest and largest observations (in the range not considered as outliers) are shown as the error bars. Data for Arctic grayling and rainbow trout collected in 2011 and 2012 were combined as there were no significant difference in duration of time between species or year.

References

Adelman, I. R. 1987. Uptake of radioactive amino acids as indices of current growth rate of fish: a review. Pages 65–79 *in* R. C. Summerfelt and G. E. Hall. 1987, editors. Age and growth of fish. Iowa State University Press, Ames, Iowa.

Albanese, B., P. L. Angermeier, and S. Dorai-Raj. 2004. Ecological correlates of fish movement in a network of Virginia streams. Canadian Journal of Fisheries and Aquatic Sciences 61:857–869.

Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447–482 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland

Armstrong, J. B. 2010. Comment on "Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)" Appears in Canadian Journal of Fisheries and Aquatic Sciences 66: 1546–1553. Canadian Journal of Fisheries and Aquatic Sciences 67:2052–2054.

Armstrong, J. B., and D. E. Schindler. 2011. Excess digestive capacity in predators reflects a life of feast and famine. Nature 476:84–87.

Armstrong, J. B., and D. E. Schindler. 2013. Going with the flow: spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. Ecosystems 16:1429–1441.

Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology 91:1445–1454.

Armstrong, J. B., D. E. Schindler, C. P. Ruff, G. T. Brooks, K. T. Bentley, and C. E. Torgersen. 2013. Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. Ecology 94:2066–2075.

Baker, T. T., F. W. West, G. B. Buck, X. Zhang, S. Fleischman, and J. Erickson. 2009. Review of Salmon Escapement Goals in Bristol Bay, Alaska, 2009. Alaska Department of Fish and Game Fishery Manuscript Series No. 09-05, Anchorage, Alaska, USA.

Beckman, B. R. 2011. Perspectives on concordant and discordant relations between insulin-like growth factor 1 (IGF1) and growth in fishes. General and Comparative Endocrinology 170:233–252.

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. BioScience 54:413–427.

Bentley, K.T., and D.E. Schindler. 2013. Body condition correlates with instantaneous growth in stream-dwelling rainbow trout and Arctic grayling. Transactions of American Fisheries Society 142:747-755.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, R. Zhang, C. P. Ruff, and P. J. Lisi. 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. Ecosphere 3(12):113. http://dx.doi.org/10.1890/ES12-00231.1

Berg, O. K., G. Rød, Ø. Solem, and A. G. Finstad. 2011. Pre-winter lipid stores in brown trout *Salmo trutta* along altitudinal and latitudinal gradients. Journal of Fish Biology 79:1156–1166.

Bergeron, P., D. Reale, M. Humphries, and D. Garant. 2011. Anticipation and tracking of pulsed resources drive population dynamics in eastern chipmunks. Ecology 92:2027–2034.

Bervoets, L., and R. Blust. 2003. Metal concentrations in water, sediment and gudgeon (*Gobio gobio*) from a pollution gradient: relationship with fish condition factor. Environmental Pollution 126:9–19.

Bestgen, K. R., and J. M. Bundy. 1998. Environmental factors affect daily increment deposition and otolith growth in young Colorado squawfish. Transactions of the American Fisheries Society 127:105–117.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53:164–173.

Bilby, R. E., B. R. Fransen, J. K. Walter, C. J. Cederholm, and W. J. Scarlett. 2001. Preliminary Evaluation of the Use of Nitrogen Stable Isotope Ratios to Establish Escapement Levels for Pacific Salmon. Fisheries 26:6–14.

Biro, P. A., and J. R. Post. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proceedings of the National Academy of Sciences 105:2919–2922.

Bond, M., C. Hanson, R. Baertsch, S. Hayes, and R. B. MacFarlane. 2007. A new low-cost instream antenna system for tracking passive integrated transponder (PIT)-tagged fish in small streams. Transactions of the American Fisheries Society 136:562–566.

Brink, S. R. 1995. Summer habitat ecology of rainbow trout in the Middle Fork of the Gulkana River, Alaska. M.S. Thesis, University of Alaska, Fairbanks.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Cade, B. S., J. W. Terrell, and B. C. Neely. 2011. Estimating geographic variation in allometric growth and body condition of blue Suckers with quantile regression. Transactions of the American Fisheries Society 140:1657–1669.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129–136.

Chícharo, M. A., and L. Chícharo. 2008. RNA:DNA ratio and other nucleic acid derived indices in marine ecology. International Journal of Molecular Sciences 9:1453–1471.

Clarke, K. 1993. Non-parametric multivariate analyses of changes in community structure. Australian journal of ecology 18:117–143.

Cone, R. S. 1989. The need to reconsider the use of condition indices in fishery science. Transactions of the American Fisheries Society 118:510–514.

Cooke, S. J., J. F. Schreer, D. H. Wahl, and D. P. Philipp. 2002. Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth. American Fisheries Society Symposium 31: 489–512.

Couture, P., J. D. Dutil, and H. Guderley. 1998. Biochemical correlates of growth and condition in juvenile Atlantic cod (*Gadus morhua*) from Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55:1591–1598.

Cox, M. K., and K. J. Hartman. 2005. Nonlethal estimation of proximate composition in fish. Canadian Journal of Fisheries and Aquatic Sciences 62:269–275.

Crowder, L. B., E. L. Hazen, N. Avissar, R. Bjorkland, C. Latanich, and M. B. Ogburn. 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. Annual Review of Ecology, Evolution, and Systematics 39:259–278.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen der Internationale Vereinigung fu¨r Theoretische und Angewandte Limnologie 18:1–158.

Cunjak, R. A., and G. Power. 1987. The feeding and energetics of stream-resident trout in winter. Journal of Fish Biology 31:493–511.

De Raedemaecker, F., D. Brophy, I. O'Connor, and B. O'Neill. 2012. Dependence of RNA: DNA ratio and Fulton's *K* condition indices on environmental characteristics of plaice and dab nursery grounds. Estuarine, Coastal and Shelf Science 98:60–70.

Denton, K. P., H. B. Rich, and T. P. Quinn. 2009. Diet, Movement, and Growth of Dolly Varden in Response to Sockeye Salmon Subsidies. Transactions of the American Fisheries Society 138:1207–1219.

Delgado, M. M., K. A. Bartoń, D. Bonte, and J. M. J. Travis. 2014. Prospecting and dispersal: their eco-evolutionary dynamics and implications for population patterns. Proceedings of the Royal Society B: Biological Sciences 281:20132851.

DeVries, D. R., R. V. Frie. 1996. Determination of age and growth. Pages 483–512 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Duan, C. 1997. The insulin-like growth factor system and its biological actions in fish. American Zoologist 37:491–503.

Duffield, J. W., C. J. Neher, and D. A. Patterson. 2007. Economics of wild salmon ecosystems: Bristol Bay, Alaska. Trout Unlimited, Final Report, Juneau, Alaska.

Dye, J. E. 2005. Radio tracking study of rainbow trout in the Wood River watershed, Bristol Bay, Alaska. Alaska Department of Fish and Game Fishery Manuscript Series No. 05-05, Anchorage, Alaska, USA.

Eastman, D. E. 1996. Response of freshwater fish communities to spawning sockeye salmon (*Oncorhynchus nerka*). University of Washington.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2001. Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecology of Freshwater Fish 10:1–10.

Elliott, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. The Journal of Animal Ecology:923–948.

Essington, T. E., T. P. Quinn, V. E. Ewert. 2000. Intra-and inter-specific competition and the reproductive success of sympatric Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 57:205–213.

Essington, T. E., P. W. Sorensen, and D. G. Paron. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. Canadian Journal of Fisheries and Aquatic Sciences 55:2310–2316.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.

Fechhelm, R. G., W. B. Griffiths, W. J. Wilson, B. J. Gallaway, and J. D. Bryan. 1995. Intra- and interseasonal changes in the relative condition and proximate body composition of broad whitefish from the Prudhoe Bay region of Alaska. Transactions of the American Fisheries Society 124:508–519.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20:273–287.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Fryxell, J. M., J. F. Wilmshurst, A. R. E. Sinclair, D. T. Haydon, R. D. Holt, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. Ecology Letters 8:328–335.

Gabelhouse Jr, D. W. 1991. Seasonal changes in body condition of white crappies and relations to length and growth in Melvern Reservoir, Kansas. North American Journal of Fisheries Management 11:50–56.

Garvey, J. E., K. G. Ostrand, and D. H. Wahl. 2004. Energetics, predation, and ration affect size-dependent growth and mortality of fish during winter. Ecology 85:2860–2871.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917–928.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51:2626–2637.

Heggenes, J. 1988. Effects of short-term flow fluctuations on displacement of, and habitat use by, brown trout in a small stream. Transactions of the American Fisheries Society 117:336–344.

Grant, G. C. 1996. RNA-DNA ratios in white muscle tissue biopsies reflect recent growth rates of adult brown trout. Journal of Fish Biology 48:1223–1230.

Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473–1483.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25:15–21.

Guy, C. S., H. L. Blankenship, L. A. Nielsen. 1996. Tagging and marking. Pages 353–383 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin, Sea Grant Institute, Madison, Wisconsin, USA.

Hartman, K. J., and F. J. Margraf. 2006. Relationships among condition indices, feeding and growth of walleye in Lake Erie. Fisheries Management and Ecology 13:121–130.

Heintz, R. A., B. D. Nelson, J. Hudson, M. Larsen, L. Holland, and M. Wipfli. 2004. Marine subsidies in freshwater: effects of salmon carcasses on lipid class and fatty acid composition of juvenile coho salmon. Transactions of the American Fisheries Society 133:559–567.

Henderson, B. A., N. Collins, G. E. Morgan, and A. Vaillancourt. 2003. Sexual size dimorphism of walleye (*Stizostedion vitreum vitreum*). Canadian Journal of Fisheries and Aquatic Sciences 60:1345–1352.

Hewett, S. W., and C. E. Kraft. 1993. The Relationship between growth and consumption: comparisons across fish populations. Transactions of the American Fisheries Society 122:814–821.

Hilborn, R. 2006. Fisheries success and failure: the case of the Bristol Bay salmon fishery. Bulletin of Marine Science 78:487–498.

Hilborn, R., and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty/Book and Disk. Springer.

Hilderbrand, G., C. Schwartz, C. Robbins, M. Jacoby, T. Hanley, S. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77:132–138.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Holt, R. D. 2008. Theoretical perspectives on resource pulses. Ecology 89:671–681.

Holtgrieve, G. W., D. E. Schindler, C. P. Gowell, C. P. Ruff, and P. J. Lisi. 2010. Stream geomorphology regulates the effects on periphyton of ecosystem engineering and nutrient enrichment by Pacific salmon. Freshwater Biology 55:2598–2611.

Isaak, D. J., and W. A. Hubert. 2004. Nonlinear response of trout abundance to summer stream temperatures across a thermally diverse montane landscape. Transactions of the American Fisheries Society 133:1254–1259.

Jacobs, G. R., J. E. Breck, and T. O. Höök. 2011. Growth-mediated seasonal energy allocation patterns of young-of-year largemouth bass (*Micropterus salmoides*). Journal of Freshwater Ecology:1–14.

Jakob, E. M., S. D. Marshall, and G. W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Johnston, T. A., and R. A. Cunjak. 1999. Dry mass–length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada. Freshwater Biology 41:653–674.

Kebus, M. J., M. T. Collins, M. S. Brownfield, C. H. Amundson, T. B. Kayes, and J. A. Malison. 1992. Effects of rearing density on the stress response and growth of rainbow trout. Journal of Aquatic Animal Health 4:1–6.

Kline, T. C., J. J. Goering, O. A. Mathisen, P. H. Poe. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}N$ and $\delta^{13}C$ evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 50:2350–2365.

Lapointe, N. W. R., S. J. Cooke, J. G. Imhof, D. Boisclair, J. M. Casselman, R. A. Curry, O. E. Langer, R. L. McLaughlin, C. K. Minns, J. R. Post, M. Power, J. B. Rasmussen, J. D. Reynolds, J. S. Richardson, and W. M. Tonn. 2013. Principles for ensuring healthy and productive freshwater ecosystems that support sustainable fisheries. Environmental Reviews 22:1–25.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.

Levi, T., C. T. Darimont, M. MacDuffee, M. Mangel, P. Paquet, and C. C. Wilmers. 2012. Using grizzly bears to assess harvest-ecosystem tradeoffs in salmon fisheries. PLoS Biology 10:e1001303.

Liao, H., C. L. Pierce, D. H. Wahl, J. B. Rasmussen, and W. C. Leggett. 1995. Relative weight (Wr) as a field assessment tool: relationships with growth, prey biomass, and environmental conditions. Transactions of the American Fisheries Society 124:387–400.

Lichatowich, J. A. 2001. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, New York.

Lisi, P. J., D. E. Schindler, K. T. Bentley, and G. R. Pess. *In review*. Association between geomorphic attributes of watersheds, water temperature, and salmon spawn timing in Alaskan streams. Geomorphology.

Lleonart, J., J. Salat, and G. J. Torres. 2000. Removing allometric effects of body size in morphological analysis. Journal of Theoretical Biology 205:85–93.

Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology 88:140–148.

McGarigal, K. 2011. BIOSTATS documentation. (*www.umass.edu/landeco/teaching/ecodata/labs/biostats.pdf).*

Meka, J. M., E. E. Knudsen, D. C. Douglas, and R. B. Benter. 2003. Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. Transactions of the American Fisheries Society 132:717–732.

Milner, N. J., J. M. Elliott, J. D. Armstrong, R. Gardiner, J. S. Welton, and M. Ladle. 2003. The natural control of salmon and trout populations in streams. Fisheries Research 62:111–125.

Moore, J. W., D. E. Schindler, J. L. Carter, J. Fox, J. Griffiths, G. W. Holtgrieve. 2007. Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. Ecology 88:1278–1291.

Moore, J. W., and D. E. Schindler. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. Journal of Animal Ecology 77:275–284.

Moore, J. W., and D. E. Schindler. 2010. Spawning salmon and the phenology of emergence in stream insects. Proceedings of the Royal Society - Biological Sciences 277:1695–1703.

Moore, J. W., D. E. Schindler, and C. P. Ruff. 2008. Habitat saturation drives thresholds in stream subsidies. Ecology 89:306–312.

Morgan, M. J. 2004. The relationship between fish condition and the probability of being mature in American Plaice (*Hippoglossoides Platessoides*). ICES Journal of Marine Science 61:64–70.

Morita, K., and S. Yamamoto. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. Conservation Biology 16:1318–1323.

Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the Upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797–810.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98:166–170.

Northcote, T. G. 1997. Potamodromy in Salmonidae: Living and moving in the fast lane. North American Journal of Fisheries Management 17:1029–1045.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual review of ecology and systematics 4:25–51.

Oksanen, J., R. Kindt, P. Legendre, and R. B. O’Hara. 2007. The vegan package. vegan: community ecology package. R package version 1.9-25. (http://cran.r-project.org/).

Ombredane, D., J. L. Bagliniere, and F. Marchand. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile brown trout (*Salmo trutta* L.) and their use for studying movement in a small river. Hydrobiologia 371:99–106.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology & Evolution 15:232–237.

Peig, J., and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883-1891.

Peig, J., and A. J. Green. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Functional Ecology 24:1323-1332.

Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1992. Trophic Interactions in Temperate Lake Ecosystems: A Test of Food Chain Theory. The American Naturalist 140:59–84.

Peters, R. H. 1986. The ecological implications of body size. Cambridge University Press.

Piccolo, J. J., M. D. Adkison, and F. Rue. 2009. Linking Alaskan Salmon Fisheries Management with Ecosystem-based Escapement Goals: A Review and Prospectus. Fisheries 34:124–134.

Pickering, A. D., T. G. Pottinger, and P. Christie. 1982. Recovery of the brown trout, *Salmo trutta* L., from acute handling stress: a time-course study. Journal of Fish Biology 20:229–244.

Pikitch, E., E. A. Santora, A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, Dayton, P, others, P. Doukakis, D. Fluharty, and B. Heheman. 2004. Ecosystem-based fishery management. Science 305:346–347.

Pinheiro J., D. Bates, S. DebRoy, and D. Sarkar. 2009. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-96. (http://cran.r-roject.org/web/packages/nlme/index.html).

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual review of ecology and systematics 28:289–316.

Pope, K. L., and C. G. Kruse. 2007. Condition. Pages 423–471 *in* M. L. Brown and C. S. Guy, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Porto, L. M., R. L. McLaughlin, and D. L. G. Noakes. 1999. Low-head barrier dams restrict the movements of fishes in two Lake Ontario streams. North American Journal of Fisheries Management 19:1028–1036.

Post, J. R., and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040–1051.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.

Quinn, T. P., and N. P. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon

(*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences 53:1555–1564.

Quinn, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. (www.R-project.org)

Rahel, F. J., and W. A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain–Great Plains stream: biotic zonation and additive patterns of community change. Transactions of the American Fisheries Society 120:319–332.

Railsback, S. F., and K. A. Rose. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Transactions of the American Fisheries Society 128:241–256.

Rasmussen, J. B., A. N. Krimmer, A. J. Paul, and A. Hontela. 2012. Empirical relationships between body tissue composition and bioelectrical impedance of brook trout *Salvelinus fontinalis* from a Rocky Mountain Stream. Journal of Fish Biology 80:2317–2327.

Reimers, N. 1963. Body condition, water temperature, and over-winter survival of hatchery-reared trout in Convict Creek, California. Transactions of the American Fisheries Society 92:39–46.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Board of Canada 11:559–623.

Rinella, D. J., M. S. Wipfli, C. A. Stricker, R. A. Heintz, and M. J. Rinella. 2012. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Canadian Journal of Fisheries and Aquatic Sciences 69:73–84.

Rogers, D. E., and B. J. Rogers. 1998. Spawning ground surveys in the Wood River Lakes. Alaska Salmon Program, Technical Report No. FRI-UW-9803, University of Washington, Seattle, WA.

Rogers, L. A., and D. E. Schindler. 2008. Asynchrony in population dynamics of sockeye salmon in southwest Alaska. Oikos 117:1578–1586.

Rogers, L. A., and D. E. Schindler. 2011. Scale and the detection of climatic influences on the productivity of salmon populations. Global Change Biology 17:2546–2558.

Ruff, C. P., D. E. Schindler, J. B. Armstrong, K. T. Bentley, G. T. Brooks, G. W. Holtgrieve, M. T. McGlauflin, J. E. Seeb, and C. E. Torgersen. 2011. Temperature-associated population diversity in salmon confers benefits to mobile consumers. Ecology 92:2073–2084.

Sabo, J. L., J. L. Bastow, and M. E. Power. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. Journal of the North American Benthological Society 21:336–343.

Scheuerell, M. D., J. W. Moore, D. E. Schindler, and C. J. Harvey. 2007. Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52:1944–1956.

Schindler, D. E., D. E. Rogers, M. D. Scheuerell, and C. A. Abrey. 2005. Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. Ecology 86:198–209.

Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. Nature 465:609-612.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience 41:704–712.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. American Fisheries Society Symposium 17:360-370.

Schmetterling, D. A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport upstream of Milltown Dam, Montana. North American Journal of Fisheries Management 23:721–731.

Schmidt, K. A., and R. S. Ostfeld. 2008. Numerical and behavioral effects within a pulse-driven system: consequences for shared prey. Ecology 89:635–646.

Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163.

Simpkins, D. G., W. A. Hubert, C. M. Del Rio, and D. C. Rule. 2003. Physiological responses of juvenile rainbow trout to fasting and swimming activity: effects on body composition and condition indices. Transactions of the American Fisheries Society 132:576–589.

Stanford, J. A., M. S. Lorang, and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. Proceedings of the International Society of Limnology 29:123–136.

Stevenson, R. D., and W. A. Woods. 2006. Condition indices for conservation: new uses for evolving tools. Integrative and Comparative Biology 46:1169–1190.

Summerfelt, R. C., and G. E. Hall. 1987. Age and Growth of Fish. Iowa State University Press, Ames, Iowa.

Sutton, S. G., T. P. Bult, and R. L. Haedrich. 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. Transactions of the American Fisheries Society 129:527–538.

Thompson, K. G., E. P. Bergersen, R. B. Nehring, and D. C. Bowden. 1997. Long-term effects of electrofishing on growth and body condition of brown trout and rainbow trout. North American Journal of Fisheries Management 17:154–159.

Tockner, K., A. Paetzold, U. Karaus, C. Claret, and J. Zettel. 2006. Ecology of braided rivers. Braided Rivers. Blackwell Science. Oxford, UK. 36:339–359.

Tyus, H. M., and N. J. Nikirk. 1990. Abundance, growth, and diet of channel catfish, *Ictalurus punctatus*, in the Green and Yampa Rivers, Colorado and Utah. The Southwestern Naturalist 35:188–198.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Venturelli, P. A., and W. M. Tonn. 2006. Diet and growth of northern pike in the absence of prey fishes: initial consequences for persisting in disturbance-prone lakes. Transactions of the American Fisheries Society 135:1512–1522.

Wang, G., N. T. Hobbs, R. B. Boone, A. W. Illius, I. J. Gordon, J. E. Gross, and K. L. Hamlin. 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. Ecology 87:95–102.

Warren, M. L., and M. G. Pardew. 1998. Road crossings as barriers to small-stream fish movement. Transactions of the American Fisheries Society 127:637–644.

Weatherley, A. H., H. Gill, and J. M. Casselman. 1987. The biology of fish growth. Academic Press, London.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional ecology 3:385–397.

Willis, D. W. 1989. Proposed standard length–weight equation for northern pike. North American Journal of Fisheries Management 9:203–208.

Willson, M. F., and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology 9:489–497.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35:373–387.

Wipfli, M. S., J. P. Hudson, J. P. Caouette, and D. T. Chaloner. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132:371–381.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–151.

Zerrenner, A., D. C. Josephson, and C. C. Krueger. 1997. Growth, mortality, and mark retention of hatchery brook trout marked with visible implant tags, jaw tags, and adipose fin clips. The Progressive Fish Culturist 59:241–245.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, New York.

Appendix

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 each 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. Over the three years, the same snorkeler performed each survey.

For each year, abundance densities were 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/m^2). Biomass densities (kg/m^2) were estimated for each individual fish calculating the average mass for each individual fish, based on the length-mass relationship developed for each species (Bentley and Schindler 2013), 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.

Table A1. Biomass (kg/m^2) and abundance (no./m^2) densities estimates for Arctic grayling and rainbow trout in Hidden and Lynx creeks from 2010-2012. Estimates are from surveys conducted in late-August in all years to correspond with the peak of the salmon run.

	Arctic Grayling				Rainbow trout			
	Biomass		Abundance		Biomass		Abundance	
Year	Hidden	Lynx	Hidden	Lynx	Hidden	Lynx	Hidden	Lynx
2010	1.39	1.03	0.0008	0.0006	2.36	2.34	0.0030	0.0029
2011	1.44	0.76	0.0007	0.0004	3.41	2.33	0.0032	0.0045
2012	2.86	0.89	0.0014	0.0011	1.74	2.30	0.0034	0.0043
Average	1.90	0.89	0.0009	0.0007	2.50	2.33	0.0032	0.0039

Appendix B: List of dietary items used in diet analyses

Table B1. List of 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
Flesh	*Oncorhynchus nerka*	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 (Figure 2.2). 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}; $U_{158,270}$ = 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}; $U_{158, 270}$ = 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 ($U_{95,185}$ = 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 ($U_{95,185}$ = 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}; $U_{88,139}$ = 8897, p<0.0001), while the small ration of salmon derived prey items was not ($t_{88,139}$ =6251, p=0.530). In high salmon years, the salmon derived resources constituted 63and 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 ($U_{41,12}$ = 252, p=0.908), nor were the rations of salmon ($U_{41,12}$ = 248, p=0.974) and non-salmon prey ($U_{41,12}$ = 261, p=0.758).

Appendix D: AIC model results for growth as a function of salmon density

Table D1. 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 Creek, Bristol Bay, Alaska.

Species (Stream) and Model	K	-2*l*	AIC	ΔAIC	w_i
Arctic grayling (Hidden)					
Sigmoid: SD + T + T^2	8	-1882.30	-3748.6	4.46	0.0628
Sigmoid: SD + T	7	-1882.28	-3750.56	2.5	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	0.0345
Arctic grayling (Lynx)					
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)					
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	-6223.77	14.41	0.0005
Power: SD + T	6	-3119.72	-6227.43	10.75	0.0031
Power: SD	5	-3120.43	-6230.86	7.32	0.0169
Linear: SD + T + T^2	6	-3118.49	-6224.97	13.21	0.0009
Linear: SD + T	5	-3117.51	-6225.02	13.16	0.0009
Linear: SD	4	-3119.21	-6230.41	7.77	0.0135
Rainbow trout (Lynx)					
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	-3009.61	-6003.21	9.85	0.0050
Linear: SD	4	-3010.61	-6007.22	5.84	0.0372

Notes : For each model, *K* is the number of estimated parameters, ΔAIC is the difference in AIC relative to the best model, -2*l* is twice the negative log-likelihood, and w_i is the AIC weight.

Appendix E: Parameter estimates of the best-fit mixed-effect growth models.

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 (Stream)	y_o	a	s_o	b
Arctic grayling (Hidden)	0.0050 (0.0015, 0.0086)	0.0026 (0.0020, 0.0032)	0.2551 (0.2274, 0.2828)	15.54 (0.0001, 51.06)
Arctic grayling (Lynx)	0.0039 (0.0035, 0.0043)	0.0033 (0.0017, 0.0050)	0.2708 (0.0001, 1.306)	22.87 (0.0001, 580.03)
Rainbow trout (Hidden)	0.0171 (0.0162, 0.0179)	0.0060 (0.0048, 0.0073)	0.2436 (0.2401, 0.2471)	92.87 (0.0001, 207.5)
Rainbow trout (Lynx)	0.0104 (0.0083, 0.0125)	0.0217 (0.0151, 0.0283)	0.4896 (0.0317, 0.9475)	-

Appendix F: Distribution of PIT-tags deployed and returned among species, sites, and years.

Table F1. Number of Arctic grayling and rainbow trout tagged and returned (in subsequent years) by year and stream. Only "returning" fish were used in movement analyses.

		Tagged			Returned	
Species	Stream	2007-2009	2010	2011	2011	2012
Grayling	Hidden	132	128	122	38	51
	Lynx	156	108	129	34	49
	Teal	0	0	32	3	10
	Stovall	0	0	37	-	73
	Total	288	236	320	59*	121*
Rainbow trout	Hidden	344	111	200	15	34
	Lynx	509	232	371	62	108
	Teal	0	0	23	2	4
	Stovall	0	0	0	-	5
	Total	853	343	594	77*	141*

* Note: Total does not equal the sum of all streams because some fish "returned" to multiple streams

Appendix G: Length-frequency histograms of all hand-captured and tagged Arctic grayling and rainbow trout.

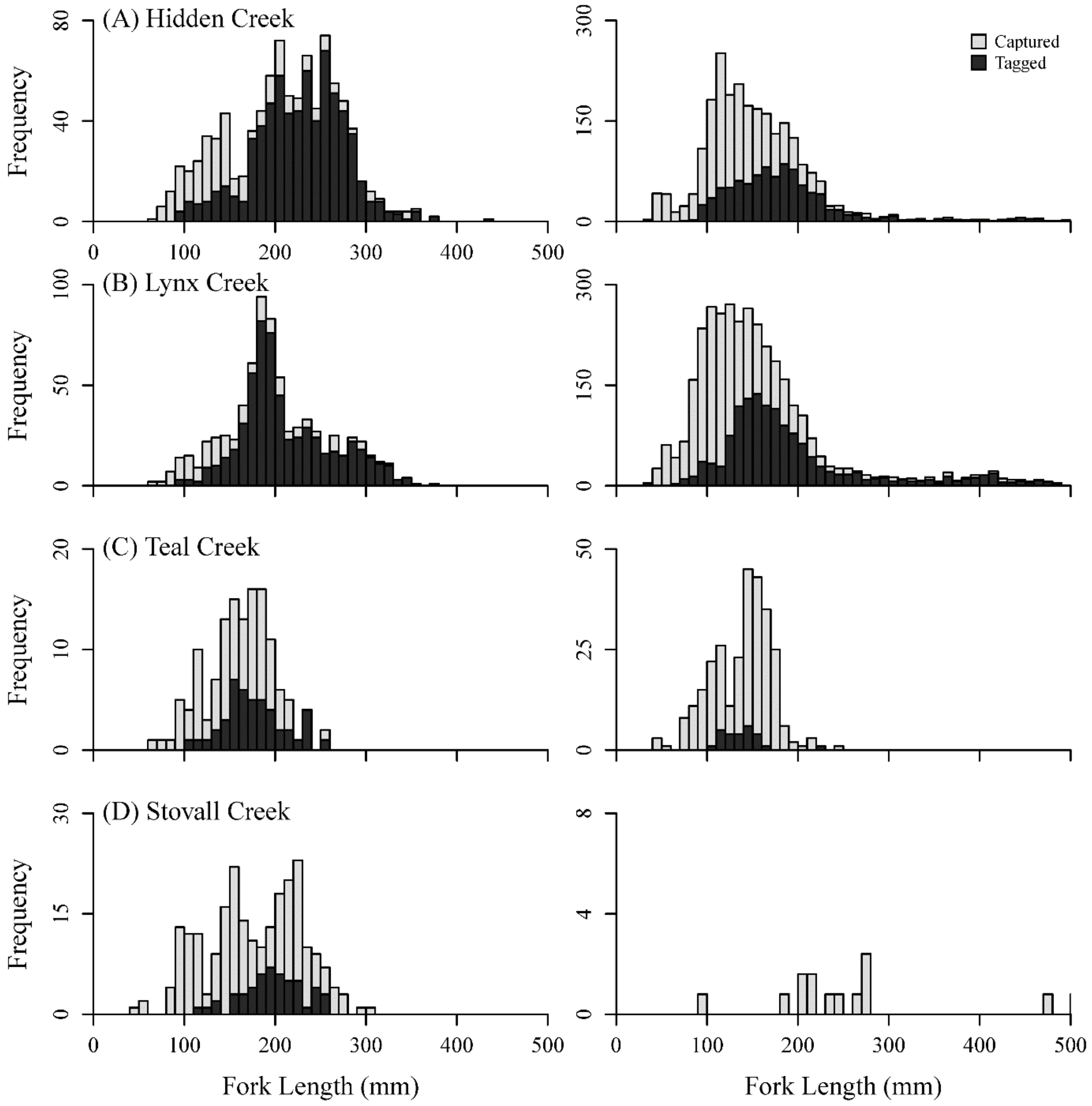

Figure G1. Length-frequency histograms of all hand-captured (light gray) and tagged (black) Arctic grayling (left) and rainbow trout (right) in (A) Hidden Creek, (B) Lynx Creek, (C) Teal Creek, and (D) Stovall Creek.

Appendix H: Antenna detection efficiency

Antenna detection efficiency was assessed two ways. First, we calculated the percent of total antenna detections that were classified as serial detections. Second, we compared the known location of recaptured individuals from our stream seining data to the predicted location of each individual (i.e., in or out of a specific stream) based on the antenna data. Over the two years of this study, a total of 8,442 antenna hits were classified as movements and overall 83.4% of the movements were serial detections (Table H1; ranging from 63.8% in Lynx during 2012 to 98.5% in Stovall during 2012). During 2011 and 2012, we recaptured 363 Arctic grayling and rainbow trout "returners" in one of our four monitored streams. Overall, 90.1% of these recaptures were correctly classified as being in the stream they were captured in based on their antenna detection (Table H2; ranging from 77.8% in Stovall during 2012 to 100% in Teal during 2011).

Table H1. Percent of antenna hits that were serial detection by stream, species, and year.

		Stream			
Species	Year	Lynx	Hidden	Teal	Stovall
Rainbows	2011	87.2	86.5	76.5	-
	2012	79.2	93.7	95.8	98.5
Grayling	2011	82.6	74.3	89.2	-
	2012	63.8	89.4	96.4	90.7

Table H2. Percent of handheld capture locations that matched predicted locations from antenna data by stream and year. Sample sizes are denoted in parentheses.

	Stream			
Year	Hidden	Lynx	Teal	Stovall
2011	84.2 (133)	94.5 (69)	100.0 (7)	- (-)
2012	98.0 (101)	78.6 (28)	91.7 (12)	77.8 (9)