FEEDING ECOLOGY OF JUVENILE SOCKEYE SALMON IN

AFOGNAK LAKE, ALASKA

By

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FEEDING ECOLOGY OF JUVENILE SOCKEYE SALMON IN AFOGNAK LAKE, ALASKA

A

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Abstract

Much attention has been given to juvenile Sockeye Salmon (*Oncorhynchus nerka*) ecology with particular focus on pelagic food webs in deep nursery lakes. In contrast, this study took place at Afognak Lake, Alaska, to better understand juvenile Sockeye Salmon foraging ecology, potential consumer interactions, and metabolic opportunities and constraints in a shallow nursery lake. I collected fish every two weeks from Afognak Lake from May through August, 2013. I described ontogenetic and temporal variation in the diets of juvenile Sockeye Salmon and a potential competitor, adult Threespine Stickleback (*Gasterosteus aculeatus*). Notably, this study revealed that adult aquatic insects are an important prey item for lake rearing juveniles. Threespine Stickleback diets showed some overlap with diets of juvenile Sockeye Salmon; however, significant differences in diet composition suggest that Sockeye Salmon and Threespine Stickleback partition prey and habitat resources. I then used my field-derived temperature, demographic, and diet data as inputs to a bioenergetics model to estimate summer consumption rate and growth efficiency of juvenile Sockeye Salmon from Afognak Lake across a range of foraging scenarios. Consumption rate was greater and mean growth efficiency was lower for all littoral-use scenarios relative to pelagic-use scenarios. Further, daily consumption was lowest and mean growth efficiency was highest for model scenarios in which insects were a dominant component of the diet relative to scenarios in which zooplankton were the dominant prey. My findings highlight the importance of benthic-pelagic coupling in Sockeye Salmon nursery lakes and the potential for juveniles to navigate trade-offs between energy acquisition and thermal conditions across lake habitats.

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Sockeye Salmon: for being beautiful, familiar yet mysterious, and integral in the lives of Alaskans.

General Introduction

Sockeye Salmon (*Oncorhynchus nerka*) return to Afognak Lake, Alaska, in the Kodiak Archipelago every summer as they have for over 7,000 years (Steffian and Counceller 2012). The area has become known to local residents as Litnik, evolving from the Russian words "lytniy domik," meaning summer house (Orth 1971). From 1981 to 2000, the Afognak Lake Sockeye Salmon run supported the largest subsistence fishery within the Kodiak Archipelago (Baer 2010) and continues to support commercial, sport, and subsistence fisheries (Thomsen and Ruhl 2015).

A federally managed hatchery was operated on Afognak Lake from 1908 to 1933 to temper high variation in adult returns (Roppel 1982). The federal Commissioner of Fisheries at that time, H. O'Malley, said Afognak Lake was "a dearth of plankton" and "there is certainly no sense in planting fish in waters that are devoid of food, for the fish simply to starve to death in a short time" (Roppel 1982, pp. 228, 230). Subsequently, Afognak Lake was considered a poor rearing environment for juvenile Sockeye Salmon and the hatchery was removed, in part, due to low production of zooplankton (Roppel 1982).

Roughly 50 years later, low return-per-spawner ratios prompted the Fisheries Rehabilitation, Enhancement, and Development (FRED) division of the Alaska Department of Fish and Game (ADF&G) to conduct ecological investigations of Afognak Lake between 1987 and 1989 (White et al. 1990). Limnological information, including zooplankton data, were collected; however, no fish diet data were gathered to quantify the dependence of juvenile Sockeye Salmon on zooplankton. In 1989, a hydroacoustic survey was conducted to estimate the population of juvenile Sockeye Salmon within the lake; however, tow-netting to characterize species composition was met with limited success as only 1 Sockeye Salmon fry and 38 Threespine Stickleback (*Gasterosteus aculeatus*) were captured (White et al. 1990). Without a reliable population estimate or information on prey selection, it was determined that “millions of voracious sockeye salmon fry fully utilize the current standing stock of macro-zooplankton” and the rearing capacity of Afognak Lake was limiting salmon productivity (White et al. 1990, p. 38). Lake fertilization (i.e., additions of phosphorus and nitrogen) subsequently took place between 1990 and 2000 (Baer 2010). The lake was concurrently stocked with sockeye salmon fry in 1992, 1994, and from 1996 to 1998, applying limnological theory that fertilization would produce excess zooplankton forage to compensate for the increased density of fish (Hyatt et al. 2004). A synthesis of long-term data from Afognak Lake is needed to understand how nutrient inputs were incorporated into the food web, including the effects of fertilization on planktivore populations.

Much attention has been given to researching the pelagic productivity of Sockeye Salmon nursery lakes (Edmundson and Mazumder 2001, Hartman and Burgner 1972). A central tenet of lake ecology focuses on a linear food web model that posits the following: nutrients contribute to primary production of phytoplankton, which support secondary production of zooplankton, which, in turn, is consumed by planktivores (Hyatt et al. 2004). This linear model proposes that sustainability of higher trophic levels hinges on nutrients that promote pelagic productivity and strong bottom-up control of production at higher trophic levels. However, the lake pelagia is not spatially discrete and aquatic ecosystems can be supported by multiple energy pathways; for instance, pelagic habitats may be subsidized by benthic production (Polis et al. 1997, Schindler and Scheuerell 2002).

In lake ecosystems, terrestrial and benthic contributions can significantly increase whole lake productivity (Cole et al. 2006, Hecky and Hesslein 1995, Vadeboncoeur et al. 2002). Dissolved and particulate terrestrial allochthonous nutrients can be input through fluvial or aeolian transport, which are then integrated into the food web through bacteria and other consumers (Cole et al. 2006). Terrestrial insects that accidently fall in littoral areas can provide an important prey subsidy to fishes (Hodgson and Hansen 2005), particularly in shallow lakes that have a high perimeter- to-area ratio (Schindler and Scheuerell 2002). Through lake mixing, nutrients in the lake sediment can be re-suspended and integrated into the water column (Søndergaard et al. 2003). Benthic periphyton serves as a prey resource for primary consumers such as snails, chironomids, and zooplankton (Vadeboncoeur et al. 2002). Studies have revealed a strong benthic stable isotope signature in pelagic dwelling fishes (Hecky and Hesslein 1995), indicating benthic energy transfer up to top consumers.

Few whole-ecosystem studies exist on Sockeye Salmon lakes with minimal pelagic habitat, particularly shallow lakes. Shallow lakes differ in physical, biological, and ecological processes relative to deep lakes (Wetzel 1983). For example, shallow lakes mix easily creating homogenous water temperatures and nutrient cycling whereas deep lakes thermally stratify and experience only seasonal mixing. Shallow lakes have higher benthic and littoral production relative to deeper lakes (Schindler and Scheuerell 2002, Vandeboncoeur and Steinman 2002), which can serve as a nutrient and prey energy source to the pelagia. In deeper lakes, pelagic, benthic, and littoral habitats function more discretely with less energy transferred across habitats. Afognak Lake is clear, oligotrophic, and comparatively shallow in relation to other Sockeye Salmon nursery lakes (Edmundson and Mazumder 2001, Thomsen and Ruhl 2015). The focus of this study was to gain a more holistic understanding of food webs, consumer interactions, and metabolic opportunities and constraints for juvenile Sockeye Salmon in shallow lakes, using Afognak Lake as a case study. This research also aimed to address upon in the current working knowledge of Afognak Lake ecology, using a combination of field-based and modeling approaches.

This thesis consists of two chapters. In Chapter 1, I described and quantified temporal and ontogenetic variation in diets of juvenile Sockeye Salmon and Threespine Stickleback and examined resource partitioning between juvenile Sockeye Salmon and Threespine Stickleback. In Chapter 2, I constructed and applied a bioenergetics model in conjunction with field-derived temperature and fish data to evaluate how utilization of lake resources can influence consumption rates and growth efficiency of juvenile Sockeye Salmon.

Chapter 1:

Feeding ecology of juvenile Sockeye Salmon and a potential competitor, Threespine Stickleback, in a shallow Alaskan lake[1]

Abstract

Freshwater growth of juvenile Sockeye Salmon (*Oncorhynchus nerka*) depends upon the quality and quantity of prey and biotic interactions with potential competitors in the foraging environment. To a large extent, our understanding about the ecology of lake-rearing juvenile Sockeye Salmon has emerged from studies of commercially important runs natal to deep nursery lakes, yet information from shallow nursery lakes (≤ 10 m) is limited. We examined seasonal and ontogenetic variation in diets of juvenile Sockeye Salmon (N = 219, 30-85 mm) and Threespine Stickleback (*Gasterosteus aculeatus*; N = 198, 42-67 mm) to understand their foraging ecology and potential foraging interactions in a shallow Alaska lake. This study revealed that adult insects made up 74% of all Sockeye Salmon diets by weight and were present in 98% of all stomachs in Afognak Lake during the summer of 2013. Diets varied temporally for all fishes but small Sockeye Salmon (<60 mm) showed a distinct shift in consumption from zooplankton in early summer to adult insects in late summer. We found evidence for strong partitioning of prey between Sockeye Salmon and Threespine Stickleback and the origin of their prey indicated that they also separated their use of habitat on a fine scale. Considering that aquatic insects can be a primary resource for juvenile Sockeye Salmon, we encourage the development of nursery lake carrying capacity models that include aquatic insects as a prey source for Sockeye Salmon.

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[1] Richardson, N., Beaudreau, A.H., Wipfli, M.S. & Finkle, H. 2016. Feeding ecology of juvenile Sockeye Salmon and a potential competitor, Threespine Stickleback, in a shallow Alaskan lake. Formatted for submission to Ecology of Freshwater Fish.

Introduction

Juvenile Sockeye Salmon (*Oncorhynchus nerka*) are unique among Pacific salmon species in their use of lakes, rather than rivers and streams, as nursery habitat to grow and enhance body condition in preparation for ocean life (Burgner 1991, Quinn 2005). Entering the ocean, juvenile salmon can experience high mortality from predation, which is often size selective (Duffy and Beauchamp 2011, Sogard 1997). A cohort can experience 55% to 85% mortality during this period (Ricker 1976, Quinn 2005) and, typically, smaller individuals are more susceptible to predation because they are vulnerable to a wider size range and diversity of predators (Furey et al. 2015, Parker 1971). For some Sockeye Salmon populations, smolt-to-adult survival is positively correlated to smolt size at ocean entry (Henderson and Cass 1991); therefore, maximizing growth before outmigration may enhance marine survival to adulthood (Henderson and Cass 1991, Koenings et al. 1993).

Freshwater growth of juvenile Sockeye Salmon depends upon the quality and quantity of prey and biotic interactions with potential competitors in the foraging environment (Edmundson and Mazumder 2001, Koenings and Burkett 1987). Newly emergent Sockeye Salmon fry inhabit the nearshore littoral habitat (Beauchamp et al. 2004, Narver 1966, Pella 1968, Rogers 1973), where they have been observed to forage for chironomid larvae and pupae and zooplankton (Goodlad et al. 1974, Jaenicke et al. 1987, Rogers 1973). By midsummer, Sockeye Salmon juveniles generally transition to the lake pelagia where they prey upon zooplankton for a year or two until ocean migration (Burgner 1991, Quinn 2005). Sockeye Salmon are selective foragers that prefer larger zooplankton, such as *Daphnia* and *Cyclops*, however, the particular prey species and sizes consumed depend on the composition of the available zooplankton stock (Eggers 1982, Kyle et al. 1988, Scheuerell et al. 2005). Competition among conspecifics, both within and between cohorts during limnetic rearing and with other planktivore species, can reduce the available zooplankton forage base and, ultimately, growth (Edmundson and Mazumder 2001, Hyatt et al. 2004, Kyle et al. 1988). Threespine Stickleback (*Gasterosteus aculeatus*) often co-occur with Sockeye Salmon in limnetic zones and littoral habitats, which they use for nesting and mating (Wootton 1976). Stickleback can be highly abundant in Sockeye Salmon nursery lakes (Burgner 1991, Quinn 2005) and they show diet overlap with Sockeye Salmon (Greenback and Nelson 1959, Manzer 1976); therefore, they can potentially reduce prey availability and inhibit Sockeye Salmon growth (Krogius and Krohkin 1956, O'Neill and Hyatt 1987, Rogers 1968).

To a large extent, our understanding about the ecology of lake-rearing juvenile Sockeye Salmon has emerged from studies of commercially important runs natal to large, deep nursery lakes (Burgner 1991). However, the foraging environment for juvenile Sockeye Salmon is likely to differ in shallow lakes (≤ 10 m) due to differences in habitat and biophysical processes between deep and shallow systems (Wetzel 1983). For example, the food webs of small, shallow lakes may be strongly influenced by inputs of terrestrial organic matter because of their large perimeter-to-area ratios (Schindler and Scheuerell 2002). Sockeye Salmon display population level adaptations to localized rearing habitats (Reed et al. 2010, Waples et al. 2008), yet information on their feeding ecology and resource partitioning with potential competitors in shallow nursery lakes is limited.

In a review of literature pertaining to juvenile Sockeye Salmon ecology in lakes (Appendix 1.A), we found the mean and maximum depths of 83 study lakes to be 38 m and 78 m, respectively (Figure 1.1). Of the 83 lakes, only five have an average depth of 10 m or less, and two of the five shallow lakes are connected to an alternative rearing habitat; on the Alaska

Peninsula, Black Lake is connected to the deeper Chignik Lake, and in Southeast Alaska, Speel Lake is connected to the Speel River and associated lakes and streams. To address gaps in understanding of juvenile Sockeye Salmon feeding ecology in small lakes, we examined the Sockeye Salmon foraging environment of Afognak Lake, which is unconnected to alternative freshwater rearing habitat, has an average depth of 9.17 m, and lacks substantial limnetic habitat. Afognak Lake is small, shallow, and oligotrophic (Edmundson and Mazumder 2001, Thomsen and Ruhl 2015), thereby representing an understudied category of Sockeye Salmon rearing systems.

The goal of this study was to examine juvenile Sockeye Salmon resource use and diet overlap with abundant Threespine Stickleback in the shallow rearing environment of Afognak Lake. Our first objective was to quantify the diets of juvenile Sockeye Salmon in Afognak Lake and characterize temporal and ontogenetic variation in diet composition. We hypothesized that juvenile Sockeye Salmon would consume emergent dipterans and larvae in early summer and shifts towards a greater consumption of zooplankton mid-summer as lake productivity increases in response to light and temperature (Staehr and Sand-Jensen 2006, Wetzel 1983). We also hypothesized that younger, smaller individuals would have a greater proportion of zooplankton in their diets and that the proportion of larger prey items, such as insects, would increase with size and age due to reduced gape limitation (Scharf et al. 2000).

Our second objective was to quantify the diet of Threespine Stickleback and examine resource partitioning between juvenile Sockeye Salmon and Threespine Stickleback. Due to differences in swimming capabilities, relative gape size, and location in the water column, we expected Sockeye Salmon to feed on larger, mobile, pelagic prey items and Threespine Stickleback to forage on smaller, less mobile, benthic prey (Wootton 1976). We expected to observe overlap in prey items but hypothesized there would be differences in overall diet composition between the two fish species. Newly emergent Sockeye Salmon have smaller gape; therefore, we also predicted that smaller Sockeye Salmon would have more diet overlap with Threespine Stickleback.

Methods

Study Area

Afognak Lake is located on the southeast side of Afognak Island in the Gulf of Alaska, approximately 50 km northwest of the city of Kodiak, Alaska. Afognak Lake is long and narrow (length 8.8 km, maximum width 0.96 km), and is drained by the 5.2 km long Afognak River into Afognak bay, which is part of the Alaska Marine National Wildlife Refuge. The lake has a surface area of 5.3 km^2, a volume of 46.0 km^3, and lake-water resident time of 0.4 years (Thomsen and Ruhl 2015, White et al. 1990). The lake is shallow (mean depth 9.17 m, maximum depth 25.97 m) and has an extensive, littoral shoreline composed of soft sand and fine sediments, gravel, and cobble. The euphotic zone depth (EZD) average is 9.8 m, suggesting the majority of the lake is photosynthetically active (Thomsen and Ruhl 2015). The zooplankton community is relatively low in diversity; *Bosmina* spp. and *Epischura* spp. together make up 81% of the total zooplankton density (Thomsen and Ruhl 2015). Other fish species present are Coho Salmon (*Oncorhynchus kisutch*), Rainbow Trout (*Oncorhynchus mykiss*), Pink Salmon (*Oncorhynchus gorbuscha*), and Dolly Varden (*Salvelinus malma*). The Alaska Department of Fish and Game (ADF&G) Sockeye Salmon escapement goal is currently set at 20,000-50,000 fish and is based on a Ricker spawner-recruit model and a limnological model, which estimates the number of smolt that can be sustained by the available zooplankton forage base (Nemeth et al. 2010).

Field and Laboratory Methods

A beach seine was used to collect Sockeye Salmon and Threespine Stickleback biweekly from five littoral sites from May through August 2013. The beach seine was approximately 26.5 m long, 3 m deep in the center tapering to 0.5 m on the ends. Mesh size varied from 0.5 cm in the center to 1.25 cm in the wing sections. Upon capture, fish were measured (fork length, mm), weighed to the closest 0.1g, and stomachs of Sockeye Salmon and Threespine Stickleback were removed and immediately placed in ethanol to stop digestion. For juvenile Sockeye Salmon, scales were removed from between the dorsal fin and lateral line, mounted on slides, and aged at the Kodiak ADF&G laboratory (Thomsen and Ruhl 2015).

Prey items were identified to the lowest possible taxonomic resolution and life history stage using taxonomic keys (McCafferty 1983, Pennak 1989) and reference specimens collected in the field. Most prey items were identifiable to Order, however many sampled stomachs, particularly those from Sockeye Salmon, were extremely full of heavily digested prey items. The loss of defining characteristics due to digestion resulted in coarse taxonomic resolution for some prey items, resulting in heavily digested prey to be categorized into the broader prey categories of Insecta unidentified and zooplankton unidentified.

We estimated the proportion by weight of each prey category following the methods of Beauchamp et al. (2004). Because prey categories of individual fish were often too small to weigh accurately, the quantity of each prey category was first determined as the area covered on a gridded petri dish; for every sampled stomach, each prey category was grouped on the petri dish and spread to a consistent thickness over a standard grid (0.5 mm squares) and the number of covered grid squares was counted (Beauchamp et al. 2004). Next, grid counts were converted to weight based on regressions fitted to data for each of six dominant prey categories: Insecta unidentified, Diptera adult, Diptera larvae, zooplankton unidentified, mollusca and crustacea, and Stickleback eggs. Separate regressions were fitted for each prey category, to account for differences in morphology that could lead to variation in the relationships between grid count and weight; for example, the same grid count of insects and zooplankton would yield different weights, due to the greater body depth of insects relative to zooplankton. For each prey category, 20 stomachs containing that taxon were randomly selected and measured for grid count, blotted, and weighed. We regressed the grid count against wet weight for each prey category and applied the fitted regression formula to obtain approximate prey weights for all prey grid counts (Beauchamp et al. 2004). For prey categories for which we did not have a grid count to weight regression, we applied the regression for the most closely related prey category. We omitted prey items that covered fewer than 5 grid cells, which were too small to accurately weigh and for which the regression formula generated negative weights in some instances.

Analytical Methods

Six biweekly sampling events occurred but due to small sample sizes for Sockeye Salmon, they were combined into three sampling periods for statistical analyses: Period I (May 22 through June 6), Period II (June 28 through July 9), and Period III (July 23 through August 10; Table 1.1). Sampling periods also coincided with ADF&G limnological sampling events, including sampling for zooplankton, chlorophyll, nutrients (phosphorous and nitrogen), and dissolved oxygen.

Predator size influences morphological constraints on feeding and foraging capabilities (Scharf et al. 2000); therefore, Sockeye Salmon diets were examined according to fish length.

We quantified diet composition for small (0-60 mm) and large (60+ mm) size classes, which approximately corresponded to age-0 and age-1 fish, respectively. Due to overlap in sizes of age-0 and age-1 Sockeye Salmon (Figure 1.2, Table 1.1) we used the inflection point of a fitted logistic regression of age on length as the division between small and large categories (Figure 1.3). All Threespine Stickleback collected were greater than 45 mm, as the majority captured in beach seines (67%) were of this size or larger; few Threespine Stickleback exceeded 60 mm in length (Table 1.1).

Diet composition was summarized for each fish species and size class by computing the proportional contribution of each prey category by weight. Sand and plant debris observed in Threespine Stickleback diets were omitted, as they were likely incidentally ingested during nest building or benthic foraging (Wootton 1976). We also summarized diet composition according to prey functional groups, characterized by prey life stage, morphology and habitat origin, which helped to examine the diets in a broader ecological context. The prey functional groups were: larval fish and eggs, zooplankton, benthic molluscs and crustaceans, benthic insects, and adult insects. Benthic insects consisted mostly of aquatic insects in a larval stage. The adult insects group consisted of insects inhabiting both mid and surface waters. Most adult insects were of aquatic origin, however some terrestrially fallen adult insects were observed in the diets.

We tested for differences in diets among species, size classes, and sampling periods using multivariate statistics (PRIMER v6; Clarke and Warwick 2001). For statistical analyses, we described diets in terms of frequency of occurrence (presence/absence) for each prey category, rather than estimated prey weight to avoid the influence of variation in meal size. Prey presence/absence data were used to calculate a similarity coefficient between every pair of sampled predators to create a pairwise resemblance matrix (i.e., Jaccard matrix; Clark and

Gorley 2006). Unidentifiable stomach contents were omitted from analyses to prevent predators with large proportions of unidentifiable contents from being artificially characterized as similar in the Jaccard matrix.

To test for statistical differences in prey frequency of occurrence between the two size classes of Sockeye Salmon, we performed a two-way analysis of similarity (ANOSIM) with size class (small and large) and sampling period (periods I, II, and III) as factors. The two-way ANOSIM tests for differences among size classes while accounting for differences among sampling periods (Clarke and Warwick 2001). To understand which prey taxa accounted for differences in diets between the two size classes, a similarity percentages (SIMPER) analysis was used. SIMPER quantifies the overall percent dissimilarity between groups.

Temporal differences in prey presence/absence among species and size classes were tested using a one-way ANOSIM using sampling period as the factor. We performed this analysis individually for each fish category (small Sockeye Salmon, large Sockeye Salmon, and Threespine Stickleback). To evaluate seasonal shifts in occurrence of major prey taxa in Sockeye Salmon diets, we used logistic regression to estimate the probability of prey occurrence in small and large Sockeye Salmon stomachs as a function of sampling date. Inflection points from fitted regressions were used to define the periods in which the probability of observing a specific prey in Sockeye Salmon stomachs shifted. Separate regressions were fit to data on major prey categories (Insecta unidentified, Diptera adult, Diptera larvae, Hymenoptera, zooplankton unidentified, Cladocera, Copepoda) and prey functional groups (adult Insecta, immature Insecta, and zooplankton).

Resource partitioning between juvenile Sockeye Salmon and Threespine Stickleback was examined using a two-way ANOSIM, which allowed us to test for differences between species while accounting for differences among sampling periods. Because Sockeye Salmon from the two size classes may exhibit variation in foraging strategy and diets, we also used a two-way ANOSIM to compare Stickleback diets with diets of small and large Sockeye Salmon individually to determine if resource partitioning was greater for a particular size class. We used SIMPER to examine the percent dissimilarity between the two species and to identify which prey types contributed most to those differences.

Results

To address our first objective, we quantified the diets of juvenile Sockeye Salmon by describing the percent contribution by estimated weight (Table 1.2). The dominant prey by weight for all juvenile Sockeye Salmon across all sampling periods were Diptera adults (44.6%), Insecta unidentified (27.5%), and zooplankton unidentified (22.3%). When diets were examined according to functional group, adult insects made up 74.3% and zooplankton made up 25.3% of all Sockeye Salmon diets. Small Sockeye Salmon diets contained a higher proportion of zooplankton (34.9%) than large Sockeye Salmon diets (17.1%) and large Sockeye Salmon diets contained a higher proportion of adult insects (82.5 %) than Small Sockeye diets (64.6%). Diets differed significantly among size classes and sampling periods (two-way ANOSIM; size class: Global R=0.324, p=0.01; sampling period: Global R=0.230, p=0.02; Table 1.3). Based on the SIMPER analysis, the diets of the two size classes were 55.2% dissimilar and prey items that contributed most to those differences were Insecta unidentified, Cladocera, and Copepoda (Table 1.3).

When separate analyses were performed on small and large Sockeye Salmon, diets of small Sockeye Salmon differed significantly across sampling periods but diets of large Sockeye Salmon did not, based on an ANOSIM (small Sockeye Salmon: Global R=0.249, P=0.01; large Sockeye Salmon: Global R=0.217, P=0.2; Table 1.4). Temporal variation in diet composition appeared to be primarily related to shifts in the relative contribution of zooplankton and insects to small Sockeye Salmon diets across sampling periods. Small Sockeye Salmon diets shifted from proportionately more zooplankton during sampling period I (May 22-June 6) to proportionately more Diptera adults in periods II (June 28-July 9) and III (July 23-August 10; Table 1.2). Fitted logistic regressions showed significant shifts in the probability of Diptera adults and zooplankton occurrence in small Sockeye Salmon diets (Figure 1.5); no other prey categories evaluated showed significant temporal shifts. A shift towards consumption of Diptera adults occurred around June 10, based on an inflection point of 20.29 Julian days calculated from the fitted regression model ($\beta = 0.080$, $z = 3.966$, $P < 0.001$; Figure 1.5), whereas a shift away from consumption of zooplankton occurred around July 18, based on an inflection point of 58.28 Julian days ($\beta = -0.035$, $z = -3.257$, $P = 0.001$; Figure 1.5). Large Sockeye Salmon diets were similar during sampling periods I and III but showed a qualitative increase in the contribution zooplankton during sampling period II (Table 1.2); however, this result should be interpreted cautiously, as the sample size of Large Sockeye Salmon was small (N=4) during period II. No significant shifts were detected for large Sockeye Salmon diets.

To address our second objective, we quantified the diets of Threespine Stickleback in terms of percent contribution by estimated weight. Qualitatively, Threespine Stickleback consumed a wider variety of prey compared to Sockeye Salmon. Across all sampling periods, major prey items included Diptera larvae (21.6%), Diptera adult (18.0%), bivalves (10.6%), Insecta unidentified (10.2%), Stickleback eggs (8.5%), and Ostracoda (7.7%). We characterized diet composition according to the same prey functional groups described above and found that Stickleback diets were dominated by prey items of benthic origin (Figure 1.4; Table 1.2). A one-way ANOSIM showed significant differences in diets across sampling periods (Global R=0.125, p=0.01, Table 1.4). We observed a decrease in the proportion of Stickleback eggs, zooplankton, and dipteran larvae and an increase in the proportion of gastropods, bivalves, and adult insects to Threespine Stickleback diets from May to August.

We tested for differences in prey frequency of occurrence between all Sockeye Salmon and Threespine Stickleback, small Sockeye Salmon and Threespine Stickleback, and large Sockeye Salmon and Threespine Stickleback using 2-way ANOSIM tests. Diet composition differed significantly between Threespine Stickleback and all categories of Sockeye Salmon (all Sockeye Salmon: Global R=0.497, p= 0.01; small Sockeye Salmon: Global R=0.346, p=0.01; large Sockeye Salmon: Global R=0.482, p=0.01, Table 1.3). Across all periods, Sockeye Salmon diets were 74.5% dissimilar to Threespine Stickleback diets, although a greater dissimilarity occurred between Threespine Stickleback and large Sockeye Salmon (80.4%) compared to small Sockeye Salmon (69.2%; Table 1.3). Dissimilarities were attributed to Diptera adult, Insecta unidentified, Diptera larvae, and to a lesser extent Cladocera, Copepoda, and Arachnida, based on a SIMPER analysis (Table 1.3).

Discussion

This study provides new information on the feeding ecology of Sockeye Salmon fry and resource partitioning with Threespine Stickleback, a dominant co-occurring planktivore, in Afognak Lake, Alaska. Our results contribute to a better understanding of the ecology of small, shallow, Sockeye Salmon nursery lakes. Notably, adult insects were a major prey resource for age-0 and age-1 Sockeye Salmon throughout summer; on average, adult insects made up 74% of Sockeye Salmon diet by weight and were present in 98% of 219 sampled stomachs. These findings challenge the prevailing view that juvenile Sockeye Salmon in Afognak Lake and other systems are primarily planktivores that prefer zooplankton prey (White et al.1990). This assumption is based on studies from larger and deeper lake systems where juvenile Sockeye Salmon are predominantly planktivorous, such as in Lake Washington (Beauchamp et al. 2004 , Scheuerell et al. 2005), Chignik Lake (Narver 1966), Great Central Lake (Manzer 1976), and Frazer Lake (Koenings and Kyle 1997). Adult insects have been found to make up a large proportion of Sockeye Salmon diets in other shallow lakes. In Black Lake, Alaska, chironomids of all life stages dominated the summer diets of juvenile Sockeye Salmon until August, after which they switched to zooplankton forage (Griffiths and Schindler 2012, Ruggerone 1994). Jaenicke et al. (1987) also found emergent dipterans, mainly chironomids, to be the primary food source in the summer for age-0 Sockeye Salmon in shallow habitats of Lake Nunavaugaluk near Dillingham, Alaska. Because insects are larger and higher in energy content (2,856 J/g, Cummins and Wuycheck 1971) than zooplankton (1,674-2,382 J/g, Schindler and Eby 1997), they may act as a substantial energetic subsidy to juvenile Sockeye Salmon in shallow rearing environments. Thus, benthic and terrestrial food resources can serve as an important subsidy to pelagic food webs (Hecky and Hesslein 1995) and may have particular importance for energy flow in shallow lakes, where the opportunity for habitat coupling is greater (Polis et al. 1997, Schindler and Scheuerell 2002).

Our results also demonstrated ontogenetic and temporal shifts in Sockeye Salmon diets, similar to other studies (Scheuerell et al. 2005, Beauchamp et al. 2004, Griffiths and Schindler

2012). We observed an increase in insect consumption by small Sockeye Salmon from May to August and a peak in zooplankton consumption by large Sockeye Salmon mid-summer. These temporal shifts may relate to both size-based changes in Sockeye Salmon foraging capabilities and seasonal availability of prey in the lake. Small Sockeye Salmon may be incapable of ingesting large insects due to gape limitation. Furthermore, at small sizes, it may be more energetically cost effective to forage on smaller, more easily captured zooplankton prey. Small Sockeye Salmon incorporated more insects into their diets as they grew throughout the summer (Table 1.2) and, on average, the percent contribution did not exceed that observed in large Sockeye Salmon diets. A peak in proportional contribution of zooplankton to large Sockeye Salmon diets coincided with the period of peak zooplankton density in Afognak Lake during summer 2013 (180 mg/m^2 in July; Thomsen et al. 2014). We hypothesize that large Sockeye Salmon may consume larger, more energy rich insect prey in favor of smaller, lower energy zooplankton except when encounter rates with zooplankton are high. However, we did not observe a similar diet trend in small Sockeye Salmon during this period, and a larger sample size of large Sockeye Salmon would be needed to support this hypothesis.

Sample sizes were low for small Sockeye Salmon during sampling period I and large Sockeye Salmon after sampling period I. We believe this to be a function of fry emergence and outmigration timing. The smallest Sockeye Salmon (≤ 30mm) captured during sampling period I (May 21-June 10) had attached yolk sacs, suggesting a proportion of the population had yet to emerge or were newly emerged from gravel redds (Quinn 2005). Historically, approximately 80% of Afognak Lake Sockeye Salmon smolt outmigrate from early May through June, exiting the lake after one year of inhabitance (Thomsen and Ruhl 2015). By July, the Sockeye Salmon assemblage in Afognak Lake is generally comprised of smaller age-0 fish with only 20% of the larger age-1 cohort remaining in the lake. This shift in population structure temporally aligns with increased catches of small Sockeye Salmon and decreased catches of large Sockeye Salmon.

Exploitative competition for prey resources between Stickleback and juvenile Sockeye Salmon has been suggested as a possible limit to Sockeye Salmon production; however, evidence for competition has been equivocal. Enclosure experiments (O'Neill and Hyatt 1987) and lake fertilization studies (Hyatt et al. 2004) have suggested interspecific competition, however observational studies in natural systems have alternatively suggested resource partitioning (Jaenicke et al. 1987) or that Sockeye Salmon are superior competitors (Rogers 1968). Each of these scenarios may depend on ecological conditions in a particular system, but the ubiquitous co-existence of these fishes suggests that resource partitioning may serve to limit their competitive interactions. In deep lakes, Threespine Stickleback and Sockeye Salmon temporally partition habitats such that they both use littoral and limnetic regions, but at different times (Manzer 1976). Spatial and temporal separation may also occur in pelagic habitats, as patterns of diel vertical migration differ between Threespine Stickleback and juvenile Sockeye Salmon (Quinn et al. 2012). Sockeye Salmon and Threespine Stickleback appear to partition prey resources, as evidenced by significant differences in their diet composition. Although Sockeye Salmon and Threespine Stickleback were captured at the same locations, differences in the origin of their prey indicated that they also separated their use of habitat on a fine scale. For example, Threespine Stickleback diets contained a higher proportion of benthic prey compared to Sockeye Salmon. Threespine Stickleback diets also showed greater overlap with diets of small Sockeye Salmon compared to diets of large Sockeye Salmon, suggesting that the degree of resource sharing could depend on the size structure of Sockeye Salmon in the lake.

Our study showed that the feeding ecology of juvenile Sockeye Salmon in shallow lakes may differ in important ways from deep lake ecosystems. This suggests that inferences derived from ecological knowledge of large lakes may not be appropriate for assessing the capacity of small, shallow systems to support Sockeye Salmon production. Sockeye Salmon lake ecosystems have often been managed as a linear food chain (nutrients → phytoplankton → zooplankton → Sockeye Salmon), driven either by bottom-up or top-down processes (Carpenter et al. 2009). Decisions pertaining to escapement goals, nutrient enrichment, and stocking of hatchery fish can hinge on a lake's carrying capacity, or the amount of secondary production that can be supported by phytoplankton. Considering that aquatic and terrestrial insects can serve as primary prey for juvenile Sockeye Salmon, Sockeye Salmon productivity models based on zooplankton production may not be applicable to Afognak Lake or similarly shallow systems. Jaenicke et al. (1987) suggested that further research was needed to determine if survival and growth of Sockeye Salmon fry was related to chironomid production and encouraged the development of carrying capacity models that include insects as a prey source for sockeye. We too encourage the development of alternative models and caution against generalized assumptions about the ecological functioning of Sockeye Salmon rearing lakes.

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in compliance with the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks (approval #453388) and under ADF&G fish collection permit #CF-2012-20.

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Figures

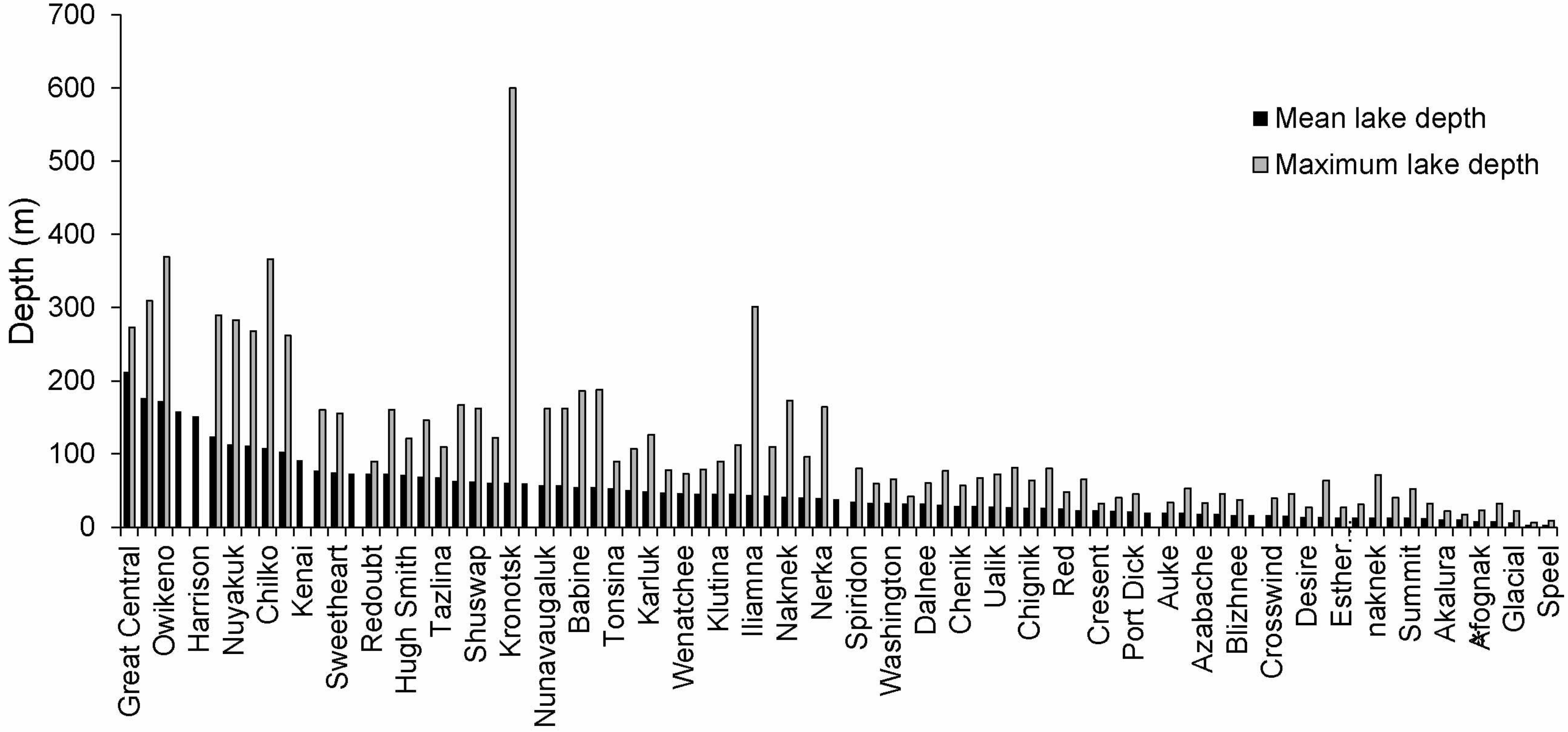

Figure 1.1 Distribution of mean and maximum depths of 83 Sockeye Salmon nursery lakes from published literature. Maximum depth data are missing from 8 lakes as they were not reported in literature source. The study system, Afognak Lake, is marked with an asterisk. For a full list of lake names see Appendix 1.A.

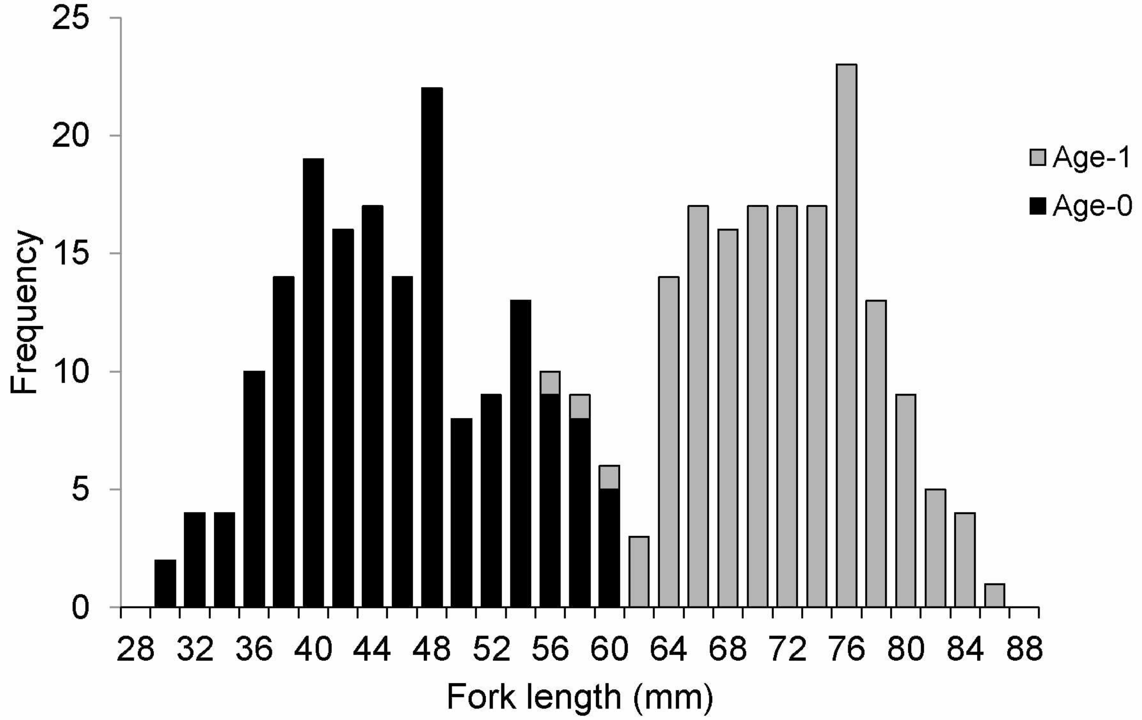

Figure 1.2 Length frequency distribution of juvenile Sockeye Salmon (n=219) captured in Afognak Lake. Fish were captured from May through August 2013. A total of 120 age-0 (29 – 60 mm FL) and 99 age-1 (56 – 85 mm FL) were caught.

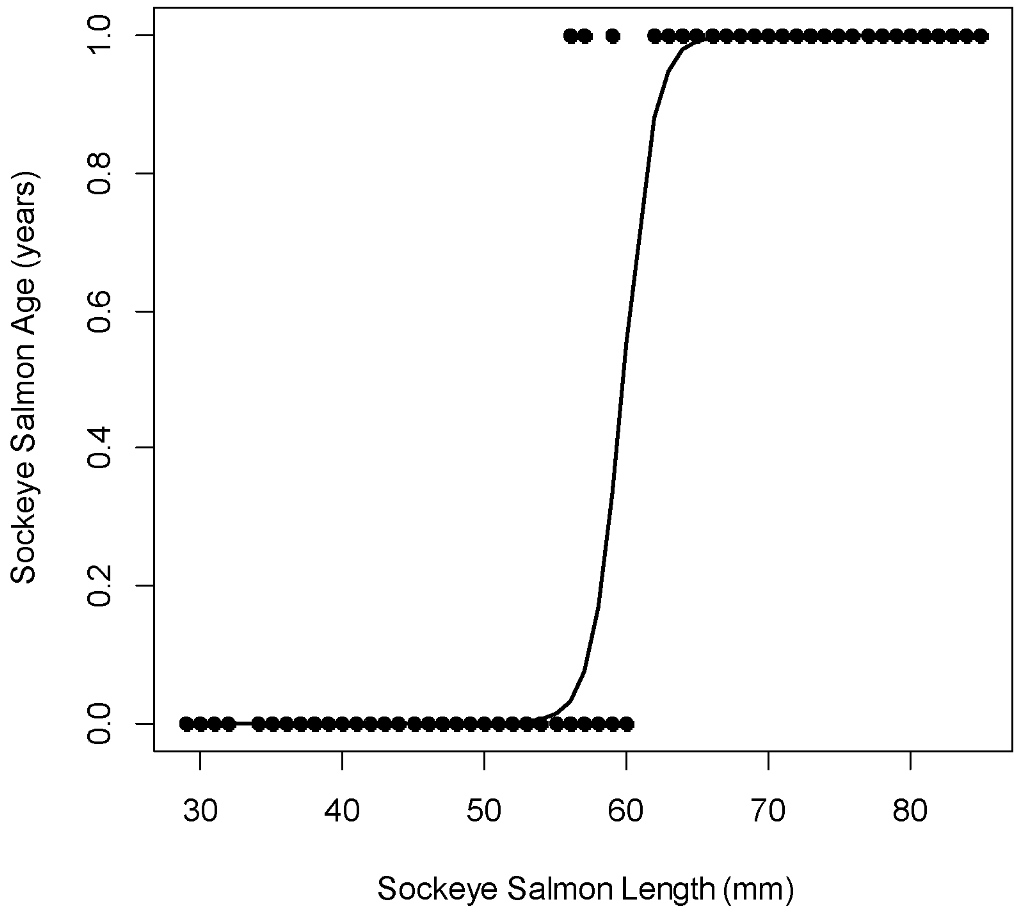

Figure 1.3 Fitted logistic regression used to determine Sockeye Salmon size classes for diet comparisons. The inflection point (~60 mm) was used to separate small and large size classes, which approximately corresponded to age-0 and age-1 Sockeye Salmon, respectively.

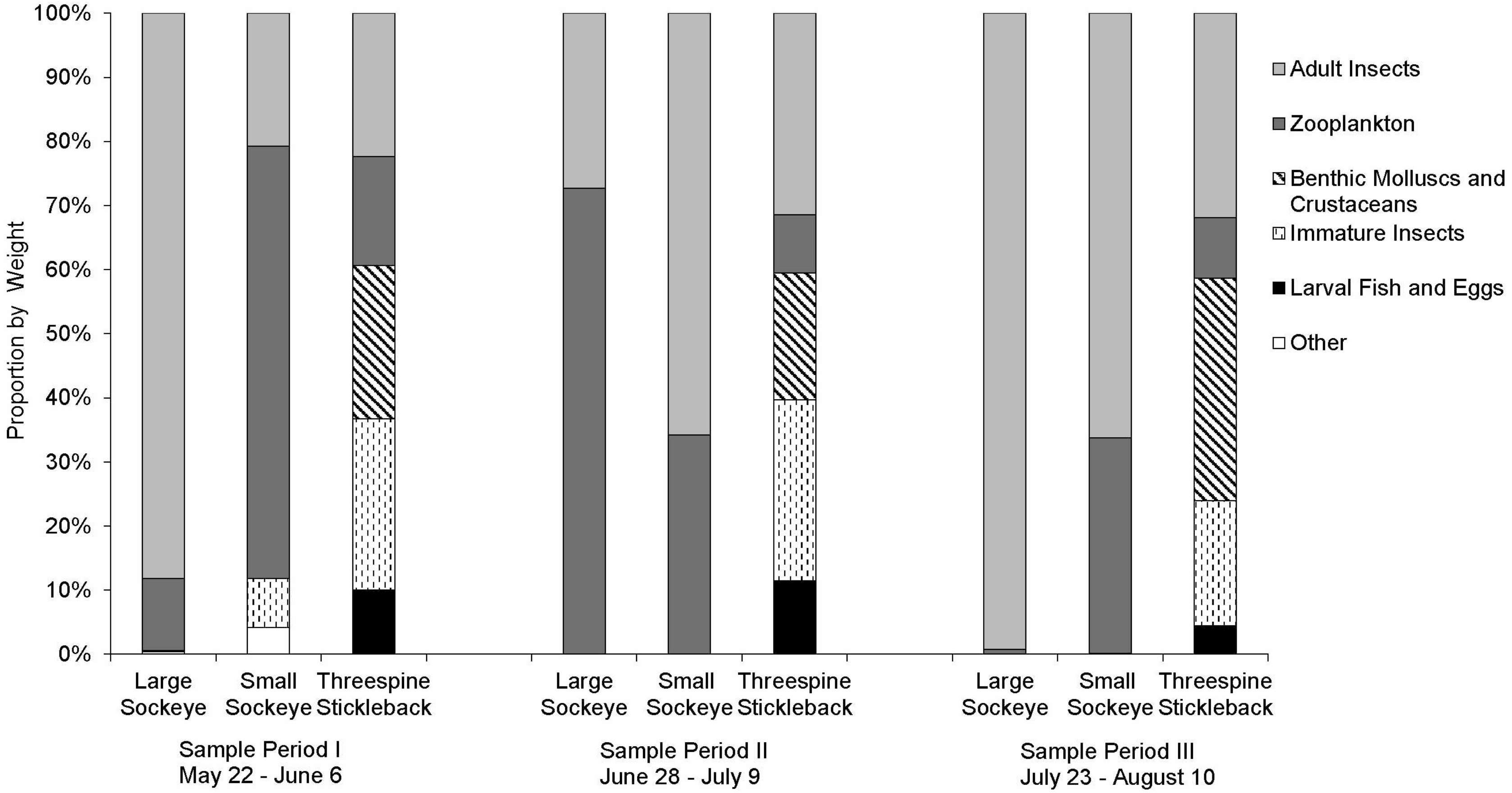

Figure 1.4 Diet composition for juvenile Sockeye Salmon and Threespine Stickleback. Proportion of the diet was estimated by prey weight for large Sockeye Salmon (>60 mm), small Sockeye Salmon ($\leq$ 60 mm), and Threespine Stickleback across sampling periods. Prey items were identified to the lowest possible taxonomic resolution then assigned to prey functional groups, characterized by prey life stage, morphology and habitat origin. Adult insects were of mid-water or surface origin and immature insects were of benthic origin.

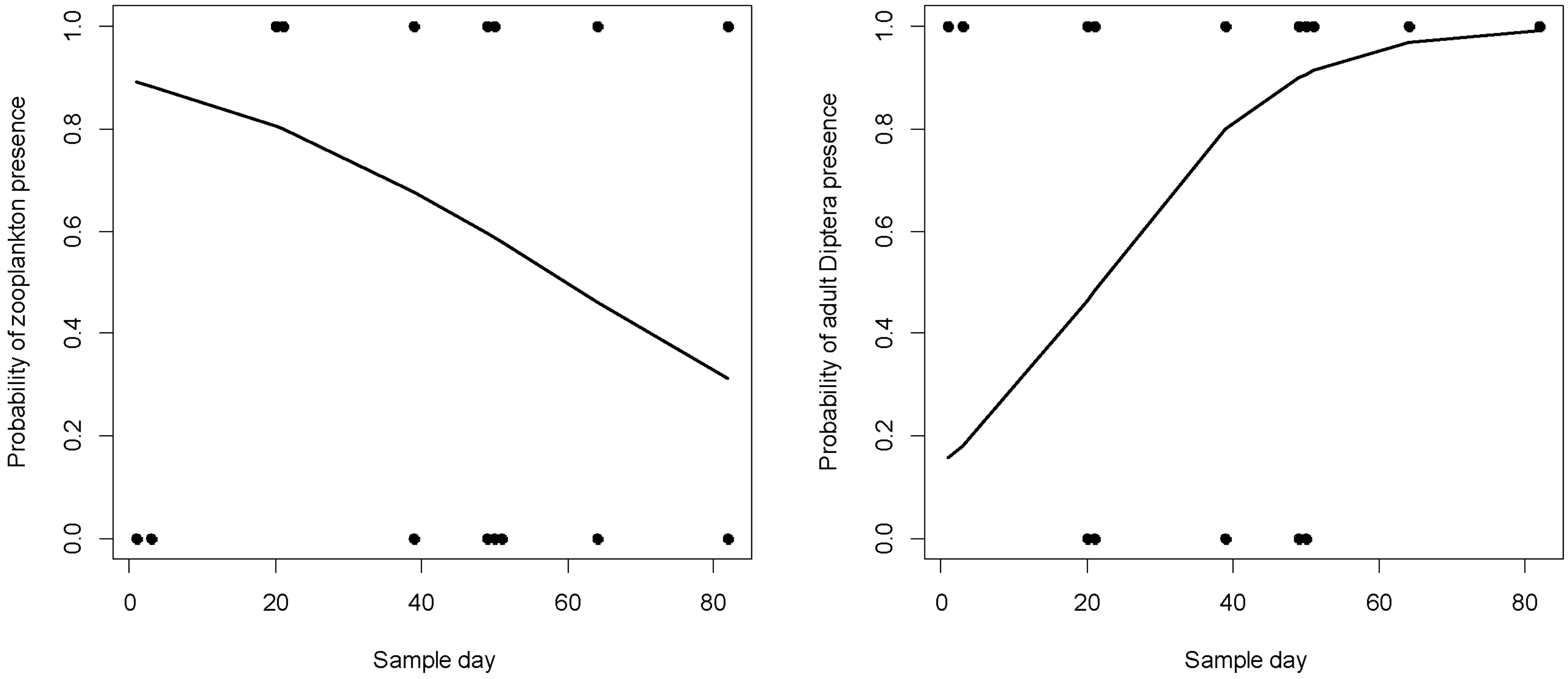

Figure 1.5 Fitted logistic regressions showing shifts in small Sockeye Salmon diets. A significant shift towards consumption of adult Diptera occurred around June 10, based on an inflection point of 20.29 calculated from the fitted regression model ($\beta = 0.080$, $z = 3.966$, $P < 0.001$). A significant shift away from consumption of zooplankton occurred around July 18, based on an inflection point of 58.28 ($\beta = -0.035$, $z = -3.257$, $P = 0.001$).

Tables

Table 1.1 Summary of the total fish sampled and fish sizes. Number of small Sockeye Salmon, large Sockeye Salmon, and Threespine Stickleback sampled for diets and mean fork length with standard deviation and range of fork lengths are summarized for each sample period.

	Period I May 22 - June 6		Period II June-28 - July 9		Period III July 23 - August 10	
	N fish sampled	Length Mean (SD), Range	N fish sampled	Length Mean (SD), Range	N fish sampled	Length Mean (SD), Range
Small Sockeye Salmon (≤60 mm)	12	38.8 (9.2) mm, 30-59 mm	52	41.9 (4.8) mm, 32-59 mm	56	51.5 (5.7) mm, 41-60 mm
Large Sockeye Salmon (>60 mm)	78	71.3 (5.9) mm, 62-85 mm	4	72.5 (3.3) mm, 70-77 mm	17	74.5 (4.5) mm, 67- 84 mm
Threespine Stickleback	72	55.7 (3.2) mm, 47-62 mm	59	56.6 (3.7) mm, 45-67 mm	67	54 (3.9) mm, 42-65 mm

Table 1.2 Diet composition as the proportion of prey by weight of large Sockeye Salmon, small Sockeye Salmon, and Threespine Stickleback. Sampling occurred every two weeks but diets were combined and summarized for three sampling periods. Prey items were identified to the lowest possible taxonomic resolution and assigned to prey functional groups, characterized by prey life stage, morphology, and habitat origin.

	Large Sockeye Salmon (>60 mm)			Small Sockeye Salmon (≤60 mm)			Sockeye Salmon (all size classes)			Threespine Stickleback		
	Sampling Period			Sampling Period			Sampling Period			Sampling Period		
Prey Taxa	I	II	III	I	II	III	I	II	III	I	II	III
Benthic Mollusca and Crustacea												
Gastropoda	-	-	-	-	-	-	-	-	-	1.0	0.5	12.7
Bivalve	0.2	-	-	-	-	-	0.2	-	-	7.6	11.2	13.7
Amphipoda	-	-	-	-	-	-	-	-	-	5.0	2.2	1.5
Ostracoda	-	-	-	-	-	-	-	-	-	10.3	5.9	6.8
Cumulative	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	23.9	19.7	34.7
Benthic Insecta												
Arhynchobdellida	-	-	-	-	-	-	-	-	-	-	0.6	-
Coleoptera Larvae	-	-	0.1	-	-	-	-	-	-	-	-	-

Table 1.2 Continued

	Large Sockeye Salmon (>60 mm)			Small Sockeye Salmon (<60 mm)			Sockeye Salmon (all size classes)			Threespine Stickleback		
	Sampling Period			Sampling Period			Sampling Period			Sampling Period		
Prey Taxa	I	II	III	I	II	III	I	II	III	I	II	III
Diptera Larvae	-	-	-	-	-	-	-	-	-	24.9	23.0	16.1
Ephemeroptera Larvae	-	-	-	7.6	-	-	0.3	-	-	-	-	-
Insecta Larvae	-	-	-	-	-	-	-	-	-	-	0.2	0.8
Trichoptera Larvae	-	-	-	-	-	-	-	-	-	1.8	4.5	2.7
Cumulative	0.0	0.0	0.1	7.6	0.0	0.0	0.3	0.0	0.0	26.7	28.3	19.6
Larval Fish and Eggs												
Fish Egg	-	-	-	-	-	0.1	-	-	-	10.0	11.4	3.1
Larval Fish	-	-	-	-	-	-	-	-	-	-	-	1.3
Cumulative	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	10.0	11.4	4.4
Zooplankton												
Cladocera	0.1	-	0.2	2.2	11.2	0.8	0.2	6.5	0.6	1.0	8.7	5.9
Copepoda	-	8.0	0.6	1.4	4.4	0.9	0.1	5.9	0.8	16.0	0.4	3.4
Zooplankton Unid.	11.2	64.6	-	63.9	18.6	32.0	13.5	38.0	23.2	-	-	0.2
Cumulative	11.3	72.6	0.7	67.5	34.2	33.7	13.7	50.5	24.7	17.0	9.2	9.5

Table 1.2 Continued

	Large Sockeye Salmon (>60 mm)			Small Sockeye Salmon (<60 mm)			Sockeye Salmon (all size classes)			Threespine Stickleback		
	Sampling Period			Sampling Period			Sampling Period			Sampling Period		
Prey Taxa	I	II	III	I	II	III	I	II	III	I	II	III
Adult Insecta												
Trichoptera Adult	0.1	0.2	1.1	-	0.2	0.6	0.1	0.2	0.7	-	0.2	-
Arachnida	0.2	-	-	-	-	-	0.2	-	-	-	-	-
Coleoptera	-	-	0.4	-	-	0.2	-	-	0.3	-	-	-
Collembola	0.1	-	0.1	-	-	1.2	0.1	-	0.9	-	-	-
Diptera	49.1	13.3	48.6	7.1	41.2	48.1	47.3	29.4	48.3	1.6	28.8	25.6
Homoptera	-	-	0.3	-	-	0.4	-	-	0.3	-	-	-
Hymenoptera	0.2	0.2	4.0	-	0.5	1.0	0.2	0.4	1.8	-	-	-
Insecta	38.4	13.7	44.9	13.6	23.8	14.8	37.3	19.5	23.0	20.7	2.4	6.3
Cumulative	88.1	27.4	99.2	20.7	65.8	66.2	85.2	49.5	75.3	22.4	31.4	31.9
Other												
Seed	0.4	0.0	0.0	4.1	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Total	100	100	100	100	100	100	100	100	100	100	100	100

Table 1.3 Results of two-way analysis of variance (ANOSIM) and similarity percentages (SIMPER). Two-way ANOSIM tests were used to determine significant differences between fish size or species and sampling period. ANOSIM tests were based on a Jaccard matrix using presence/absence data, with 9,999 permutations and significance set at α=0.01. SIMPER results were based on a Jaccard similarity matrix and were used to determine the percent differences in fish diets and the percent that prey items contributed to those differences.

	Small Sockeye & Stickleback	Large Sockeye & Stickleback	All Sockeye & Stickleback	Small Sockeye & Large Sockeye
Two-way ANOSIM				
Factor: Size or Species				
Global R	0.346	0.482	0.497	0.324
Significance level (p-value)	0.01	0.01	0.01	0.01
Factor: Sampling period				
Global R	0.162	0.160	0.127	0.23
Significance level (p-value)	0.01	0.01	0.01	0.02
SIMPER (across all sampling periods)				
% Dissimilarity	69.2	80.4	74.5	55.2
% Contribution to difference				
Diptera emergent	7.9	18.2	13.2	9.2
Insecta	12.2	12.5	12.3	12.7
Diptera larva	12.9	12.9	12.9	4.4
Bivalve	3.6	3.1	3.3	-
Ostracoda	3.2	2.7	2.9	-

Table 1.3 Continued

	Small Sockeye & Stickleback	Large Sockeye & Stickleback	All Sockeye & Stickleback	Small Sockeye & Large Sockeye
SIMPER (across all sampling periods)				
% Contribution to difference				
Zooplankton unid.	2.9	-	2.5	7.3
Cladocera	12.0	8.5	10.2	14.7
Hymenoptera	5.8	5.2	5.5	8.1
Copepoda	9.4	11.0	10.2	12.7
Trichoptera adult	-	-	-	-
Homoptera	-	-	-	2.8
Stickleback egg	-	-	4.5	-
Tricoptera larva	3.1	-	2.4	-
Collembola	5.7	5.5	5.6	8.2
Egg	3.0	2.5	2.7	-
Arachnida	9.3	5.7	7.5	8.6
Thysanoptera	-	2.5	-	-
Coleoptera	-	-	-	3.5
Gastropoda	-	-	-	-
Cumulative %	90.9	90.2	91.3	92.0

Table 1.4 Results of one-way analysis of similarity (ANOSIM). ANOSIM was used to test for temporal differences in fish diets. ANOSIM tests were run separately for each fish category (small Sockeye Salmon, large Sockeye Salmon, and Threespine Stickleback) across three sample periods spanning from May through August, 2013. ANOSIM tests were based on a Jaccard matrix of presence/absence data, with 9,999 permutations and significance set at α=0.01.

1-way ANOSIM Factor: Sampling Period	Small Sockeye Salmon	Large Sockeye Salmon	Threespine Stickleback
Global R	0.249	0.217	0.125
Significance level (p-value)	0.01	0.2	0.01

Appendix

Appendix 1.A Summary of 83 Sockeye Salmon lakes, depths, and literature source.

Lake	Mean lake depth (m)	Maximum lake depth (m)	Reference
Great Central	212	273	Manzer 1976
Kuril	180	316	Milovskaya et al. 1998
Owikeno	172	369	McKinnell et al. 2001
Quesnal	158	530	Hume et al. 1996
Harrison	151		Shortreed et al. 2001
Tustemena	124	290	Edmundson and Manzumder 2001
Nuyakuk	113	283	Burgner 1991
Chauekuktuli	111	268	Burgner 1991
Chilko	123	330	Hume et al. 1996
Clark	103	262	Burgner et al. 1969
Kenai	91	165	Tarbox et al. 1993
Kulik	77	160	Burgner 1991
Sweetheart	74	155	Edmundson and Manzumder 2001
Long	73		Shortreed et al. 2001
Redoubt	73	90	Edmundson and Manzumder 2001
Skilak	73	160	Tarbox et al. 1993
Hugh Smith	71	121	Edmundson and Manzumder 2001
Badger	69	146	Edmundson and Manzumder 2001
Tazlina	68	110	Edmundson and Manzumder 2001
Naknek	63	167	Hartman and Burgner 1972
Shuswap	62	162	Hume et al. 1996
Chelatna	60	122	Edmundson and Manzumder 2001
Kronotsk	60	600	Burgner 1991
Sproat	59		LeBrasseur et al. 1978
Nunavaugaluk	57	162	Jaenicke et al. 1987
Babine	55	186	Hartman and Burgner 1972
Beverly	55	188	Burgner 1991
Tonsina	53	90	Edmundson and Manzumder 2001
Grosvenor	50	107	Burgner 1991
Karluk	49	126	Hartman and Burgner 1972
Coghill	47	78	Edmundson and Manzumder 2001
Wenatchee	46	73	Burgner 1991
Brooks	45	79	Burgner 1991

Appendix 1.A continued

Lake	Mean lake depth (m)	Maximum lake depth (m)	Reference
Klutina	45	90	Edmundson and Manzumder 2001
McDonald	45	112	Edmundson and Manzumder 2001
Iliamna	44	301	Rich et al. 2009
Aleknagik	43	110	Schindler et al. 2005
Naknek	41	173	Hartman and Burgner 1972
Ozette	40	96	Beauchamp et al. 1995
Nerka	39	164	Burgner 1991
Kennedy	38		O'Neill and Hyatt 1987
Spiridon	35	80	Edmundson and Manzumder 2001
Frazer	33	59	Edmundson and Manzumder 2001
Washington	33	65	Beauchamp et al. 2004
Cultus	32	42	Goodlad et al. 1974
Dalnee	32	60	Krogius and Krokhin 1948
Little Togiak	30	77	Rogers et al. 1982
Chenik	29	57	Edmundson and Manzumder 2001
Cresent SE	29	67	Edmundson and Manzumder 2001
Ualik	28	72	Burgner 1991
Upper Russian	27	81	Edmundson and Manzumder 2001
Chignik	64		Westley et al. 2008
Upper Station	26	80	Edmundson and Manzumder 2001
Red	25	48	Edmundson and Manzumder 2001
Amanka	23	65	Burgner 1991
Cresent	23	32	Edmundson and Manzumder 2001
Delight	22	40	Edmundson and Manzumder 2001
Port Dick	21	45	Edmundson and Manzumder 2001
Stuart	20		Burgner 1991
Auke	19	34	Edmundson and Manzumder 2001
Coveille	19	53	Burgner 1991
Azabache	18	33	Burgner 1991
Hidden	18	45	Edmundson and Manzumder 2001
Blizhnee	16	37	Burgner 1991
Bowron	16		Burgner 1991
Crosswind	16	39	Reed et al. 2010
Tikchik	15	45	Burgner 1991
Desire	14	27	Edmundson and Manzumder 2001
Osoyoos	14	64	Burgner 1991

Appendix 1.A continued

Lake	Mean lake depth (m)	Maximum lake depth (m)	Reference
Esther Passage	13	27	Edmundson and Manzumder 2001
Fraser	13	31	Goodlad et al. 1974
Naknek	13	71	Hartman and Burgner 1972
Salmon	13	40	Edmundson and Manzumder 2001
Summit	13	52	Reed et al. 2010
Packers	12	32	Edmundson and Manzumder 2001
Akalura	10	22	Edmundson and Manzumder 2001
Bear	10	17	Edmundson and Manzumder 2001
Afognak	8	23	Edmundson and Manzumder 2001
Lakelse	8	32	Brett 1950
Glacial	6	22	Edmundson and Manzumder 2001
Black	1.5	4	Westley et al. 2008
Speel	3	9	Edmundson and Manzumder 2001

Chapter 2:

Bioenergetic tradeoffs among foraging environments for lake rearing juvenile Sockeye Salmon[1]

Abstract

Freshwater growth of salmon is influenced by environmental conditions, particularly water temperature and the abundance and quality of prey. Temporal and spatial habitat heterogeneity exists within a lake and how juvenile Sockeye Salmon utilize foraging opportunities within the lake environment can contribute to growth and, ultimately, survival. We applied a bioenergetics model in conjunction with field-derived temperature, diet, and growth data to evaluate how use of lake resources can influence consumption rates and growth efficiency of juvenile Sockeye Salmon in a shallow Alaska lake. We estimated the summer consumption rate and growth efficiency of age-0 and age-1 juvenile Sockeye Salmon across a range of foraging scenarios (habitat temperature and diet composition). Seasonal mean consumption rates for an individual fish were 0.23 ± 0.02 g/g/d and 0.14 ± 0.05g/g/d and seasonal mean growth efficiency was 14.6 ±7.3% and 7.0± 3.8% for age-0 and age-1 fish, respectively. Across 27 model scenarios, total consumption was greater and mean growth efficiency was lower for all littoral-use scenarios relative to pelagic-use scenarios. Daily consumption was lowest for model scenarios in which insects were a dominant component of the diet and mean growth efficiency was 20.3% higher for high insect diet scenarios relative to high zooplankton diet scenarios. We posit that the optimal foraging scenario, in which juvenile Sockeye Salmon consume predominantly insect prey and use pelagic habitat, could occur through donor or recipient controlled benthic prey subsidization. Our bioenergetics model results

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[1] Richardson, N., Beaudreau, A.H. & Finkle, H. 2016. Bioenergetic tradeoffs among foraging environments for lake rearing juvenile Sockeye Salmon. Formatted for submission to Ecology of Freshwater Fish.

lay the foundation to predict and test future hypotheses on energy pathways for mobile consumers in lakes.

Introduction

Ecological and environmental conditions experienced by juvenile Sockeye Salmon in nursery lakes may have implications for their survival upon ocean entry (Kaeriyama and Ueda 1998, Rice et al. 1994, Wood 1987). Upon marine entry, smaller individuals are more susceptible to predation and higher rates of mortality than larger individuals (Henderson and Cass 1991, Koenings et al. 1993). Freshwater growth of juvenile Sockeye Salmon is influenced by environmental conditions, particularly lake temperature and abundance of prey (Edmundson and Mazumder 2001, Hyatt and Stockner 1985). Within a lake, temperature and prey conditions are temporally and spatially heterogeneous, creating diverse foraging habitats for juveniles. Understanding how juvenile Sockeye Salmon may utilize a suite of foraging opportunities within the lake environment can give insight into processes that contribute to growth and, ultimately, survival.

Where and when a fish chooses to forage can impact its metabolic processes, with ultimate consequences for growth. When temperatures are too cold, growth is slowed or arrested (Brett et al. 1969, Elliot 1976). When temperatures are too high, increased metabolic demands can result in an energy deficit (Brett et al. 1969, Elliot 1976). Juvenile Sockeye Salmon have a range of temperatures that favor growth (5°-17°C) and under maximum rations, growth efficiency peaks at 15°C (Brett et al. 1969). Juvenile Sockeye Salmon can regulate their thermal environment by moving between nearshore and offshore habitats (Beauchamp et al. 2004, Quinn 2005), undergoing diel vertical migrations (Levy 1987, Scheuerell and Schindler 2003), or migrating between connected bodies of water (Burgner 1991, Westley et al. 2008). Fish may also economize their energy consumption to achieve optimal growth through selective foraging (e.g., Werner and Hall 1974). Sockeye Salmon have been shown to be selective foragers that consume large zooplankton prey, such as *Daphnia* and *Cyclops* (Eggers 1982, Kyle et al. 1988, Scheuerell et al. 2005), and high energy dipteran insects of all life stages (Griffiths and Schindler 2012; Richardson 2016).

If a spatial mismatch exists between optimal metabolic temperature and preferred prey, Sockeye Salmon may be faced with tradeoffs in their foraging environment. For example, Black Lake, Alaska, is shallow and during summer months lake temperatures can exceed 15°C, which is above the optimal growing temperature for Sockeye Salmon (Brett et al. 1969). Some juveniles remain in Black Lake while others migrate downstream in the watershed to deeper, cooler Chignik Lake (Westley et al. 2008). Those fish remaining in Black Lake incur high metabolic costs; however, they are potentially rewarded with an abundance of energy-dense aquatic insect prey (Griffiths and Schindler 2012). Individuals that migrate to Chignik Lake may forfeit high energy prey in exchange for temperatures that are less physiologically taxing.

Some fish may strategize to take advantage of both optimal temperatures and high quality prey through habitat cycling, or moving between habitats. For example, in the Wood River basin of Alaska, juvenile Coho Salmon gorge on Sockeye Salmon eggs in cold spawning habitats but move to warmer areas to increase digestive capacity (Armstrong et al. 2013). Additionally, Sockeye Salmon that undergo diel vertical migrations may do so, in part, to exploit zooplankton concentrated at the lake’s surface but then return to or below the cooler thermocline to limit their exposure to high surface temperatures that increase bioenergetic expenditures (Levy 1987).

A combination of modeling and field-based approaches can offer insight into the relationships between a fish and its foraging environment. Models have been used to explore how juvenile Sockeye Salmon metabolically respond to environmental changes, such as decreases in lake volume (Griffiths and Schindler 2012) or increasing temperature as a result of climate change (Schindler et al. 2005). Additionally, bioenergetics models expanded to the population level have examined predator-prey dynamics, comparing prey supply with consumer demand (Beauchamp et al. 2004). We used a unique application of a bioenergetics model parameterized for juvenile Sockeye Salmon (Beauchamp et al. 1989) to understand the metabolic constraints and opportunities that can exist within a single lake, owing to diversity in foraging habitat.

We applied our bioenergetics model in conjunction with field-derived temperature, diet, and growth data to evaluate how use of lake resources can influence consumption rates and growth efficiency of juvenile Sockeye Salmon in a shallow Alaska lake. Our first objective was to estimate summer consumption rates and growth efficiency of age-0 (newly emerged) and age-1 juvenile Sockeye Salmon from Afognak Lake, based on observed temperatures and diet composition. We hypothesized that age-0 juveniles would have higher mass-specific consumption and growth efficiency due to smaller body size. Our second objective was to assess consumption rates and growth efficiency of age-0 Sockeye Salmon across a range of thermal conditions and diet compositions, representing different foraging scenarios within Afognak Lake. We hypothesized that fish residing in warmer, littoral habitats would have a higher consumption demand and that fish foraging primarily on insects would be most efficient at converting consumed energy into growth.

Methods

Study system

Afognak Lake, located within the Kodiak Archipelago, is a small, shallow lake. The majority of the lake consists of extensive littoral zones that are less than 10m in depth. Pelagic habitat is limited to three small areas that reach depths of 24.5, 20.5, and 26.0 m (Ruhl 2016; Figure 2.1). Mean summer lake temperature is 10.4 °C (from 1989 to 2014); however, Afognak Lake shows large inter-annual and seasonal variability in temperature (Thomsen and Ruhl 2015). The zooplankton community is relatively low in biomass and diversity. *Bosmina* spp. and *Epischura* spp. together make up 81% of the total zooplankton density (Thomsen and Ruhl 2015); however, substantial alternative terrestrial and benthic prey are exploited by juvenile Sockeye Salmon (Richardson 2016). Sockeye Salmon returns to Afognak Lake are among the earliest within the Kodiak Archipelago and mature adults spawn on lake shoals and stream tributaries in late summer and fall (White et al. 1990). Fry emerge the following spring and most juveniles rear in the lake for one summer, overwinter, then migrate to the ocean early in the subsequent summer (May-June). Approximately 25% of individuals overwinter a second year, and head to sea as age-2 smolt (Thomsen and Ruhl 2015). Eggs, fry, and fingerling Sockeye Salmon are at risk of predation by other lake inhabitants including Coho Salmon (*Oncorhynchus kisutch)*, Rainbow Trout (*Oncorhynchus mykiss)*, and Dolly Varden (*Salvelinus malma)*. The lake supports a prodigious population of Threespine Stickleback (*Gasterosteus aculeatus)* which have the potential to compete for shared resources with Sockeye Salmon fry (O'Neill and Hyatt 1987).

Field Methods

Juvenile Sockeye Salmon were collected from Afognak Lake every two weeks from May through August, 2013. A beach seine was used to collect fish (n=317) at five littoral sites and a trawl net was towed in deeper areas to collect fish (n=16) offshore. Upon capture, fish were measured (fork length, mm), weighed to the closest 0.1g, and a scale was removed and slide mounted for age determination at the Kodiak Alaska Department of Fish and Game (ADF&G)

laboratory. Juveniles were randomly selected for either energy density or diet analysis. Stomachs were removed and immediately placed in ethanol or whole fish were frozen and sent to the ADF&G Soldotna Lab for bomb calorimetry to measure energy density. Prey items were identified to the lowest possible taxonomic resolution and life history stage (McCafferty 1983, Pennak 1989). Diet composition was calculated as the proportion of each prey type by weight (Richardson 2016). Lake temperatures were continuously recorded at depths of 1m, 5m, 10m, and 13m using a water temperature logger (HOBO pro V2©).

Model formulation

The bioenergetics model was based on a standard mass balance bioenergetics equation (Kitchell 1977), where energy consumed is equal to energy lost through metabolic processes:

$$C = R + SDA + F + U + G$$

where R is respiration, SDA is specific dynamic action (digestive costs), F is egestion, U is excretion, and G is growth. We assumed constant swimming speed and calculated respiration as a function of body size, temperature, and swimming speed, according to a respiration model parameterized for Sockeye Salmon by Beauchamp et al. (1989). Digestive costs, egestion, and excretion were calculated as a constant proportion of consumption (Beauchamp et al. 1989).

Model inputs

We used bimonthly weight and length data to develop separate growth models for age-0 and age-1 Sockeye Salmon for estimating daily growth (g/d). We calculated seasonal mean energy density for each fish age class (age-0 = 2,834 J/g and age-1 = 3,844 J/g), which was held constant throughout model simulations. The model was run from May 14 through August 11, 2013 (90 days), which corresponds to the timeframe for which diet data were available. Diets were analyzed and input separately for each age class. Due to small sample sizes, biweekly diet data were combined for model input in monthly steps (Table 2.1). Energy density of prey items were obtained from the literature (Table 2.1). Hourly temperatures were averaged to obtain a mean daily temperature at each depth. Temperatures were then integrated across all depths to obtain a mean daily temperature for each day of model input (Figure 2.2).

For objective two, we applied the same physiological and growth parameters, predator energy density, and prey energy density from the age-0 model. We chose this model to represent the lake rearing population, as the majority of Afognak Lake smolt migrate to the ocean after one year (Thomsen and Ruhl 2015). We ran 27 scenarios that represented a range of thermal conditions and prey combinations, described in detail below. The model was run from May 14 through Sept 18 (128 days), the duration of recorded lake temperatures.

We created nine diet scenarios to encompass a range of prey choices potentially available to Sockeye Salmon in the lake. Diets were simplified to the broad prey categories of insects and zooplankton, as the majority of measured prey items (>95%) fell into one of those two categories. Mean energy densities values were calculated for the broad zooplankton and insect prey categories by averaging individual zooplankton and insect taxa observed in the diets. The first diet scenario represented a diet made of 90% zooplankton and 10% insects. For succeeding diet scenarios, zooplankton contribution was adjusted down by 10% while the insect contribution was adjusted up by 10% (i.e., the next diet scenario was 80% zooplankton and 20% insects). This was repeated eight times until a diet composition of 10% zooplankton and 90% insects was achieved. Diet inputs were held constant across the model simulation period for each scenario.

Recorded temperatures were used to simulate thermal experiences of Sockeye Salmon within three habitats: littoral, pelagic, and whole lake utilization. For pelagic scenarios we used daily mean temperature at 13 m, which was located below the lake thermocline during the period of stratification. We used 1 m lake temperatures for littoral model inputs, as both littoral and surface waters are shallow and responsive to changes in air temperature (Arhonditsis et al. 2004). For the whole lake scenarios, temperatures were averaged across all depths to obtain daily mean lake temperature. This represents the thermal experience of a fish that is using all lake depths uniformly.

We summarized model outputs in terms of daily consumption (g/d) and mass-specific consumption (daily consumption/consumer weight, g/g/d). We calculated the growth efficiency, or the efficiency with which consumed prey are converted to growth, by dividing fish growth (g/d) by consumption (g/d).

Results

For our age-1 growth model, we fit a linear regression model that related weight (W) to Julian day (JD) (β_0=0.0284, β_1=-1.5, R^2= 0.6243, $p < 2.2\times10^{-16}$). A linear regression model displayed non-constant variance and was determined a poor fit when applied to age-0 fish, therefore, a separate model was used to describe age-0 growth. We first constructed a Von Bertalanffy growth curve to determine fish length for each Julian day ($L=78.32 \times (1-e^{-0.0085\times(JD-98.24)})$). We then fit a non-linear model on weight-length data ($W=5.782\times10^{-6}\times L^{3.17}$) to predict weight from length.

Mass-specific consumption and growth efficiency were higher for age-0 juvenile Sockeye Salmon compared to age-1 juveniles (Figure 2.3 and Figure 2.4). Seasonal mean consumption rates were 0.23 ± 0.02 g/g/d and 0.14 ± 0.05g/g/d and seasonal mean growth efficiency was 14.6 ±7.3% and 7.0± 3.8% for age-0 and age-1 fish, respectively. On June 20 (Julian day 179), age-1 fish shifted their diets to include a greater proportion of zooplankton forage, which resulted in a 34% increase in consumption rate and a 35% decrease in growth efficiency. At the same time, age-0 fish increased their foraging capacity to include a higher proportion of insects in the diet, which led to a 16% reduction in consumption rate and 17% increase in growth efficiency. Both age classes showed a physiological response to temperature, particularly during peak temperatures when consumption demand reached a maximum and growth efficiency decreased.

When examining the outputs from the 27 model scenarios, estimated cumulative consumption by an individual age-0 juvenile Sockeye Salmon over the simulation period ranged from 24.65 g (pelagic habitat, 10% zooplankton / 90% insect diet) to 39.81 g (littoral habitat, 90% zooplankton / 10% insect diet), almost a twofold difference across model scenarios (Figure 2.5). Total consumption was greater for all littoral scenarios relative to pelagic scenarios (Figure 2.5). Mass-specific consumption rates were higher and showed greater variance across the simulation period for littoral scenarios (maximum= 0.40 g/g/d, seasonal mean= 0.25 ± 0.05 g/g/d) compared to pelagic scenarios (maximum=0.25 g/g/d, seasonal mean= 0.19± 0.01 g/g/d) (Figure 2.6 and Figure 2.7). A fish that fed on insects in littoral habitats would require greater consumption to achieve the same seasonal growth than a fish foraging in the lake pelagia, regardless of prey choice. Elevated consumption demand due to habitat choice led to consequences for conversion efficiency. Mean growth efficiency for littoral scenarios was lower than pelagic scenarios (10.5% vs.12.8%, Figure 2.8 and Figure 2.9).

Daily rations were lowest for model scenarios in which insects were a dominant component of the diet (seasonal mean = 0.21 ± 0.04 g/g/d for a 90% insect diet and seasonal mean = 0.26 ± 0.05 g/g/d for a 90% zooplankton diet, Figure 2.6 and Figure 2.7). Irrespective of habitat, every 10% increase in zooplankton in the diet resulted in approximately a 2.9% increase in mass-specific consumption rate. Therefore, a fish feeding on a diet of 90% zooplankton would need to consume 25.4% more prey mass than a fish feeding on a diet of 90% insects (Figure 2.6). Growth efficiency improved when the proportion of insects increased in the diet. Mean growth efficiency was 20.3% higher for high insect diet scenarios relative to high zooplankton diet scenarios (Figure 2.8 and Figure 2.9).

Daily consumption (g/d) increased and growth efficiency decreased across the simulation period due, in part, to increasing body size as fish grew throughout the summer. Mean growth efficiency declined from 26.5 % in May to 15.9% and 8.0% in June and July, respectively, before reaching an asymptote at approximately 5.5% in August and September (Figure 2.8 and Figure 2.9). When controlling for body size, temporal patterns in consumption rates related to temperature emerged. Thermal experience was relatively consistent between littoral and pelagic scenarios in May, but diverged in July when surface temperatures peaked. Mass-specific consumption rates peaked with temperature in July, particularly in littoral and whole lake scenarios. This introduced greater differences in mass-specific consumption between littoral and pelagic foraging scenarios (Figure 2.6 and Figure 2.7).

Discussion

Our model provided insight in to the physiological constraints and opportunities of juvenile Sockeye Salmon, which is influenced by fish size, thermal experience, and prey quality. We found that mass-specific consumption and growth efficiency were higher for age-0 juvenile Sockeye Salmon compared to age-1 juveniles. Seasonal mean consumption rates were 0.23 g/g/d and 0.14 g/g/d and seasonal mean growth efficiency was 14.6 % and 7.0% for age-0 and age-1 fish, respectively. Differences in age-0 and age-1 values are likely due to allometric scaling of size dependent physiological parameters, small initial mass of age-0 fish, and differences in growth allocation (i.e., age-0 fish allocated more initial growth to length than weight). Our consumption estimates were slightly higher than consumption rates reported in other Sockeye Salmon bioenergetics studies (0.16 g/g/d Black Lake, Griffiths and Schindler 2012; 0.08 g/g/d Babine Lake, Beauchamp et al. 1989). Higher mean mass-specific consumption estimates for Afognak Lake Sockeye Salmon could be due to warmer temperatures experienced within the lake and lower initial mass of fish in the model.

Bioenergetics models generate plausible consumption rates that can be used for qualitative comparisons among model scenarios that represent different ecological conditions; however, this approach has some limitations. We applied species-specific parameters (Beauchamp et al. 1989) but assumed constant swimming speed, as is common in many bioenergetics models. We also recognize that physiological parameters for one population of Sockeye Salmon may not mirror those of another. Furthermore, our model scenarios were simplifications of reality and do not fully represent the foraging environment for Sockeye Salmon in Afognak Lake. Our model did not account explicitly for foraging movements or habitat switching by mobile consumers. While this is a major caveat of the model, the model scenarios were useful for bracketing the range of potential consumption by Sockeye Salmon under different combinations of prey quality and temperature, and examining the metabolic costs and benefits of choosing one foraging scenario over another.

Our model estimates suggest that the foraging scenario for age-0 Sockeye Salmon to achieve the highest growth efficiency is to consume insects while residing in the lake pelagia. The ecological consequences to juvenile Sockeye Salmon from utilizing the lake’s insect forage base would depend on the mechanism of prey acquisition. The delivery of insects to juvenile Sockeye Salmon may be recipient-controlled or donor-controlled (Polis et al. 1997). If a spatial mismatch exists between pelagic habitat and insect availability, we posit that through a recipient-controlled process, Sockeye Salmon could seek and control the rate of prey consumed from littoral, benthic, or surface water habitats. Given that Afognak Lake is shallow and narrow and that juvenile Sockeye Salmon are capable of sustained swimming speeds of 0.54 m/s (Brett 1967), it is feasible that Sockeye Salmon forage within multiple habitats of Afognak Lake. Although this strategy would incur extra swimming costs and increased risk of predation, some evidence suggests that if fish undergo short (< 60 minute) inter-habitat excursions, thermoregulatory costs are minimal (Pépino et al. 2015).

We hypothesize that the optimal foraging scenario could also arise from donor control, in which the insect prey (i.e., donor) is delivered directly to Sockeye Salmon. Benthic production of Dipterans, particularly chironomids, can contribute substantially to total secondary productivity in lakes (Armitage et al. 1995) and during their pelagic ascendance from benthic pupae to surface emergent adult, chironomids are temporarily available as pelagic prey. Benthic-pelagic coupling has been observed across a range of lakes and a growing number of studies have shown that benthic prey can make up over 50% of total fish consumption (Vander Zanden and Vadeboncoeur 2002, Schindler and Scheuerell 2002, Wagner et al. 2012). Because habitat coupling and chironomid production are higher in shallow lakes (Babler et al. 2008, Butkas et al. 2011), a donor-controlled benthic prey subsidy is possible, considering the shallow character of Afognak Lake. Furthermore, a donor-controlled subsidy could result in higher growth potential for Sockeye Salmon by reducing their energetic costs of foraging. However, both donor and recipient controlled processes exist along a gradient, making it possible for both mechanisms to function during Sockeye Salmon prey acquisition.

When comparing our observed foraging patterns in context of bioenergetic model results, juvenile Sockeye Salmon in Afognak Lake may not forage under the optimal scenario due to ecological constraints that are not included in the modeling framework. Sockeye Salmon, as mobile consumers, may adapt their foraging not only in response to temperature and prey supply, but also to other environmental factors such as perceived predation risk and competitive interactions. Predation risk varies spatially and temporally across lake habitats and across body size; fish will forego foraging opportunities when the threat of predation is high (Power 1984, Sih 1980, Werner et al. 1983). Shallow habitats are known areas of refuge from pelagic piscivores (Crowder et al. 1994, Werner et al. 1983), yet fish residing in littoral habitats are susceptible to avian and terrestrial predators in addition to aquatic predators (Power 1984). Both pelagic and littoral habitats may pose risks, and juvenile Sockeye Salmon must balance energetic reward with predation risk when making foraging decisions. Competition, either for space or food, can also guide an individual's decision on where to forage and what type of prey to pursue. In Afognak Lake, Threespine Stickleback have the potential to outcompete juvenile Sockeye Salmon for shared resources, particularly in pelagic habitats where Threespine Stickleback densities are high (approximately 225-fold higher than Sockeye Salmon; Richardson, unpublished data). Limited food or high densities of competitors can result in prey switching (O'Neill and Hyatt 1987, Werner and Hall 1979). Thus, there are numerous, interacting factors that contribute to foraging decisions of fishes.

The behavioral responses of fish to temperature, quantity and quality of prey, potential competition, and predation risk are dynamic and difficult to represent in a simple model. However, the bioenergetics model was a useful heuristic tool to help understand the consequences of changing thermal conditions and available prey types for juvenile Sockeye

Salmon consumption demand and growth efficiency in Afognak Lake. Our results generated hypotheses about potential mechanisms leading to alternative foraging scenarios and may be used to direct future research. For example, potential food supply for juvenile Sockeye Salmon has traditionally been evaluated through pelagic production estimates for phytoplankton and zooplankton (Koenings and Burkett 1987); however, we propose continued investigation to characterize the magnitude, timing, and variability in consumption of insects by Sockeye Salmon. Additionally, evidence of diel horizontal movements (DHM) of fishes, including salmonids, is increasing (e.g., Armstong et al. 2013) and juvenile Sockeye Salmon may undergo DHM to take advantage of littoral prey resources and optimal temperatures of pelagic habitats. Future investigations of potential Sockeye Salmon DHM in the lacustrine environment are warranted. By understanding how juvenile Sockeye Salmon use their rearing environments, we will better understand what limits population productivity and, in turn, carrying capacity. This knowledge would contribute to habitat-based models that are currently used to set escapement goals for many Sockeye Salmon stocks in Alaska.

Acknowledgements

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compliance with the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks (approval #453388) and under ADF&G fish collection permit #CF-2012-20.

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Figures

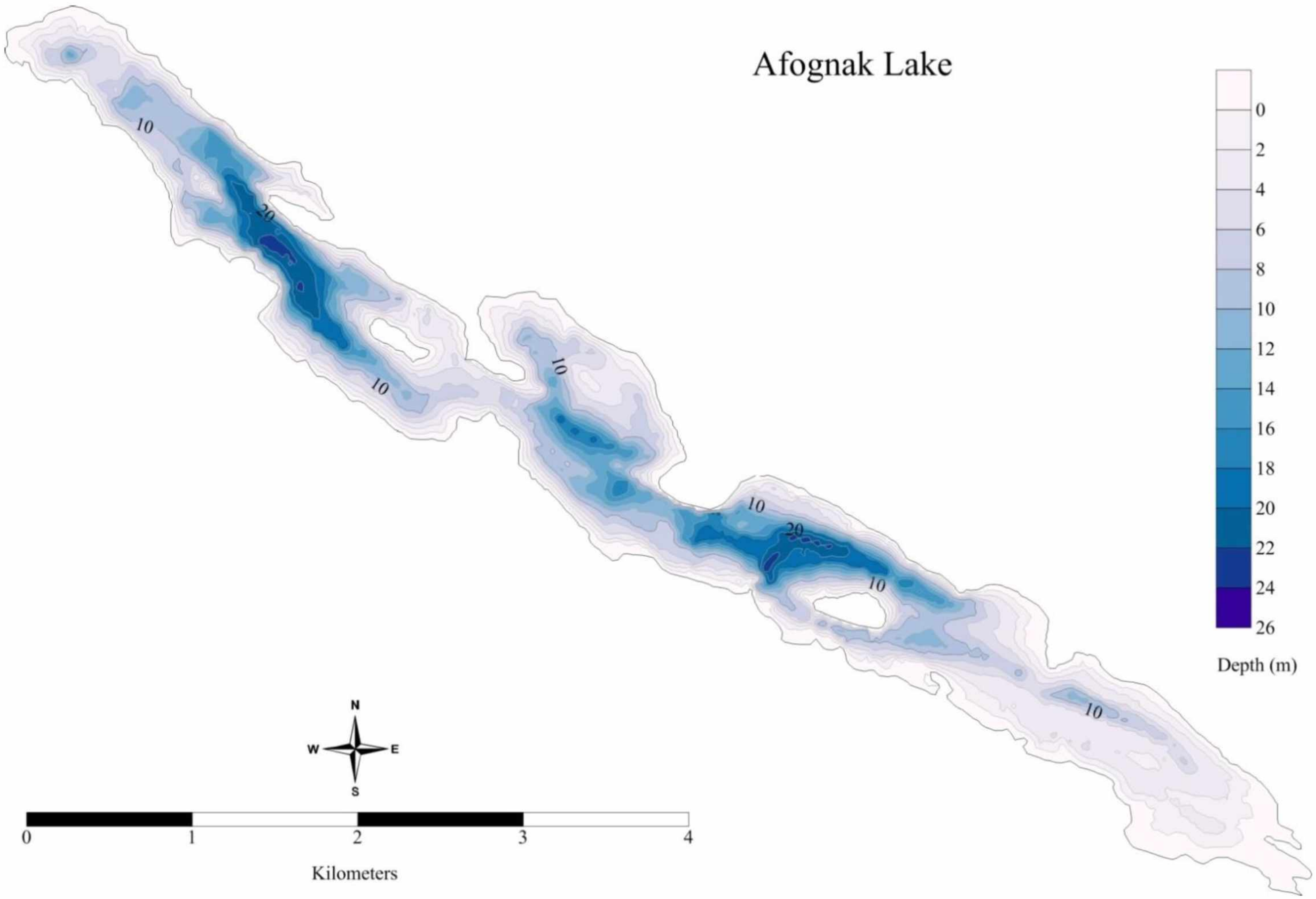

Figure 2.1 Map of Afognak Lake, Kodiak Archipelago, Alaska. The lake is characterized by extensive shallow littoral habitat with a mean depth of 9.17 m and a maximum depth of 25.97 m. (Image credit; Heather Finkle.)

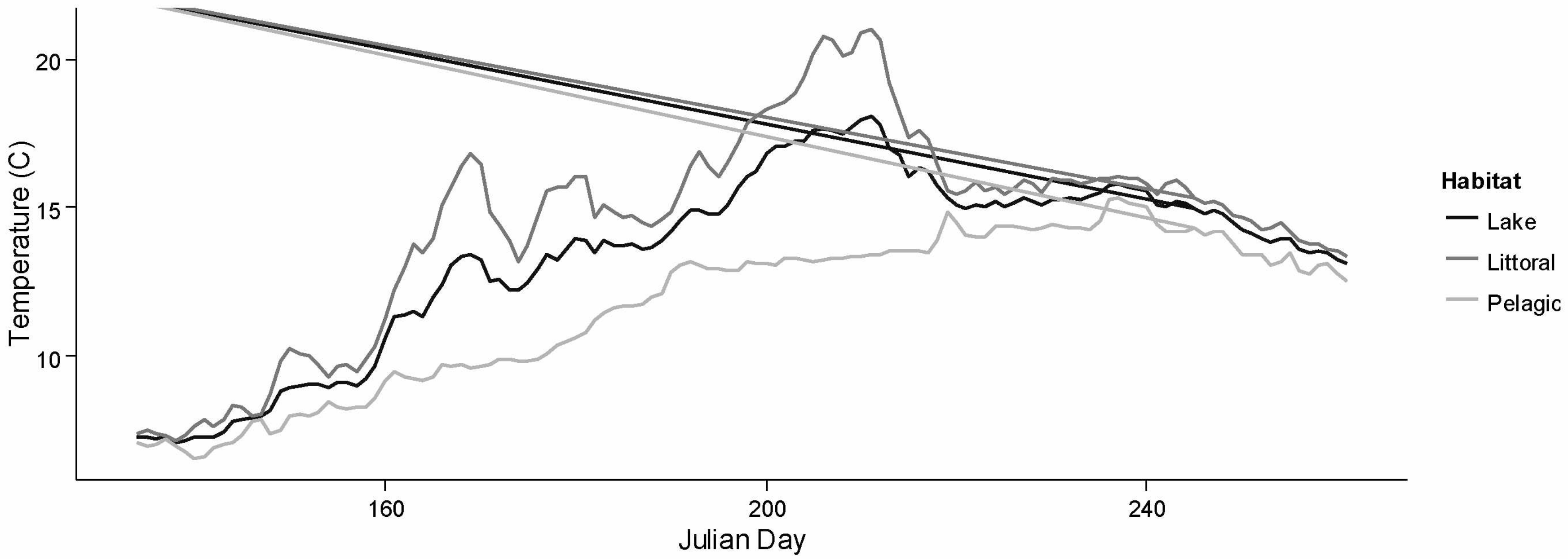

Figure 2.2 Thermal profiles of three habitats within Afognak Lake. Hourly temperatures were recorded from May 14 through August 11, 2013 and averaged to obtain a mean daily temperature. Pelagic temperatures were recorded at 13 m, located below the lake thermocline if one was established. Recorded 1 m temperature data were applied as littoral temperatures. Whole lake temperatures are represented by temperatures integrated across 1, 5, 10, and 13 m depths.

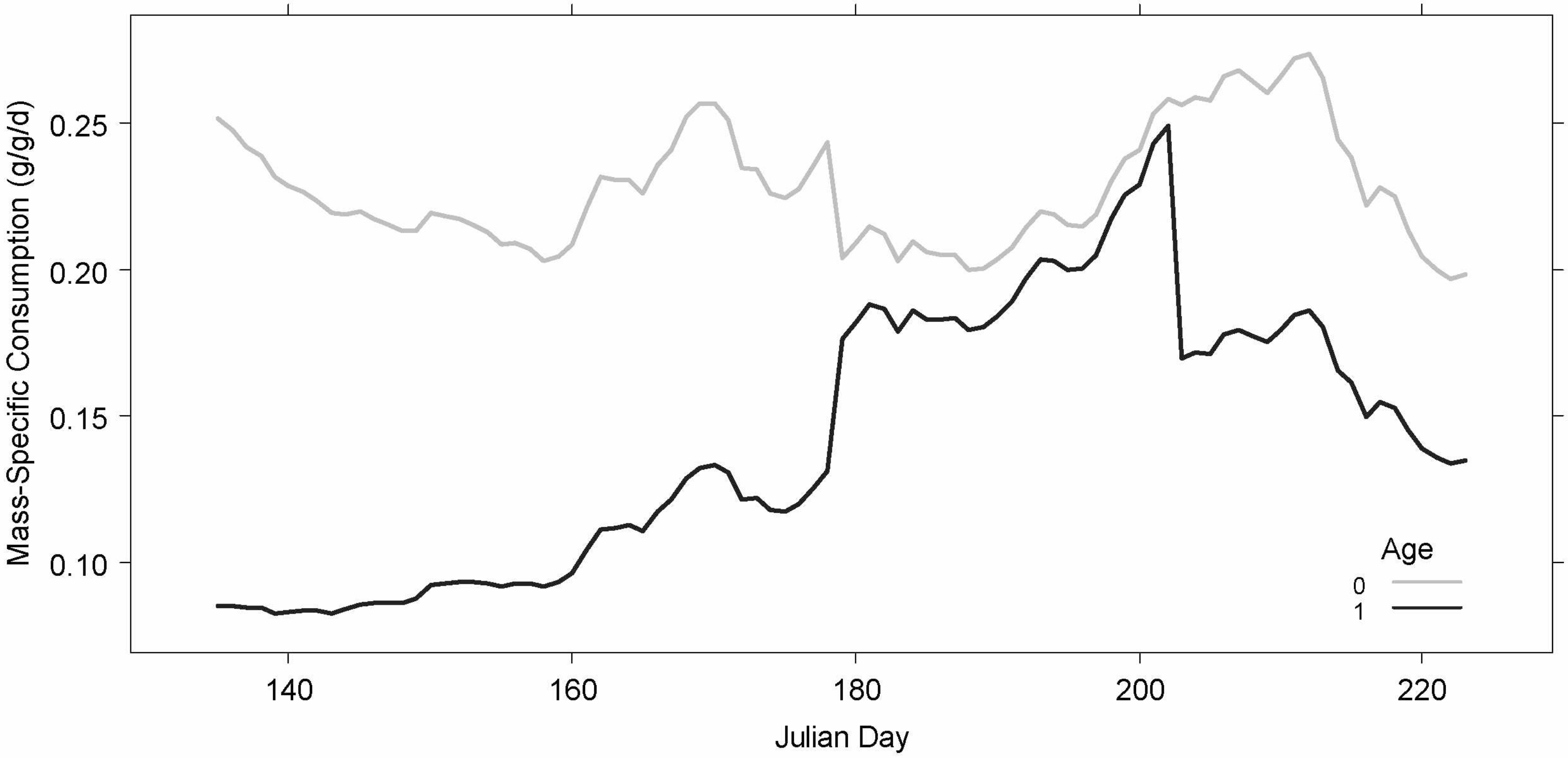

Figure 2.3 Daily mass-specific consumption (g/g/d) for age-0 and age-1 juvenile Sockeye Salmon. Consumption rate was estimated separately for age-0 and age-1 individuals from Afognak, Lake from May 14 through August 11, 2013. Seasonal mean consumption rates were 0.23 ± 0.02 g/g/d and 0.14 ± 0.05g/g/d for age-0 and age-1 fish, respectively. On Julian day 179 (June 20), shifts in diets resulted in a 34% increase in consumption rate for age-1 fish and 16% reduction in consumption rate for age-0 fish.

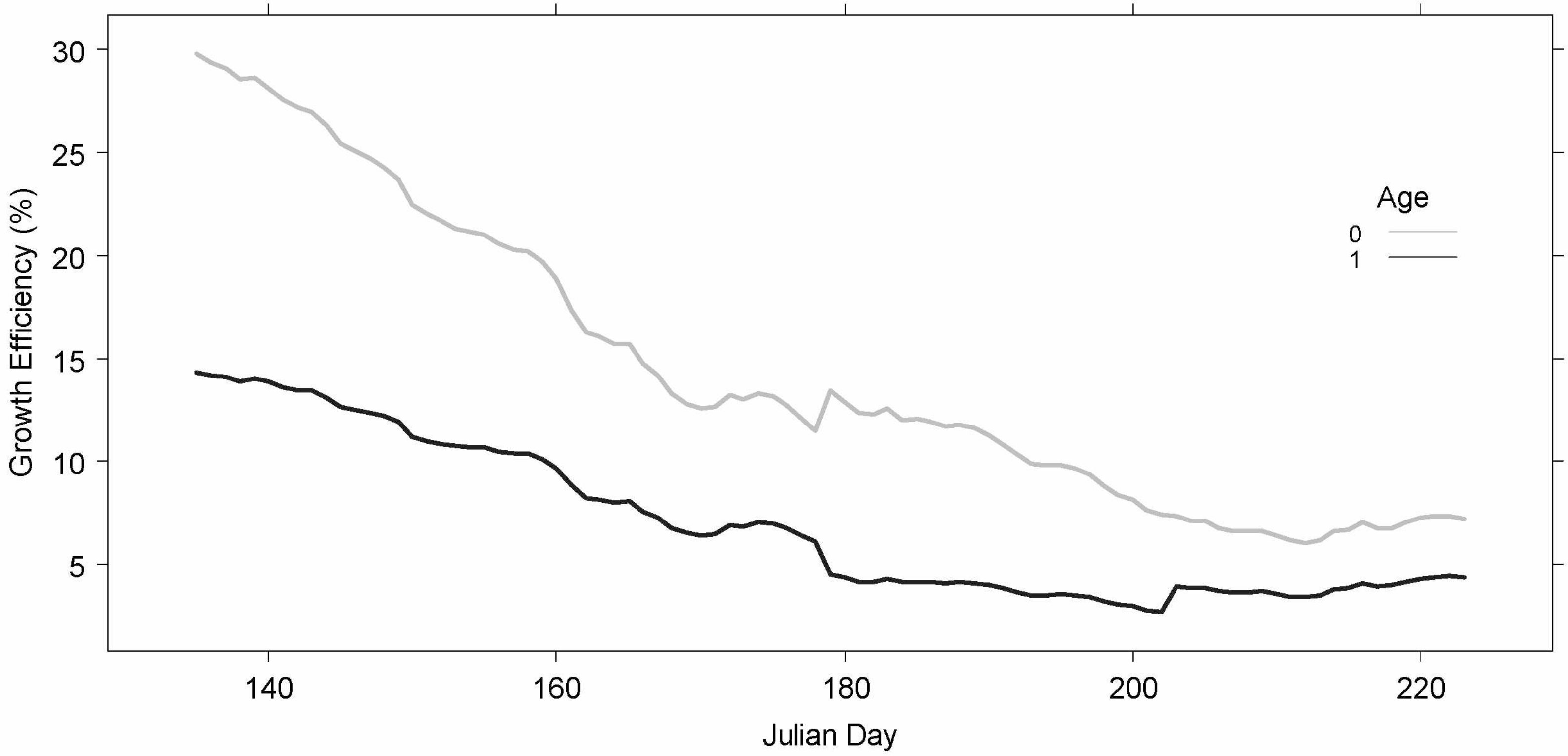

Figure 2.4 Daily growth efficiency (%) of age-0 and age-1 juvenile Sockeye Salmon. Growth efficiency was estimated for an individual age-0 and age-1 juvenile Sockeye Salmon in Afognak Lake, from May 14 through August 11, 2013. Seasonal mean growth efficiency was 14.6 ±7.3% and 7.0± 3.8% for age-0 and age-1 fish, respectively. On June 20 (Julian day 179), age-1 fish shifted their diets to include a greater proportion of zooplankton forage, which resulted in a 35% decrease in growth efficiency.

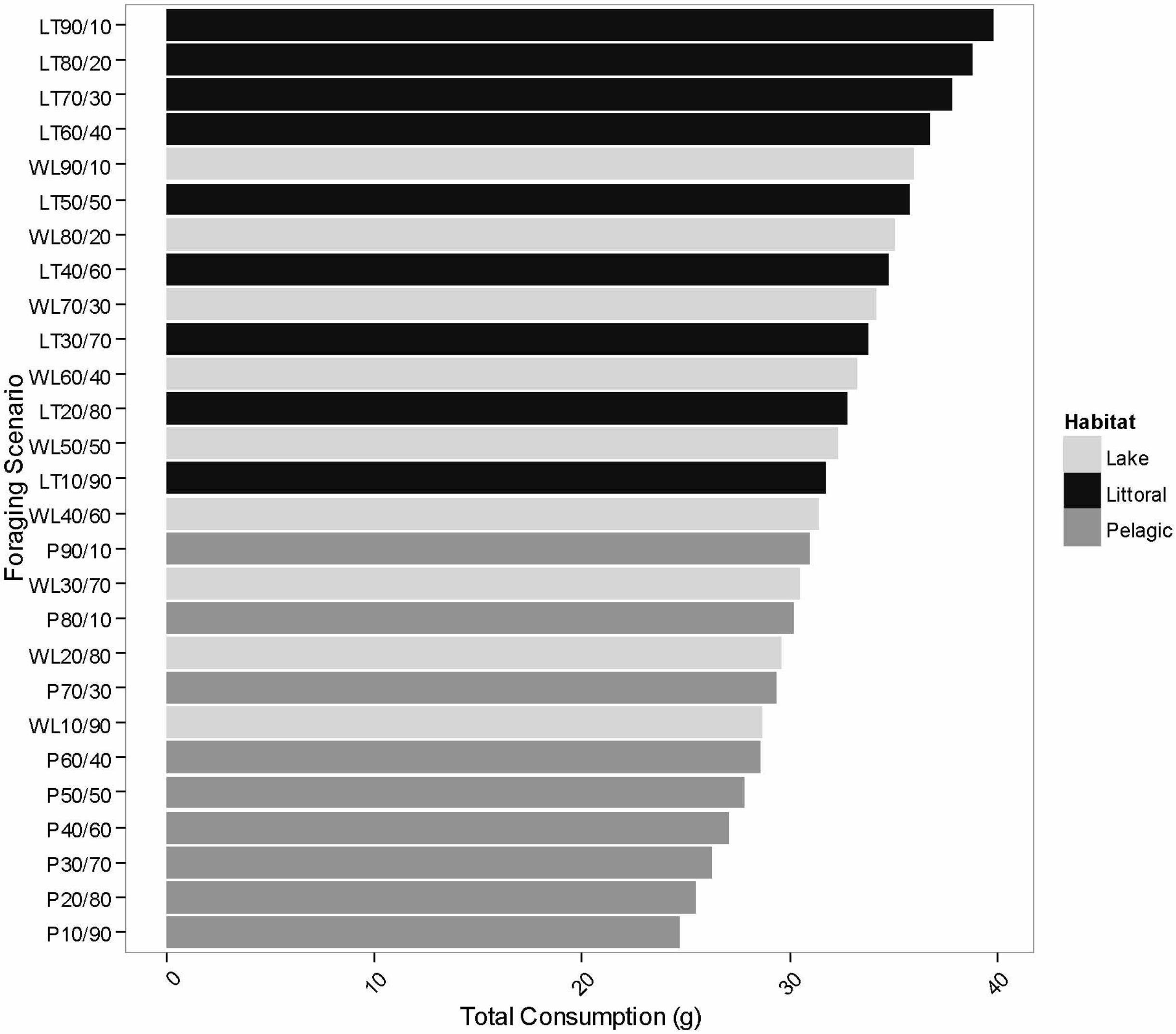

Figure 2.5 Cumulative consumption by an individual age-0 juvenile Sockeye Salmon across model scenarios in Afognak Lake. Total consumption was estimated from 14 May through 18 September, 2013. Twenty seven scenarios were run to represent a range of thermal conditions and prey combinations. LT, P, and W represent thermal experience of Sockeye Salmon within three habitats: littoral, pelagic, and whole lake utilization. Numbers indicate the percentage of zooplankton and insects (% zooplankton / % insects) used for diet inputs. Estimated cumulative consumption ranged from 24.65g (P10/90) to 39.81g (LT90/10) and total consumption was greater for all littoral scenarios relative to pelagic scenarios.

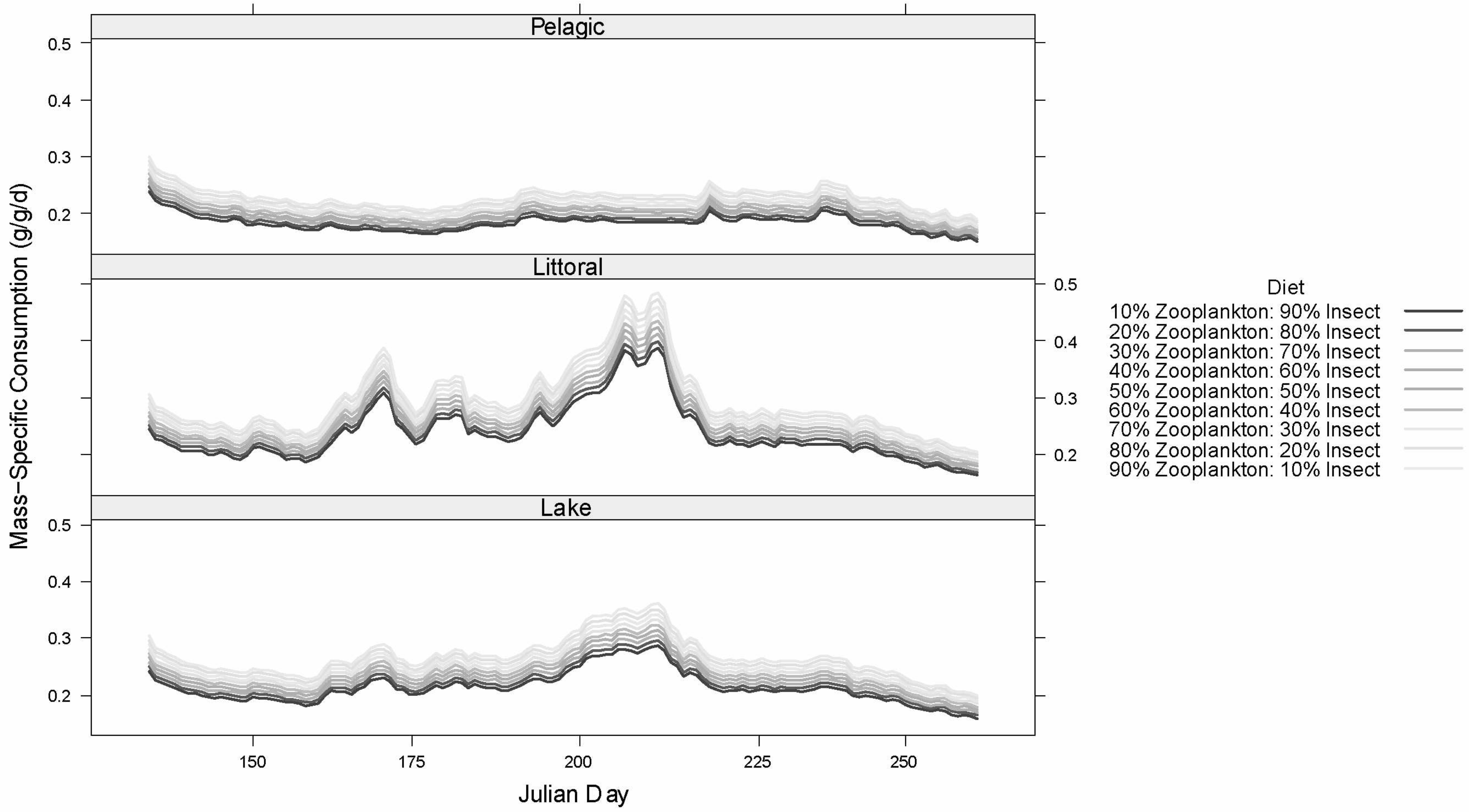

Figure 2.6 Daily mass-specific consumption of age-0 juvenile Sockeye Salmon across model scenarios in Afognak Lake. Consumption rate was estimated from 14 May through 18 September, 2013. Recorded temperatures were used to simulate thermal experience within three habitats (littoral, pelagic, and whole lake utilization) and 9 diet compositions were simulated within each habitat to create 27 model scenarios. Consumption rates were higher and showed greater variance across the simulation period for littoral scenarios compared to pelagic scenarios. Consumption rate was lowest for model scenarios in which insects were a dominant component of the diet and every 10% decrease in proportion of insects in the diet resulted in a 2.9% increase in consumption.

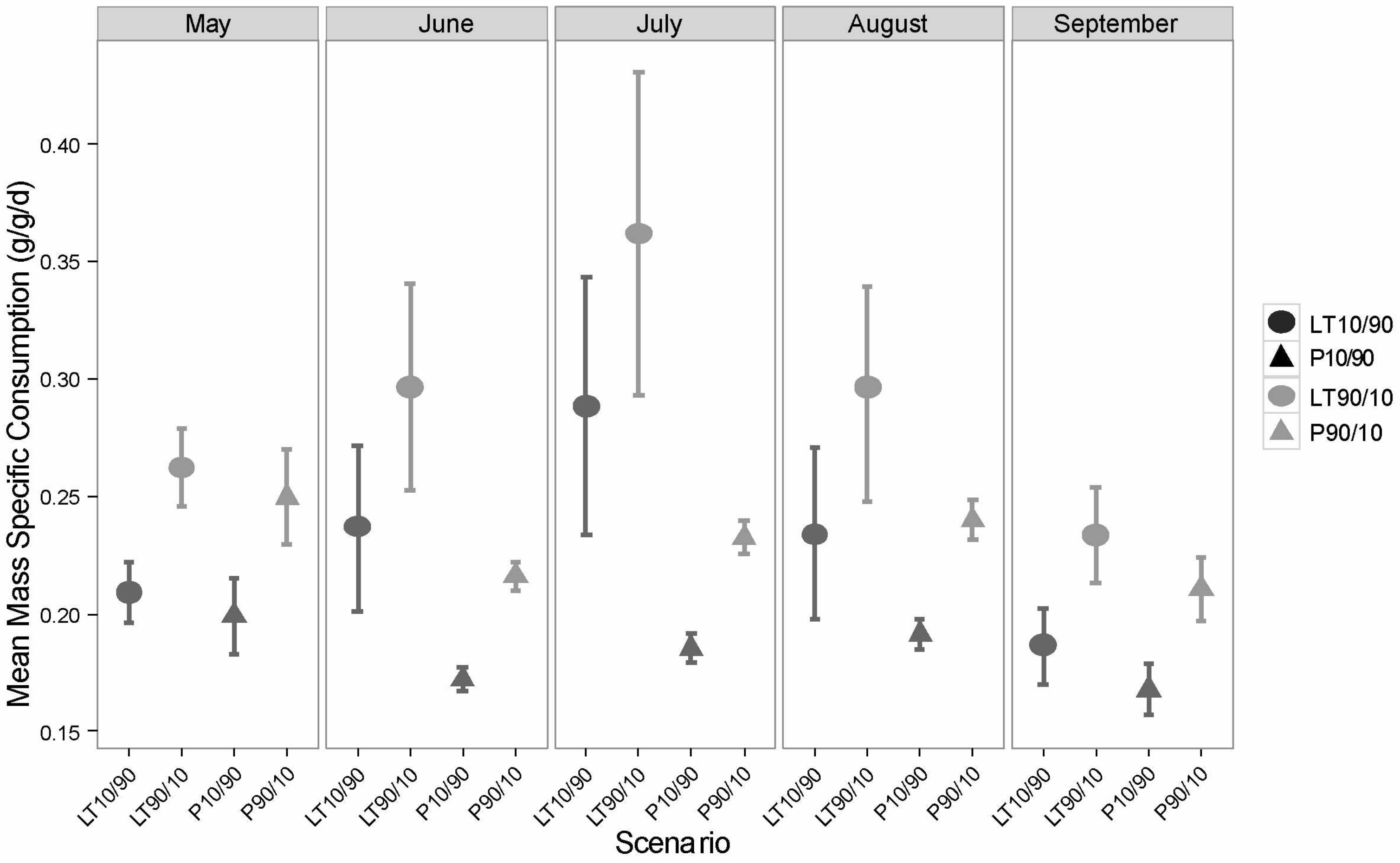

Figure 2.7 Mean mass-specific consumption (g/g/d) of age-0 juvenile Sockeye Salmon by month, habitat, and diet. Four model scenarios that bracket the range of habitat and prey model inputs are shown. Consumption rates were similar between littoral and pelagic scenarios in May and September, but diverged due to temperature increase, particularly in July when littoral temperatures peaked. LT, P, and W represent thermal experience of Sockeye Salmon within three habitats: littoral, pelagic, and whole lake utilization. Numbers indicate the percentage of zooplankton and insects (% zooplankton / % insects) used for diet inputs.

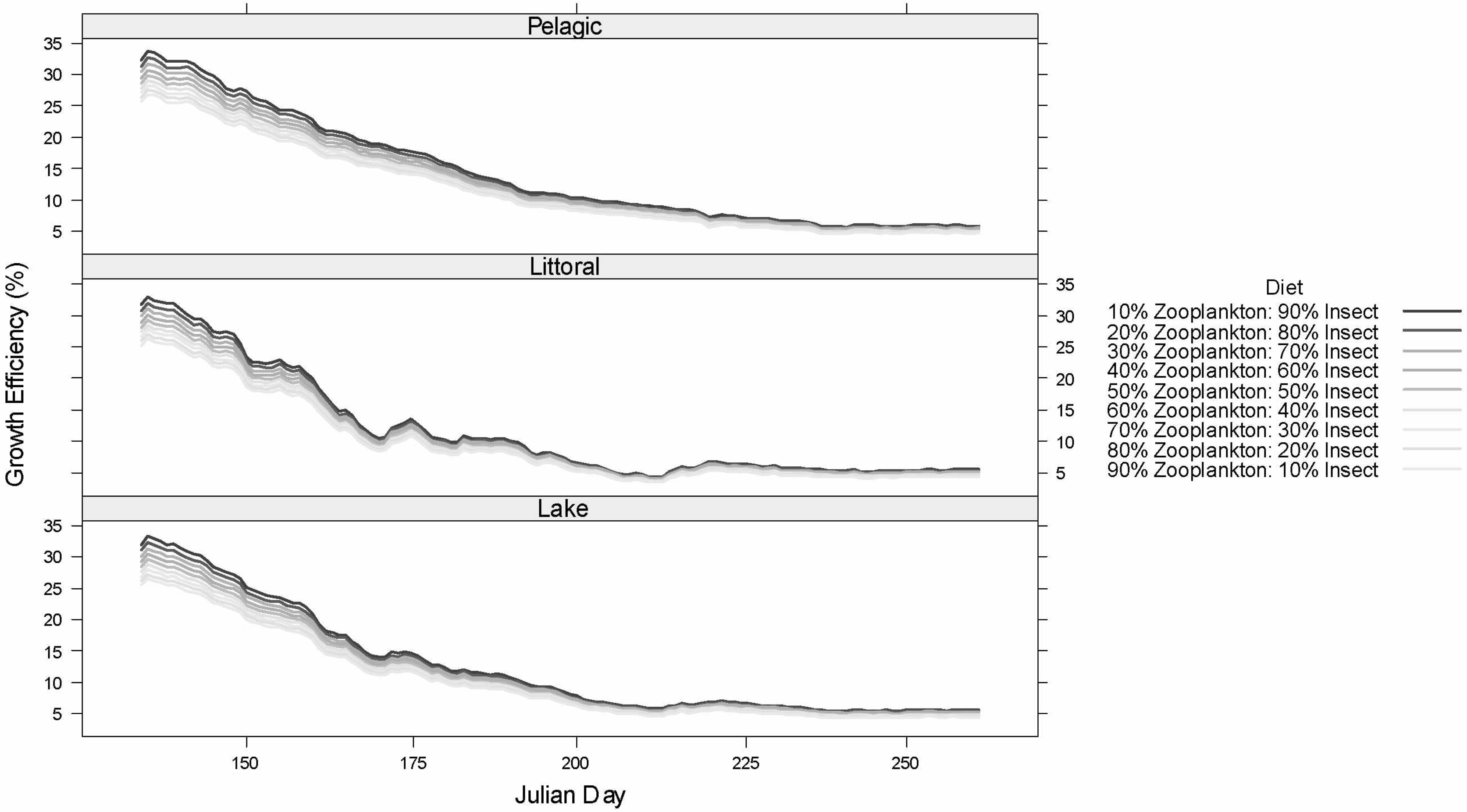

Figure 2.8 Daily growth efficiency of age-0 juvenile Sockeye Salmon across model scenarios in Afognak Lake. Model simulations were run from 14 May through 18 September, 2013. Recorded temperatures were used to simulate thermal experience within three habitats (littoral, pelagic, and whole lake utilization) and 9 diet compositions were simulated within each habitat to create 27 model scenarios. Growth efficiency decreased across the simulation period due, in part, to increasing body size as fish grew throughout the summer. Mean growth efficiency was higher for high insect diet scenarios relative to high zooplankton diet scenarios and for pelagic scenarios relative to littoral scenarios.

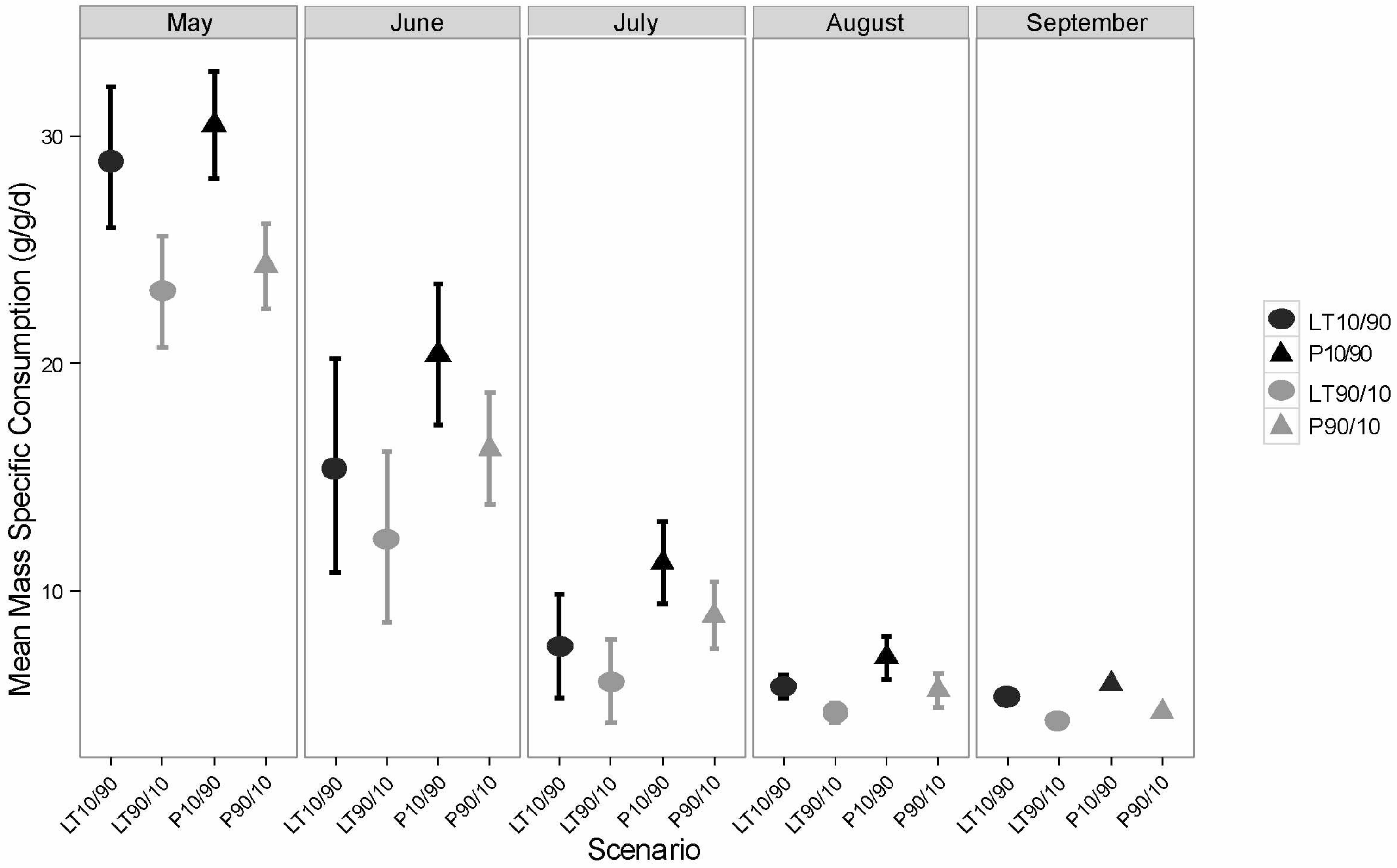

Figure 2.9 Mean growth efficiency of age-0 juvenile Sockeye Salmon by month, diet, and habitat. Four model scenarios that bracket the range of habitat and prey model inputs are shown. Mean growth efficiency declined from 26.5 % in May to 15.9% and 8.0% in June and July, respectively, before reaching an asymptote at approximately 5.5% in August and September. For each month Growth efficiency was always greatest for the P 10/90 scenario (pelagic habitat; 10% zooplankton / 90% insect diet) and lowest for the LT 90/10 scenario (littoral habitat; 90% zooplankton / 10% insect diet).

Tables

Table 2.1 Bioenergetic model inputs of prey energy density and diet proportions for age-0 and age-1 juvenile Sockeye Salmon in Afognak Lake. Diets were analyzed as a % by prey weight and input separately for each age class at approximately monthly steps. Prey energy densities were obtained from the literature and mean values were calculated when multiple references were available.

		Age-1 Sockeye Salmon Simulation Input			Age-0 Sockeye Salmon Simulation Input		
Prey Taxa	Energy Density (J/g)	Julian Day 134-178	Julian Day 179-202	Julian Day 203-223	Julian Day 134-178	Julian Day 179-202	Julian Day 203-223
Bivalve	814[a]	0.16	0	0	0	0	0
Coleoptera Larvae	4272[b]	0	0	0.07	0	0	0
Ephemeroptera Larvae	3076[b]	0	0	0	7.63	0	0
Fish Egg	5000[c]	0	0	0	0	0	0.06
Cladocera	2757[acde]	0.11	0	0.16	2.18	11.23	0.75
Copepoda	2558[acdefg]	0	8.01	0.55	1.42	4.42	0.93
Zooplankton Unid.	2745[acdefg]	11.23	64.63	0	63.9	18.58	32
Trichoptera Adult	4209[a]	0.12	0.23	1.07	0	0.23	0.55
Arachnida	4597[a]	0.22	0	0	0	0	0
Coleoptera	5144[a]	0	0	0.39	0	0	0.21
Collembola	4769[a]	0.12	0	0.06	0	0	1.17
Diptera	3647[bcfhi]	49.05	13.28	48.62	7.09	41.24	48.12
Homoptera	4721[a]	0	0	0.28	0	0	0.36
Hymenoptera	5030.5[ab]	0.2	0.17	3.95	0	0.54	1
Insecta	3647[abcde]	38.41	13.68	44.86	13.63	23.77	14.79
Seed	3000	0.36	0	0	4.14	0	0
Total		100	100	100	100	100	100

[a] Chittaro et al. 2014; [b] McCarthy et al. 2009; [c] Cummins and Wuycheck 1971; [d] Schindler and Eby 1997; [e] Luecke and Brandt 1993; [f] Schaeffer et al. 1999; [g] Krokhin 1957; [h] Hansen et al. 1997; [i] Gray 2005

General Conclusions

Benthic and pelagic production pathways in Afognak Lake

A major finding of this research is that adult insects, primarily emergent aquatic Dipterans, are an important prey resource for juvenile Sockeye Salmon (freshwater age-0 and age-1) rearing in Afognak Lake, Alaska, throughout the summer. Adult insects (mostly aquatic) made up 74% of juvenile Sockeye Salmon diets by weight and were present in 98% of all sampled stomachs. Our results challenge the long standing view that juvenile Sockeye Salmon in Afognak Lake and potentially other systems are primarily planktivores that prefer zooplankton prey (White et al.1990). We also demonstrated ontogenetic and temporal shifts in juvenile Sockeye Salmon diets that may relate to both size-based constraints on feeding and seasonal availability of prey in the lake.

Considering that insects can serve as primary prey for juvenile Sockeye Salmon, lake productivity models could be improved upon by incorporating both benthic and pelagic energy pathways. Benthic resources are thought to contribute more to small, shallow lake ecosystems (Babler et al. 2008, Butkas et al. 2011, Schindler and Scheuerell 2002); however, current research has shown the importance of benthic periphyton in large deep lakes (Vadeboncoeur et al. 2008). Furthermore, many Sockeye Salmon lakes are characterized as oligotrophic, particularly in Alaska, and benthic production is greater in clear, oligotrophic lakes relative to deep, mesotrophic or eutrophic lakes (Vandeboncoeur and Steinman 2002). More research is needed to quantify the degree to which benthic resources contribute to whole lake and sockeye salmon productivity, across a gradient of Sockeye Salmon lakes. Results from such research, could improve current models used to determine lake carrying capacity, and better inform managers when considering escapement goals and stocking of hatchery fish.

Nutrient additions to Afognak Lake from 1990 through 2000 were intended to promote pelagic productivity and bottom up controls on higher trophic levels. However, Afognak Lake has a high flushing rate (water residency time of 0.4 years; White et al. 1990) and a low depth ratio (maximum depth / mean depth; 0.353 m), two factors which can reduce the effects of fertilization (Holtham et al. 2004, Vadeboncoeur et al. 2008). Yet, mean zooplankton density was higher during years of fertilization (Thomsen and Ruhl 2015), suggesting nutrients did increase pelagic plankton productivity to some degree. Although data on benthic productivity are lacking, other fertilization studies have shown benthic primary production (i.e., algae, periphyton, and bacteria) may respond to nutrient additions (Blumeshine et al. 1997). Furthermore, the biomass of chironomids, a family of Diptera and important prey for Afognak Lake juvenile Sockeye Salmon and Stickleback, have shown a positive response to increased nitrogen and phosphorous levels (Blumeshine et al. 1997, Welch et al. 1988). Therefore, I hypothesize that benthic primary and secondary production in Afognak Lake may have increased as a result of increased nitrogen and phosphorous. Additional research is needed about the effects of fertilization on benthic and pelagic food web components as well as the extent to which increased prey production confers benefits to Sockeye Salmon populations through enhanced growth and survival.

Potential for competition between Threespine Stickleback and Sockeye Salmon

Interspecific competition occurs when species inhibit each other's access to a shared, limiting resource, thereby reducing the fitness of one or more species (Pianka 1983). In ecological studies, the reduction of fitness due to a lack of resources and not from other confounding effects is difficult to determine. Because competition can drive coexisting species to differ in their resource use, studies of resource partitioning can help describe when the potential for competition exists (Ross 1986). In Afognak Lake, Sockeye Salmon and Threespine Stickleback appear to partition prey and habitat resources. Threespine Stickleback diets showed greater overlap with diets of small Sockeye Salmon compared to diets of large Sockeye Salmon, mostly as result of shared zooplankton prey. This suggests that the degree of resource sharing could depend on the age and size structure of Sockeye Salmon in the lake and the availability of alternative prey. This study shows that Sockeye Salmon and Threespine Stickleback may use different prey resources, which may help alleviate interspecific competition.

Despite evidence for resource partitioning, Sockeye Salmon and Threespine Stickleback may still adversely affect each other through exploitative competition. Stickleback may indirectly compete by cropping down prey resources (i.e., chironomid larvae) before they become available as emergent adults for Sockeye Salmon. Although we did not investigate apparent competition, abundant Stickleback could attract and support a greater predator population, which in turn would invite increased predation pressure on Sockeye Salmon. However, Krogius and Krokhin (1956) suggested Dolly Varden feeding on Stickleback benefit Sockeye Salmon by releasing interspecific competitive pressure and Ruggerone (1992) found that Sticklebacks, with their defensive spines, can deter predators and serve as a predation refuge for juvenile Sockeye Salmon.

Heterogeneity in lake foraging habitat for Sockeye Salmon

Diversity in juvenile Sockeye Salmon foraging led us to consider the spatial heterogeneity of lakes and the variety of foraging opportunities available. To understand how juveniles may utilize a suite of thermal and prey resources within the lake environment, we applied a bioenergetics model in conjunction with field-derived data to evaluate how exploitation of lake resources can influence consumption rates and growth efficiency of juveniles. We estimated the consumption rate and growth efficiency of age-0 and age-1 juvenile Sockeye Salmon from Afognak Lake and across a range of foraging scenarios (thermal conditions and prey selection) potentially available within the lake. Across 27 model scenarios, total consumption was lowest and mean growth efficiency was highest for all cool, pelagic habitat scenarios. Daily consumption was lowest for model scenarios in which insects were a dominant component of the diet and mean growth efficiency was 20.3% higher for high insect diet scenarios relative to high zooplankton diet scenarios. Our models results highlighted the role of temperature and prey quality on consumption demand and metabolic processes in juvenile Sockeye Salmon.

Lake ecosystems are sensitive to changes in air temperature (Schindler et al. 1990, Wetzel 1983) and future climate models project increasing temperatures, particularly in northern latitudes (Stocker et al. 2013). Increased water temperatures in Sockeye rearing lakes could increase physiological stress for foraging juveniles, which could have implications for growth. Under current conditions, Afognak Lake littoral and whole lake temperatures often exceed the optimal level of 15° C, and can reach lethal temperatures of 20° C. Higher temperatures could create a rearing environment in which the majority of the lake is physiologically taxing or even uninhabitable. This thermal change in habitat would not only increase metabolic costs and consumption demand, but could also lead to reduced growth as a result of competition for space and prey resources. Temperature changes could also affect Sockeye Salmon through shifts in prey production, timing, or available species (Winder and Schindler 2004). In the face of a shifting climate, will there be sufficient high quality prey, at the right time, to compensate for increased consumption demand by Sockeye and their competitors? The bioenergetics model developed here could be paired with models forecasting changes in lake temperature and prey production to help elucidate how a changing climate may affect juvenile Sockeye Salmon bioenergetics and growth.

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