LINKING FRESHWATER GROWTH TO SIZE-DEPENDENT MARINE SURVIVAL OF

SOCKEYE SALMON: INTERACTIONS BETWEEN PROCESSES OF CLIMATE, DENSITY,

AND NATURAL SELECTION

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Abstract

Due to the mediating role of body size in determining fitness, the 'bigger is better' hypothesis still pervades evolutionary ecology despite evidence that natural selection on phenotypic traits varies in time and space. For Pacific salmon (genus *Oncorhynchus*), the size at which juveniles migrate to sea (i.e., smolts) has been linked to survival during the early marine period, where larger smolts typically survive at a higher rate than their smaller counterparts. However, the relationship of smolt size and survival becomes more ambiguous when considering confounding factors of age, ocean entry timing, and environmental variability. Despite equivocal results, smolt size appears to be a key trait and therefore changes in freshwater conditions may have consequences for population productivity. Furthermore, due to differences in site-specific habitats, trophic dynamics, and population traits the response of specific populations to these changes is likely to be context specific. The objective of this thesis was to 1) quantify the direction and magnitude of natural selection on smolt size for three age classes of sockeye salmon in a small watershed on Kodiak Island, AK and 2) explore stock-specific effects of temperature and conspecific density on smolt size over a multi-decade time-series to understand historic and possible future trends. To address our first objective, we calculated standardized selection differentials by comparing observed size distributions of out-migrating juvenile salmon to back-calculated smolt length from the scales of surviving, returning adults. Results reveal the magnitude of selection on size was very strong and consistent among years. However, the direction of selection on size consistently varied among age classes. The absolute magnitude of selection was negatively correlated to apparent marine survival and positively correlated to late mean ocean entry timing. To address our second objective, we back-calculated smolt size from returning adult scales to reconstruct a time-series of smolt length of two stocks within a small Alaska watershed on Kodiak Island. Using a dynamic linear model framework, we detected evidence that for one

stock, temperature was important in explaining smolt length, and density effects influenced both stocks utilizing the same lakes. Furthermore, forecasts of smolt length showed highly variable responses under scenarios of increasing temperature and high and low densities. Collectively, these results demonstrate that interactions between processes of climate, density, and natural selection are highly context-specific in terms of both inter- and intra- population variability.

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Introduction

Body size is a profoundly important phenotypic trait, as it has inter- and intra-specific fitness consequences for aquatic and terrestrial species (Brown et al. 1993; Choudhury et al. 1996; Sokolovska et al. 2000; Wikelski and Romero 2003). In many fishes, traits measuring reproduction and survival are strongly influenced by body size. Body size is positively correlated with female fecundity (Coates 1988; Eenennaam and Doroshov 1998), can mediate the outcome of territorial aggression in juvenile fish (Johnsson et al. 1999), and has survival advantages such as decreased susceptibility to starvation, predation, and environmental extremes (Sogard 1997). Moreover, in some cases, increased body size may incur competitive advantages during specific times in the life history, such as overwinter survival (Quinn and Peterson 1996) or predator avoidance among juveniles (Parker 1971).

Fish length is determined by a set of heritable alleles that control for body size and growth rate (Devlin et al. 2004; Biro and Post 2008). However, the phenotype for fish length is also plastic and can shift dramatically due to fish density (Holm et al. 1990), temperature (Brett et al. 1969), and other abiotic and biotic factors. The role of the environment in shaping specific phenotypic traits (e.g., increases in temperature resulting in a large body size) and imposing selection on a phenotypic trait (e.g., small fish may be more likely to be consumed by a size-selective predator) is an important focus of research in evolutionary ecology. Populations at equilibrium are predicted to experience stabilizing selection around a local fitness optimum; however, ecological change driven by abiotic or biotic factors can impose selection away from the current fitness peak, resulting in directional selection toward a new local or global optimum (Hendry 2017). Directional selection is likely to occur if there is 1) a shifting adaptive landscape among years and 2) opposing selection at some other life stage (e.g., Carlson et al. 2009). Life-history trade-offs between growth, survival, and reproduction at different life stages are predicted

to be particularly strong in migratory or metamorphosing species, because individuals are exposed to selection across ecosystems within and among generations. Therefore, directional selection is likely, as phenotypic traits that prove beneficial in one environment may incur a fitness disadvantage in the next or vice versa (Schluter et al. 1991; Waples et al. 2004; Gillis et al. 2008).

For anadromous Pacific salmon (genus *Oncorhynchus*), individual length of juveniles at ocean entry (i.e., 'smolts') from the same brood year can vary greatly based on initial growth, time of ocean entry, and age at maturity (Beckman et al. 2003; Morita and Fukuwaka 2006). Specifically, populations of sockeye salmon *O. nerka* show considerable variation in freshwater and marine age composition from year to year and among populations; juveniles may spend a few weeks to three years in freshwater after emergence from the gravel and up to four years at sea (Quinn 2018). Residence time in freshwater is largely a function of size and growth rate, where the largest fish of any cohort tend to migrate and smaller fish are more likely to spend at least one additional year in freshwater (Burgner 1991; Tillotson and Quinn 2016). Several fitness related trade-offs exist for an individual fish that may overwinter in freshwater or migrate out to sea at a given age and size. Fish that reside in freshwater for an additional winter incur another year of predation risk (Beauchamp et al. 1995) and parasitism (Boyce 1974) that may cause decreases in growth opportunities and survival during the winter (Metcalfe and Thorpe 1992); however, when these fish migrate to sea they tend to be larger on average than their younger counterparts. In contrast, juvenile salmon that migrate to the ocean at a younger age increase the probability of surviving to the ocean phase but are also susceptible to high rates of predation in the early marine period when smolts are small enough to be targeted by a greater number of piscivorous fishes, birds, and mammals (Ricker 1976).

In general, smolt-to-adult survival increases with increasing smolt size at ocean entry for sockeye salmon (Foerster 1954) and other salmonids (Ward et al. 1989; Bond et al. 2008). Higher survivability of larger smolts is presumably linked to increased escape ability, faster growth, and a shorter time to attain a size less susceptible to predation (Holtby et al. 1990), though the ecological agents of predation or mortality are usually unknown. However, the evidence for size-biased survival becomes more ambiguous when considering the confounding factors of age, ocean entry timing, and environmental variability (Bilton et al. 1982; Holtby et al. 1990; Henderson and Cass 1991; Koenings and Geiger 1993). Smolt size is correlated to ocean entry timing within a season, where the largest and oldest smolts are more likely to migrate earlier in the season; therefore, size may be confounded with the benefit of migrating at an optimum time. For example, due to a difference in ocean entry timing, age 2 smolts had lower marine survival than comparably sized age 1 smolts (Koenings and Geiger 1993). Alternatively, trade-offs between smolt size and ocean entry timing may result in more than one optima, where smolts migrate early and small or later in the season after attaining a larger size (Bilton et al. 1982). Therefore, describing the variability in natural selection on size among ages and marine cohorts has become necessary in order to understand the realized fitness advantages of increases in smolt body size. This is especially true when salmon populations are characterized by a diverse freshwater age structure.

Despite equivocal results, overall smolt size appears to be a key trait in predicting marine survival and population productivity (Foerster 1954; Henderson and Cass 1991). With potential changes in growth conditions for Pacific salmon, the effect of climate on freshwater growth is important to consider in regard to future productivity. Currently, the climate system is warming and regions in the northern high latitudes are warming at over twice the global rate (IPCC 2014). The general effects of climate warming on freshwater habitats will likely include increases in water temperature and decreased dissolved oxygen levels (Ficke et al. 2007). As

lake temperatures increase it is expected that the maintenance metabolism for juvenile sockeye salmon will increase, requiring a greater food demand and may result in slower growth if food is limiting. Conversely, if food is not limited and of sufficient quality, growth is expected to increase as temperatures warm. In addition, with warming temperatures changes in plankton phenology could lead to a mismatch between the spring zooplankton bloom and their phytoplankton prey leading to lower zooplankton densities and less food for juveniles (Healey 2011). In contrast, earlier spring break-up can increase zooplankton biomass and consequently increase growth of juvenile sockeye salmon (Schindler et al. 2005). However, because of variation in filtering of climate by the physical landscape and trophic dynamics, the effects of climate-driven changes on freshwater growth will likely be site- or population-specific (Griffiths et al. 2014).

Diversity in smolt age and maturation timing serves to decrease variability in numerical abundance of meta-populations and buffer against environmental change by decreasing the probability that all individuals of a cohort will experience adverse conditions (Greene et al. 2010; Schindler et al. 2010). As a consequence, commercial fisheries and mobile consumers have greater consistency and options for acquiring salmon resources (Hilborn et al. 2003) and similarly, harvesters that exploit a diverse set of species often have less variable income (Anderson et al. 2017; Cline et al. 2017). Life history diversity in both the marine and freshwater phases of sockeye salmon may become increasingly vital as populations experience more variable environmental conditions, long-term shifts in climate, and homogenizing effects of development. However, processes of natural selection on size in sockeye salmon populations with diverse freshwater age structure are not well understood and, in many systems, the links between freshwater growth and marine survival are unknown.

The overarching goal of this thesis was to explore the linkages between freshwater growth

and survival of sockeye salmon, to better understand how the effects of climate on size may have consequences for population productivity. I addressed this goal by quantifying the direction and magnitude of natural selection on smolt size for three age classes of sockeye salmon in a small watershed on Kodiak Island, AK. In addition, I explored the stock-specific effects of temperature and conspecific density on smolt size over a multi-decade time-series to understand historical trends and possible future trajectories.

The objective of my first chapter was to understand how the magnitude and direction of natural selection on size at ocean-entry may vary by age by quantifying differences in smolt size before and after their ocean residency for three sockeye salmon age classes. I utilized out-migrating smolt length and age information collected by the Alaska Department of Fish & Game (ADF&G) from Olga lakes from 1990 - 1993 to determine the mean length of smolts at ocean entry (i.e., observed smolt length). I then determined the mean length of smolts after selection at sea by back-calculating smolt length from the scales of returning adult salmon (i.e., back-calculated smolt length). By obtaining a difference in mean smolt length before and after selection I was able to determine 1) the magnitude and direction of standardized selection on size for multiple age classes, 2) the relative strength of selection compared to a global database, and 3) the relationship of the magnitude of selection on size with apparent marine survival and ocean entry timing.

The objective of my second chapter was to explore the relationship between freshwater growth and smolt size to quantify stock-specific responses to climate and intraspecific density for sockeye salmon in a small watershed. To address this objective, I reconstructed a multi-decade time-series of freshwater age 2 smolt size (1971 – 2010) for two distinct stocks of Olga lakes, AK, and related trends in size to spring air temperature and conspecific density. By using a dynamic linear model framework, I was able to 1) determine whether smolt size at age for two

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stocks in the same watershed differed in their response to climate and density over time and 2)

explore potential future outcomes of smolt size at age under varying scenarios of increasing

temperature and conspecific density.

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Chapter 1 Direction and magnitude of natural selection on body size differs among age classes of marine cohorts in sockeye salmon[1]

Abstract

Due to the mediating role of body size in determining fitness, the 'bigger is better' hypothesis still pervades evolutionary ecology despite evidence that natural selection on phenotypic traits varies in time and space. For Pacific salmon (genus *Oncorhynchus*), most individual studies quantify selection across a narrow range of sizes and ages; therefore, uncertainties remain concerning how selection on size may differ among diverse life-histories. Here, we explore how natural selection on body size may vary among age classes and among years in marine cohorts of sockeye salmon (*O. nerka*). We calculated standardized selection differentials by comparing observed size distributions of out-migrating juvenile salmon to back-calculated smolt length from the scales of surviving, returning adults. Results reveal the magnitude of selection on size was very strong (> 90th percentile compared to a database of 3,759 linear selection differentials) and consistent among years. However, the direction of selection towards size consistently varied among age classes. Selection was positive for fish migrating to sea after two years in freshwater (age 2) and in their first year of life (age 0), but negative for fish migrating after 1 year in freshwater (age 1). The absolute magnitude of selection was positively correlated to apparent marine survival and negatively correlated to mean ocean entry timing, which may underpin negative selection favoring small age 1 fish. Collectively, these results challenge the assumption that 'bigger is better' in terms of survival and emphasize trade-offs that may exist between fitness components for organisms with similarly diverse migratory life-histories.

Introduction

Few phenotypic traits are as important as body size given its influence on fitness across taxa (Brown et al. 1993; Choudhury et al. 1996; Sokolovska et al. 2000; Wikelski and Romero 2003). In many species, traits associated with reproduction and survival are strongly influenced, both directly and indirectly, by body size. Body size is often positively correlated with female fecundity (Coates 1988; Honek 1993), can mediate the outcome of territorial aggression (Tokarz 1985; Hastings 1989; Johnsson et al. 1999), and affect the probability of starvation and rate of predation (Gliwicz 1990; Sogard 1997; Scharf et al. 2000). Yet, despite the fitness benefits of increased body size, countervailing selection can occur as a result of the costs of increased detectability, higher energy requirements, reduced agility etc. for individuals of a larger size (Blanckenhorn 2000). For example, hypoxia limits body size in *Drosophila melanogaster* that otherwise are strongly selected for larger mass (Klok and Harrison 2009). Similarly, obtaining a large size before overwintering can be costly under certain conditions for juvenile steelhead trout *Oncorhynchus mykiss*, where relatively warm winter temperatures and low food availability appeared to be more physiologically demanding for large fish (Connolly and Petersen 2003). Furthermore, divergent selection can simultaneously favor both large and small body size in a population depending on the season and alternative life-history strategies (Gross 1985; Siepielski et al. 2009). These few examples, of many, demonstrate that the expression of body size reflects the balance between fitness costs and gains.

Ecological agents of selection that represent the causes of evolution (e.g. predation, parasitism) vary across the landscape and years (Siepielski et al. 2009, 2011; MacColl 2011). For example habitat-driven selection on acoustic signals is associated with song divergence in the little greenbul *Andropadus virens* (Slabbekoorn and Smith 2002) and varying water levels influence the magnitude of selection on size-at-maturity in sockeye salmon due to risk of

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stranding and predation by bears *Ursus arctos* (Carlson and Quinn 2007). Moreover, selection can vary within seasons or across other fine temporal scales (Wood 1987). This is demonstrated by the variation in sexual selection observed on male golden orb-web spider *Nephila plumipes* body size due to changes in competitive challenges males encountered at different times of the season (Kasumovic et al. 2008).

Selection can also be opposing at different stages of the life history, resulting in trade-offs between fitness components, which in turn can underpin life-history divergence and adaptive radiations (Schluter et al. 1991). Life-history trade-offs are predicted to be particularly strong in migratory or metamorphosing species, because individuals are exposed to selection across ecosystems within and among generations. Phenotypic traits that prove beneficial in one environment may incur a fitness disadvantage in the next or vice versa (Schluter et al. 1991; Waples et al. 2004; Gillis et al. 2008). Furthermore, body size is often associated with the phenology of key life history events, such as migratory timing, that are predicted to occur when conditions are most favorable (Cushing 1990).

Pacific salmon and other migratory salmonids are ideal species for exploring fitness trade-offs as a result of selection on traits, such as body size and migratory timing (Quinn et al. 2009). For anadromous salmonids, high mortality occurs during a brief period after juveniles (i.e., 'smolts') enter the ocean (Parker 1971; Healey 1982) and correspondingly, population dynamics are largely influenced by this life stage (Rogers and Schindler 2011; Cunningham et al. 2018). Smolt size and ocean-entry timing are two correlated traits that influence survival; however, with few exceptions, the ecological agents of selection are usually unknown (MacColl 2011). In general, smolt-to-adult survival increases with increasing smolt size at time of ocean entry for anadromous salmonids (Foerster 1954; Ward et al. 1989; Koenings and Geiger 1993). Higher survivability of larger juvenile fish is thought to arise from increased escape ability, faster

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growth, and a shorter time to attain a size less susceptible to predation and starvation (Sogard 1997; Heintz and Vollenweider 2010).

Despite its intuitive appeal and general assumption in the literature, the evidence for size-biased survival is equivocal. Size-based patterns of survival are less obvious when comparing across populations spanning many degrees of latitude (Koenings and Geiger 1993) or different brood years within populations (Henderson and Cass 1991; Quinn et al. 2005). Positive size-selective survival for freshwater age 1 and age 2 coho salmon *O. kisutch* smolts was detected only in years of poor marine conditions, suggesting that variability in ocean conditions may affect smolt growth rates and the susceptibility of smolts to a size-selective predator (Holtby et al. 1990). In addition, size at seaward migration for some species of Pacific salmon may not be as important as the size attained during their first marine growing season (Moss et al. 2005; Tomaro et al. 2012). The effects of smolt age at ocean entry can also affect size-dependent survival because of the influence of out-migration timing (Bilton et al. 1982). In some cases, earlier migrating age 2 smolts had lower marine survival than comparably sized age 1 smolts, where age 2 smolts needed to be approximately 20 mm larger to survive at a rate equal to age 1 smolts (Koenings and Geiger 1993).

Though the mechanisms of differential smolt survival across entry dates are generally unknown, smolt ocean entry relative to the spring bloom of their marine zooplankton prey is a predictor of within-year variation in survival rates of *Oncorhynchus* spp. (Scheuerell and Williams 2005; Satterthwaite et al. 2014). For Chinook salmon juveniles entering the ocean from the Snake and Columbia rivers, an earlier migration was associated with increased survival although peak survival varied by ocean entry day among years (Scheuerell et al. 2009). Decreases in survival have been observed with a general increase in predatory fish such as the Pacific hake *Merluccius productus* (Emmett et al. 2006) and an increased predation rate

on migrating juvenile salmon by colonial seabirds (Roby et al. 2003). Due to the variability in agents of selection over time, juvenile life history diversity provides stability and resilience to overall smolt production (Schroeder et al. 2016; Carr-Harris et al. 2018; Hovel et al. 2018). This "bet-hedging" strategy increases the probability that a component of smolts will experience favorable conditions and serve to buffer meta-populations against environmental variability (Miller et al. 2010; Schindler et al. 2010; Moore et al. 2014). Though significant advancement has been made regarding our knowledge of the role of size-selective survival for salmon smolts, most studies have been correlational by comparing mean smolt length across geographic regions, across years, and most often for a single age class (Henderson and Cass 1991; Koenings and Geiger 1993). Our understanding of how size-selective pressure may affect contemporary evolution of size at age, migratory timing, and the maintenance of age structure *within* a single breeding population is more limited.

The purpose of this study was to understand the realized fitness advantages or disadvantages of body size across different life-histories within a phenotypically diverse migratory population of sockeye salmon. The specific objectives of this study were to 1) quantify the magnitude and direction of natural selection on smolt size among age classes and cohorts, 2) compare observed selection on body size to a global database that includes 3,579 estimates from 91 species, and 3) determine the relationship of the magnitude of selection to apparent marine survival and ocean entry timing. We hypothesized that selection generally favors larger sockeye salmon smolts but that the magnitude of selection varies among age classes and among years. In addition, we hypothesized that decreasing magnitude of selection will be correlated with increasing apparent marine survival and the magnitude of selection will also be positively correlated with late ocean entry timing.

Methods

Model study system

The South Olga lakes system on the southern end of Kodiak Island, Alaska, supports one of the largest sockeye salmon runs in the Kodiak Archipelago and has a long-term average sockeye salmon run of approximately half a million fish (Jackson et al. 2012; Finkle and Loewen 2015). The system is composed of two lakes, Upper Olga Lake and Lower Olga Lake (Figure 1.1), and has two temporally distinct sockeye salmon runs that return from late May through mid-July (Early run) and from mid-July through September (Late run; Gomez-Uchida et al. 2012). This system is phenotypically diverse in terms of years spent in freshwater, with substantial expression of an "ocean-type" life history of the Late run, which describes juveniles that go to sea in their first year of life (Figure 1.2). The life history of sockeye salmon has been reviewed extensively elsewhere, but in brief, juvenile anadromous sockeye salmon rear in lakes for one to three years after emergence from the gravel, though some migrate to sea soon after emergence. After migrating to sea, adult sockeye spend one to four years in the ocean before returning to fresh water, where they spawn and die in late summer and autumn (Burgner 1991).

Observed smolt length of Olga lakes sockeye salmon

To assess smolt length at ocean entry, sockeye salmon smolts were sampled at ocean entry by the Alaska Department of Fish & Game (ADF&G) from May 20 – July 30, 1990; May 11 – August 4, 1991; May 5 – July 31, 1992; and May 10 – August 6, 1993 using a Canadian fan trap 1.6 km downstream of Lower Olga Lake (Finkle and Loewen 2015). A smear of scales was pulled from individuals and mounted on glass slides and age and length data were recorded (Finkle and Loewen 2015). Length measured directly from smolts at ocean entry will be hereafter referred to as *observed smolt length*.

Back-calculated smolt length of returning Olga lakes sockeye salmon

Adult sockeye salmon have been enumerated and sampled for age and length at the Upper Station weir since 1928. Based on stock-specific run timing, fish returning through July 15 are considered the Early run, where fish returning after July 15 are assumed to be the Late run (Gomez-Uchida et al. 2012). Run reconstructions based on escapement and scale pattern analysis are available beginning in 1969 for the Early run and 1970 for the Late run. As such, the collection of archived adult scales begins in 1969-1970 and continues on an annual basis by ADF&G.

Archived scales sampled by ADF&G from returning adult fish during 1969 – 2016 were preserved as impressions in acetate cards and include corresponding information on length, age, and sex (based on physical examination of external characteristics). Scales and impressions were included in the study based on the following criteria: 1) we agreed with ADF&G age determination, 2) annuli are clearly defined and not affected by regeneration or reabsorption of the scale, and 3) the shape of the scale indicates it was taken from the preferred area, which is immediately above the lateral line and slightly forward of the adipose fin (Koo 1962; Ruggerone et al. 2007). Smolt scales were randomly sampled (n = 1300) for each age class (0 – 3) from when smolts were sampled (1990 – 1993) with stratified random sampling for each age and year (0 – 2). A random sample of age 3 smolts were sampled across all years due to a low number of available scales (n = 100). Following the approach by Ruggerone et al. (2009), a random sample of 50 adult scales was selected from each returning age class that entered the ocean in 1990 – 1993 (Figure 1.3); in addition, age classes were included in the analysis if 25 readable scales could be obtained for both males and females, with a total of 50 scales per age class in a given year. If 25 readable scales for both females and males were available from the Early run, those samples were included in the analysis. Acetate scale impressions were digitized using a Z-Scan 46-II microfiche reader

attached to a 19.3 mm zoom lens and images were exported at high resolution (3352 x 4425 pixels) to Image-Pro software® for accurate measurements of scale patterns.

To back-calculate smolt length from returning adult scales, we measured the distance (mm) on the longest axis from the focus of the scale to the last circulus at the end of freshwater growth. In addition, we measured the total distance from the focus of the scale to the edge of the scale for both adult and smolt scales (Ruggerone et al. 2007). Random checks between two trained readers were done to assure consistency in measurements for adult scales (~5% of samples).

We used the Fraser-Lee equation (Fraser 1915; Lee 1920) to back-calculate smolt length from scales of returning adults. The Fraser-Lee method has been widely used for many species of fish (Ward et al. 1989; Bond et al. 2008; Weitkamp et al. 2011) and is preferred because the intercept, c, has a biological interpretation as the length of a fish at the beginning of scale growth. In addition, the Fraser-Lee method has been verified for $O.$ $nerka$ by comparing the lengths of tagged and recaptured sockeye salmon with their scale radii (Fukuwaka and Kaeriyama 1997). The constant c was obtained by calculating the regression of length on scale radius from adult and smolt scales (Figure 1.4):

$$g(S) = c + dS, \tag{1.1}$$

where $g(S)$ is the mean body length for fish with scale radius S, c is the estimated intercept, and d is the estimated slope. The intercept represents the theoretical length of Olga lakes sockeye salmon at the time of scale formation.

The back-calculated smolt length of returning sockeye salmon at the time of ocean-entry was then calculated using the following equation:

$$BSL = c + (L_c - c)\left(\frac{S_f}{S_c}\right), \tag{1.2}$$

where BSL is the back-calculated smolt length, L_c is the length of the returning adult, S_f is the

scale radius of the freshwater growth zone, S_c is the scale radius of the returning adult, and c is equivalent to c in Equation 1.1.

The magnitude and direction of selection on smolt size

We estimated the magnitude and direction of selection on size for Olga lakes sockeye salmon by comparing the distribution of observed smolt lengths from cohorts entering the ocean in the years 1990 – 1993 to the distribution of back-calculated smolt lengths of the corresponding cohort of surviving adults (following Bond et al. 2008). To demonstrate the intensity and direction of natural selection acting on body size at ocean-entry during the marine phase of each cohort, we calculated yearly length-based standardized selection differentials (SSDs) for each freshwater age (Kendall et al. 2009):

$$SSD_{a_y} = \frac{\overline{BSL_{a_y}} - \overline{OSL_{a_y}}}{S_{OSL_{a_y}}},\qquad(1.3)$$

where $\overline{OSL_{a_y}}$ is the mean observed smolt length for fish of age a in year y, $\overline{BSL_{a_y}}$ is the mean back-calculated smolt length for fish of age a in year y, and $S_{OSL_{a_y}}$ is the standard deviation of observed smolt length of age a in year y.

The yearly length-based standardized selection differential is a measure of the difference in mean observed smolt length migrating from Olga lakes versus mean back-calculated smolt length of surviving sockeye salmon escaping back to Olga lakes to spawn. This value was then divided by the standard deviation of observed smolt length in order to compare across years and populations (Brodie et al. 1995; Matsumura et al. 2012). We generated bootstrapped standard deviations for these selection differentials by performing weighted sampling of observed smolt lengths (n = 200) and back-calculated smolt lengths (n = 200) with replacement, applying the selection formula, and then repeating this procedure 1,000

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times. Observations were weighted by the relative contribution of its age class and run (Early or Late) to the total return in a given year. We present the mean SSD and bootstrapped standard deviation. We explored the form of selection (e.g., disruptive, stabilizing, etc.) through visual assessment of the probability density of observed smolt length at ocean-entry with the probability density of back-calculated smolt length of the return (Figure 1.5).

Comparisons to global database of selection

The relative magnitude of selection was determined by comparing SSDs to a database of linear selection differentials compiled by Kingsolver et al. (2001) and updated by Siepelski et al. (2017). The database includes 3,759 estimates from 91 different species, including both terrestrial and aquatic taxa. We calculated percentiles of the global database selection differentials and evaluated the percentiles in which our study SSDs fell. If a selection differential fell within the 90th percentile, selection was considered to be very strong relative to estimates in the database.

Relationship of magnitude of selection, survival, and ocean entry timing

Apparent marine survival was calculated using smolt enumeration estimates from the Olga lakes 1990 – 1993 smolt project and return estimates determined by daily Upper Station weir counts, catch apportionment, and age determination (Finkle and Loewen 2015). In this study apparent marine survival should be interpreted as an index rather than an absolute proportion. This is due to uncertainty around smolt estimates as well as the apportionment of mixed-fishery catch in Alitak Bay to Olga lakes stocks specifically.

Because we lacked individual ocean entry timing of returning adults, we used mean ocean entry timing calculated as the mean day of year (DOY) that smolts of age a entered the ocean in year y. Standardized mean ocean entry timing for smolts of age a in year y was calculated as a z-score in the following way:

$$Timing_{a_y} = \frac{(\bar{d}_{a_y} - \bar{D}_y)}{s_D},\tag{1.4}$$

where $\bar{d}_{a_y}$ is the mean outmigration timing of age a smolts in year y, $\bar{D}_y$ is mean run timing of

smolts in year y, and S_D is the standard deviation of outmigration timing of smolts in year y.

We explored the relationship of the magnitude of selection with apparent marine

survival and mean ocean entry timing by using a correlational analysis. We calculated the

correlation of the magnitude of selection and apparent marine survival using the Pearson

method; whereas we calculated the correlation of selection and ocean entry timing using the

Spearman method, which minimizes Type I error rates for non-normal data (Bishara and

Hittner 2012).

Results

Observed smolt length of Olga lakes sockeye salmon

A total sample of 14,401 smolts were sampled by ADF&G from 1990 – 1993, which

include juveniles of age 0 (n = 6653), age 1 (n = 2572), age 2 (n = 5176), and age 3 (n = 181).

The mean observed length of age 0, 1, 2, and 3 smolts was 58.5 mm, 91.4 mm, 103.3 mm, and

113.4 mm, respectively, and the mean length of each age class varied significantly across years

(ANOVA, $F_2 = 216.09$, $p < 0.001$; Table 1.1). Freshwater age 3 fish were excluded from further

analyses due to a small number of freshwater age 3 fish at ocean entry.

Back-calculated smolt length of returning Olga lakes sockeye salmon

A total of 1,235 adult sockeye salmon scales from the Olga lakes return (1992 – 1996)

was digitized and measured, which includes fish of freshwater age 0 (n = 346), age 1 (n = 443),

and age 2 (n = 446). The intercept c of the linear regression of fish length on scale radius from

smolt (n = 1300) and adult (n = 2361) scales was estimated as 21 mm. The average back-

calculated smolt length of freshwater age 0, 1, and 2 returning adults was 73.0 mm, 85.2 mm, and 119.5 mm, respectively, and varied significantly across ocean entry years (ANOVA, $F_2 = 18.027$, $p < 0.001$; Table 1.1). Mean back-calculated smolt length differed significantly between the Early and Late run only for age 1 smolts (t-test, $t = 18.93$, $p < 0.001$), where Early run fish were, on average, 20% smaller (Figure 1.6). Freshwater age 0 fish comprise $< 5\%$ of the Early run return; therefore, there was an insufficient number of scales to include this age class from the Early run in our analyses. Early run samples were included for all age 1 and age 2 samples, though due to an insufficient number of readable scales, Early run freshwater age 1 fish from ocean-entry year 1990 were not included.

The magnitude and direction of selection on smolt size

Standardized selection differentials (SSDs) ranged from -2.51 (indicating selection favoring smaller individuals) to 4.87 (indicating selection for larger individuals) and varied significantly among age classes (ANOVA, $F_2 = 24.00$, $p < 0.01$); however, SSDs did not vary significantly across years (ANOVA, $F_3 = 1.36$, $p = 0.34$; Figure 1.7). Selection for larger smolts was observed for age 0 and age 2 smolt in all years, with a mean SSD of 2.98 ± 1.34 and 1.80 ± 0.77 respectively, for ocean entry years 1990 – 1993. In contrast, for age 1 fish, selection favored *smaller* smolts and we observed a mean SSD of -1.61 ± 0.90.

Probability density functions comparing observed smolt length at ocean entry and back-calculated smolt length of returns show changes in the distribution shape after selection for some marine cohorts. We detected evidence of bimodal distributions of length after selection for age 1 cohorts in 1991 and 1993 (Figure 1.8), consistent with disruptive selection. For age 0 cohorts, length distributions had higher variance after selection, but consistently displayed directional selection with a shift toward larger size. In contrast, age 2 length distributions appeared to

maintain a similar distribution while shifting to a larger mean body size after selection (Figure 1.8).

Comparisons to global database of selection

The estimates of selection on Olga lakes smolt body size were strong compared to the global database of standardized selection differentials. Standardized linear selection differentials from Siepelski et al. (2017) had a mean of 0.18 ± 0.32, whereas the selection on size for Olga lakes sockeye had a mean of 2.14 ± 1.14. All twelve of the estimated SSDs fell within the 90th percentile of global selection estimates, with the SSD corresponding to age 0 smolts in 1992 falling within the 99th percentile (Figure 1.7).

Relationship of magnitude of selection, survival, and ocean entry timing

The proportion of smolts surviving to return ranged from 0.04 to 0.96 and varied significantly among age classes (ANOVA, $F_2 = 6.88$, $p = 0.03$), but not across years (ANOVA, $F_3 = 1.23$, $p = 0.38$; Table 1.1). Age 0 smolts had the lowest observed apparent marine survival rate for fish entering the ocean in 1990 – 1993, with a mean estimate of 0.075 (0.04 – 0.12) of smolts surviving to recruitment. Age 1 smolts had the highest apparent mean survival rate during the study period at 0.66 (0.40 – 0.94) and age 2 smolts also had a relatively high apparent survival rate with a mean of 0.63 (0.12 – 0.96).

The mean day of ocean entry for Olga lakes sockeye salmon during the years 1990 – 1993 was approximately June 26th $\pm$ 3.5 days and varied significantly among age classes (ANOVA, $F_2 = 242.16$, $p < 0.001$) and across years (ANOVA, $F_3 = 7.13$, $p = 0.02$). Older smolts tended to migrate to the ocean at an earlier date than younger age classes (Figure 1.9), consistent with patterns observed in Pacific salmon more generally. On average, age 2 smolts entered the

ocean at the earliest date (June 5th ± 7 days), followed by age 1 smolts (June 14th ± 4.5 days), and the mean ocean entry date of age 0 smolts was 33 days later in the season (July 17th ± 2.4 days). The magnitude of selection was negatively correlated to apparent marine survival (R = -0.61, p = 0.035), whereas the magnitude of selection was positively correlated to late ocean entry timing (R = 0.58, p = 0.048; Figure 1.10).

Discussion

Our findings indicate that selection on body size of sockeye salmon smolts at ocean entry can vary in magnitude and direction among freshwater age classes within a watershed, but trends can also be generally consistent among years. Furthermore, the magnitude of selection on size was very strong relative to linear selection values reported for other natural populations. The magnitude of selection appeared to be negatively correlated with apparent marine survival and positively correlated with late mean ocean entry timing. Taken together, our results demonstrate that bigger is not always better in regard to sockeye salmon smolt survival and smolts can experience relatively strong positive or negative selection on size after they enter the ocean, depending on the life history decision of what year to migrate to sea.

The magnitude and direction of selection on smolt size

The present study is the first to quantify the magnitude and direction of selection on size in a Pacific salmon system that includes variable age classes while also comparing selection experienced by cohorts across years. We hypothesized that selection would favor large individuals, to some extent, within all freshwater age classes (age 0 – age 2). In line with our hypothesis, our data reveal consistently strong positive selection for both age 0 and age 2 smolts; however, unexpectedly, we observed negative selection on size for age 1 smolts. Overall, our findings corroborate the general understanding that smolts of a larger size may have a survival

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advantage over their smaller counterparts (Foerster 1954; Henderson and Cass 1991; Koenings and Geiger 1993). Differential survival of large individuals could be attributed to size-biased consumption by a predator as a result of gape-limitations, behavioral selection by a predator, or increased escape ability with smolt size (Sogard 1997). The aggregation of predators (e.g., mergansers, *Mergus* spp.; gulls, *Larus* and *Chroicocephelus* spp.; and river otters, *Lontra canadensis*) at lake outlets during outmigration of salmon smolts has been documented in other systems (Clark and Furey 2016). Other known fish predators of Pacific salmon smolts include spiny dog fish *Squalus acanthias*, river lamprey *Lampetra ayresi*, Pacific staghorn sculpin *Leptocottus armatus*, and sablefish *Anoplopoma fimbria* though this is by no means an exhaustive list (Beamish et al. 1992; Beamish and Neville 1995; Sturdevant et al. 2009; Whitney et al. 2017). Salmon smolts are also predated on by seabirds throughout their range (see Cederholm et al. 2000); predation by rhinoceros auklets (*Cerorhinca monocerata*) has been shown to be size-selective, where prey were consistently shorter and lighter for their length than the general population (Tucker et al. 2016).

Contrary to our hypothesis, we observed negative selection on size for age 1 sockeye salmon smolts *O. nerka*. There is limited evidence for the selection against large juvenile salmonids, though Carlson et al. (2004) found that selection sometimes favored small/fast-growing wild trout *Salmo trutta*. In some cases bird predation can be biased by preferentially selecting large or intermediate size individuals (Sogard 1997). Steelhead smolts of intermediate length (145 – 190 mm) were more likely to be eaten by gulls; whereas smolts below or above this range were much less vulnerable to predation (Osterback et al. 2014). In pond experiments investigating size-selective predation on two size-classes of spot *Leiostomus xanthurus*, small individuals were more likely to survive when the predator field was composed of large predators (Rice et al. 1993). Harbor seals have recently been documented to preferentially consume large-

bodied juvenile salmon (i.e., coho, Chinook, and sockeye) in the Strait of Georgia (Thomas et al. 2017) and therefore large age 1 smolts could be more vulnerable to this type of predation. Overall, it appears that predation can be biased toward either large or small individuals; therefore, size-selective survival will likely be a result of the relative levels of mortality by each predator group.

It is difficult to determine whether negative selection was a function of the mean size of age 1 smolts, ocean-entry timing, or an interaction of the two, as both are intrinsically correlated (Quinn et al. 2009). Here we observed that small, presumably fast-growing, age 1 smolts entered the ocean earlier than their slower growing counterparts that entered later, but at a larger size. The timing of ocean entry is an important life history trait that can strongly influence the early marine survival of salmon smolts (Quinn 2018). For Columbia River basin Chinook salmon *O. tshawytscha* and steelhead *O. mykiss*, juveniles that migrated from early to mid-May had up to a 50-fold higher survival rate than those migrating in mid-June (Scheuerell et al. 2009). For hatchery-origin fall run Chinook salmon in California, release time relative to spring transition, among other factors, was a useful predictor of ocean survival rates (Satterthwaite et al. 2014). In hatchery operations, where size and release date can be manipulated, it has been shown that for three size classes released on four different dates, date of release had a strong effect on survival, whereas there was little variation in survival among size classes within dates (Bilton et al. 1982; Quinn 2018). Similarly, in several Alaska lakes, age 2 smolt had lower smolt-to-adult survival than comparably sized age 1 smolts until both reached approximately 100 mm (Koenings and Geiger 1993). The authors hypothesized that smaller age 1 smolts that migrated early could incur a survival advantage as predators may be satiated by large age 2 smolts migrating at the same time. This was demonstrated in the Kvichak system in Bristol Bay, Alaska where percentages of age 2 smolt were significantly and positively correlated with smolt-to-adult survival of co-

migrating age 1 smolt (Koenings and Geiger 1993; Tillotson and Quinn 2016). If selection favors smolts that migrate earlier in the season, this would explain why we observed positive selection for age 0 and age 2 smolts, as they decreased in size-at-age throughout the season, whereas age 1 smolts increased in size-at-age.

It is likely that there may not be a single combination of size and release timing that maximizes survival, but several optima may occur as a result of the interaction of the effect of size and timing. Our results support this hypothesis, although selection for age 1 smolt size was negative overall, back-calculated smolt length after selection was commonly bimodal, suggestive of disruptive selection (Brodie et al. 1995). However, there appears to be evidence of stock effects, where negative selection was driven mainly by higher survival of small individuals of the more abundant Late run stock, whereas survivors of the Early run stock were similar to the mean observed smolt length at ocean entry. Furthermore, even though we cannot assign out-migrating smolts to a specific stock, there does not appear to be any evidence of a bimodal distribution of age 1 smolt length at ocean entry; therefore, dramatic differences between stocks seem to appear after selection. One hypothesis would be that due to earlier spawning by adults, Early run juveniles would hatch earlier and would therefore be larger on average than Late run smolts out-migrating at the same time (Sparks et al. 2019). Following this logic, if Early run age 1 smolts migrate disproportionately early and at a larger size, than selection on early migration timing may not result in negative selection on size as observed for Late run smolts. Here we have demonstrated the complexity of the relationship between smolt size and survival by quantifying selection on size within multiple age classes.

We hypothesized that the magnitude of selection on size would vary among age classes, where older age classes would likely experience weaker selection as they may be less susceptible to size-selective predators following the 'critical-size hypothesis' (Henderson and Cass 1991).

However, our data reveal consistently strong selection on size for all age classes with age 1 smolts experiencing the lowest magnitude of selection on size. We found no evidence of the exclusion of age 2 fish from strong positive size-selective pressure, which would be characteristic of a critical size limit (Beacham et al. 2018).

There are a few limitations and caveats of the present study design in regard to quantifying the strength of selection on size. First, the back-calculation method used to estimate smolt size distributions from returning adults can introduce inflated variance (Wilson et al. 2009) and is sensitive to sampling effort (Siepielski et al. 2009; Beacham et al. 2018). Second, for three of the years studied (1990 – 1992) approximately 13 – 22 % of back-calculated lengths were higher than the maximum observed length at ocean entry. Since this was only an issue for age 2 smolts it suggests that the largest, oldest smolts were under-represented in the sampled juvenile population during seaward migration. Under-representation by the largest size class could be due to 1) large smolts entering the ocean earlier than smolt sampling began or 2) a higher probability of large individuals avoiding sampling gear. Finkle and Harding (2015) found that due to their large size and strong swimming ability, large smolts were efficient at avoiding the Canadian fan trap by swimming into then out of the trap. Therefore, it is highly probable that selection estimates for age 2 smolts are biased high.

Importantly, smolt length was back-calculated from scales of adults from the escapement after late-stage predation or fishing mortality has occurred that could potentially introduce bias in selection estimates (Hanson et al. 2010). Previous work has found that Pacific salmon have a higher probability of maturing at an earlier age (i.e., smaller at return) if they were large as smolts (Bilton 1971; Vøllestad et al. 2004). Olga lakes sockeye salmon are subject to both a purse seine and gillnet fishery; purse seine fisheries can disproportionately catch larger males and smaller females, whereas gillnet fisheries generally catch larger fish depending on mesh size

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(Kendall et al. 2009; Kendall and Quinn 2012). Therefore, the distribution of back-calculated smolt length could be biased high as a disproportionate number of small adults escaped into the system that are predicted to have been larger smolts at ocean entry. However, back-calculated smolt length was only significantly different by saltwater age for freshwater age 0 fish; even then, saltwater age 3 fish tended to be *larger* as smolts. In addition, larger smolts tended to be larger as adults for a given age and smolt year with correlations for cohorts ranging from 0.017 to 0.48. Furthermore, the strength of correlation between smolt length and adult length was not significantly associated with the magnitude of selection on size.

Comparisons to global database of selection

Despite variation in selection estimates among age classes, selection was very strong compared to estimates of selection in other natural populations. For example, linear selection differentials for the 3,759 estimates of 91 species compiled by Siepielski et al. (2017) have a mean absolute value of 0.18, where the mean absolute value in the present study was 2.14. All of the selection differentials for size were within the 90th percentile, which suggests that smolts experience strong size-selective pressure, either positive or negative, after they enter the ocean. Of course, it is necessary to consider that the magnitude of selection may be a result of selection favoring two correlated traits in the same direction. For example, age 2 smolts that leave early may have both the advantage of entering the ocean at an optimal time, as well as having a larger body size. Thus, the magnitude of selection on 'size' could be a compounded effect of selection on the phenotypic traits of body size and run timing. In the current study the information on ocean entry timing of individuals is limited; although we have information on smolt size and ocean entry date for smolts entering the ocean, we do not know when individual surviving adults entered the ocean. Therefore, we cannot definitively separate the effects of run timing and body

size, but only use the mean timing of ocean entry of an age class in a given year as an index. Future work that included individual-based tagging efforts (e.g., Scheuerell et al. 2009) would be illuminating in this system to parse the effects of ocean entry timing and body size for individual fish and understand the trade-offs between these two traits at a finer scale.

With such strong estimated selection on size, we might expect that there would be a mean shift in the phenotype of this population over time, given that body size (heritability, $h^2 \sim 0.44$) and timing of ocean entry ($h^2 = 0.23$) are at least in part genetically controlled (Carlson and Seamons 2008). Though the present study does not aim to predict the evolution of body size in sockeye smolts, there are reasons to consider why selection on size may not result in an evolutionary response. First, by quantifying size-selective survival from smolt-to-adult we ultimately ignore the trade-offs between growth potential and predation risk (Sogard 1997). Alternatively, growth may be limited by physiological constraints or competing requirements such as immune capacity or response to environmental stress (Conover and Schultz 1997; Arendt 2018). Although large smolts may survive at higher rates than smaller smolts, large body size comes at the cost of additional time and risk of predation for juvenile fish in freshwater before they make it to the ocean (Quinn et al. 2009). Second, ocean conditions may be variable from year to year and within a season, reflecting a shifting optimum, which in turn would be expected to maintain the expression of variable age and size structure within a population. For instance, an individual would benefit from producing offspring of variable ages and size to "hedge its bets" and increase the probability that one cohort will experience favorable conditions (Schroeder et al. 2016; Carr-Harris et al. 2018).

Relationship of magnitude of selection, survival, and ocean entry timing

By investigating mean ocean entry timing and apparent marine survival, we were able to demonstrate strong associations of each with the magnitude of selection on smolt size. As we would expect, increases in the magnitude of selection on size was associated with low apparent marine survival. In addition, cohorts that migrated earlier in the season tended to experience weaker selection on size. Though, this relationship was mainly driven by differences in freshwater age. Our results are consistent with previous findings that indicate size-selective marine survival is more difficult to detect in years where marine conditions are favorable, where size would have less of an effect on the probability of survival in years where overall survival is high (Holtby et al. 1990). It is extremely challenging to identify the mechanisms that underpin size-selective survival for salmon as they enter the ocean and therefore the drivers of selection are largely undescribed in the literature. Though the present study was not designed to identify the mechanisms behind size-selective survival, several agents of selection may contribute to the observed variation in size-selective survival. For example, year-to-year variation in parasitism rates may affect the magnitude of selection on size as infected juveniles that survive to the smolt stage exhibit reduced seawater adaptation, growth, and survival (Boyce 1979; Boyce and Clarke 1983). Environmental factors such as the strength of spring upwelling and greater freshwater discharge can contribute to higher productivity and possibly less predation risk (Scheuerell and Williams 2005; Kohan et al. 2017). If marine conditions, such as these, are less favorable, opportunities for compensatory growth may be limited, increasing the disparity among size classes and the opportunity for selection (Nicieza and Brana 1993; Nicieza et al. 1997). Smolt densities may also affect the magnitude of size-selective mortality via predators; mortality rate has been shown to decrease as overall smolt abundance increases, sometimes resulting in negligible prey size-selection effects (Wood 1987; Furey et al. 2016). It is more probable,

however, that a combination of these or other factors are responsible for the observed trends in selection on size for Olga lakes sockeye.

Conclusions

In general, population data indicate that smolts of larger average size tend to have higher marine survival (Ricker 1962) and this might lead to the assumption of the bigger-is-better hypothesis within smolt age cohorts as well. Here, we demonstrate that, within an age class, survival can favor large or small individuals depending on freshwater age. The confounded nature of migration timing and body size makes interpretation difficult and experimental approaches that isolate the effects of run timing, age, and size and the investigation of specific size-selective mechanisms would greatly increase our understanding of early marine survival of juvenile salmon with complex life histories.

Size-dependent survival has long been a concern for both conservation efforts and hatchery operations (Bilton et al. 1982; Zabel and Williams 2009) and will only continue to be as opportunities for freshwater growth are subject to change due to shifts in climate and anthropogenic disturbance or mitigation (Hyatt et al. 2004; Schindler et al. 2005; Finstad et al. 2007). Overall, we build on previous work that describes the importance of diverse juvenile life-histories for a population's resiliency to inter-annual variation (Schroeder et al. 2016; Carr-Harris et al. 2018). In addition, it underscores the maintenance of the processes that yield life history variation in Pacific salmon (Schindler et al. 2010). As lake and stream temperatures increase, decreasing thermal heterogeneity and homogenizing growth opportunities, habitat complexity may become critical for salmon populations. Therefore, the dynamics of freshwater growth and size-selective survival should be considered especially relevant when predicting future outcomes for pristine and threatened salmon populations in a changing climate.
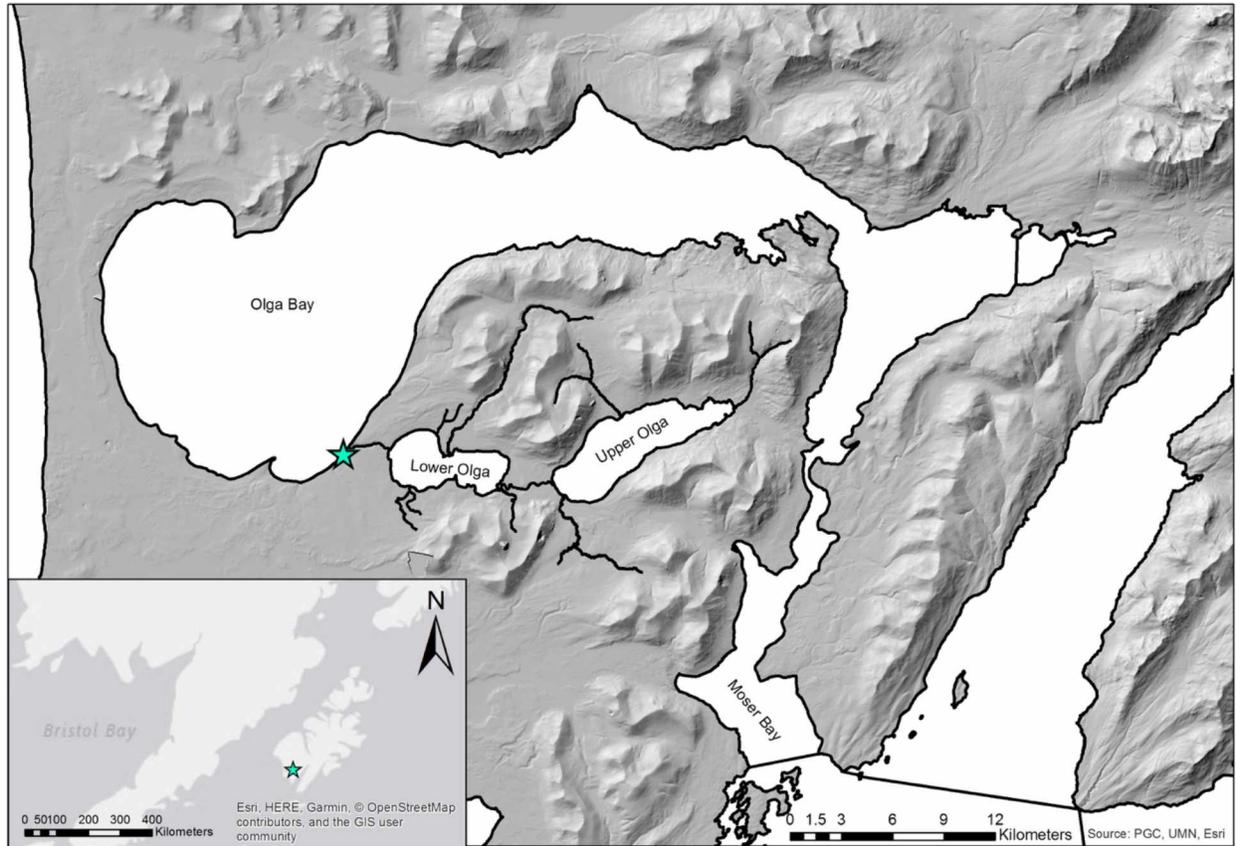
Figure 1.1 A map of Olga lakes, Kodiak, Alaska. The study area includes the Upper Station weir (star), Lower Olga Lake, and Upper Olga Lake.
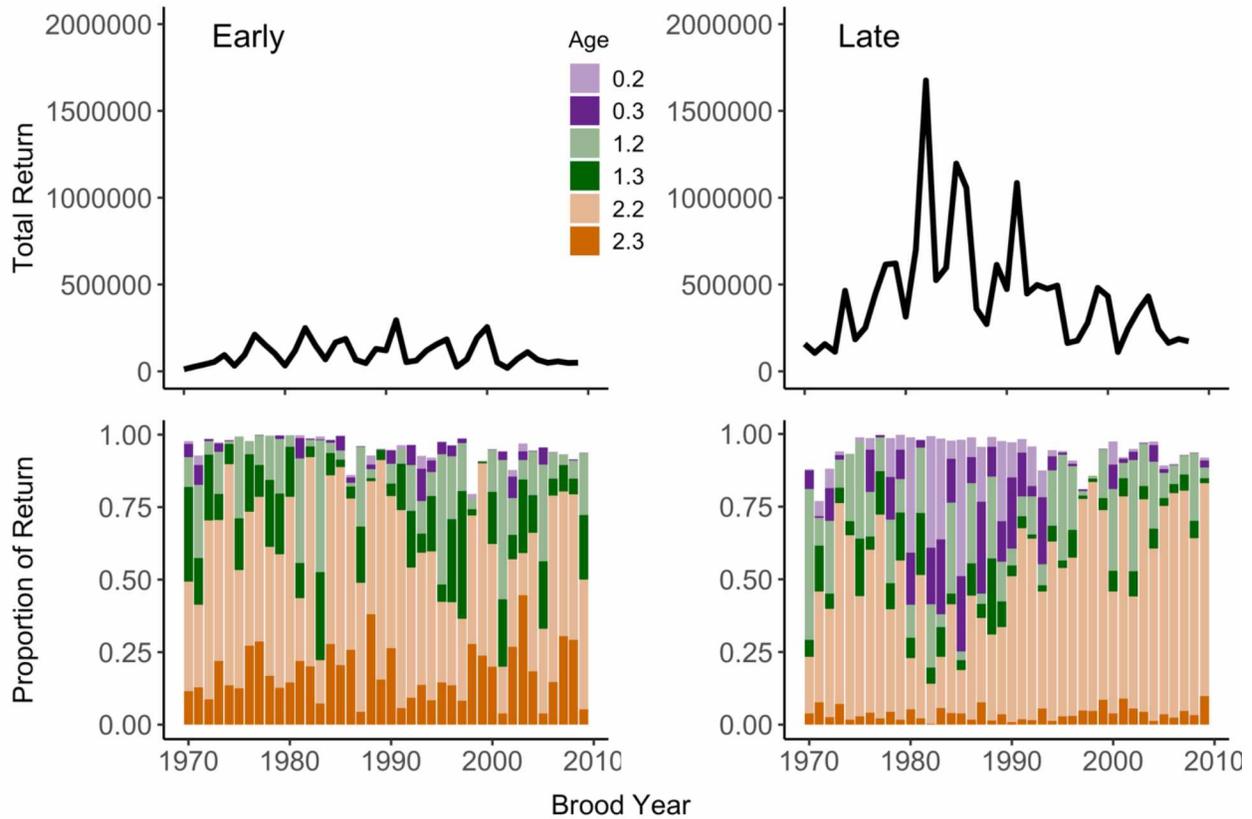
Figure 1.2 Estimated proportions of dominant age classes of Olga lakes Late run sockeye salmon (bottom panel) out of total return by brood year (top panel). Ages are represented in European notation where the number before the decimal denotes years spent in freshwater and the number after the decimal indicates the number of years spent at sea.
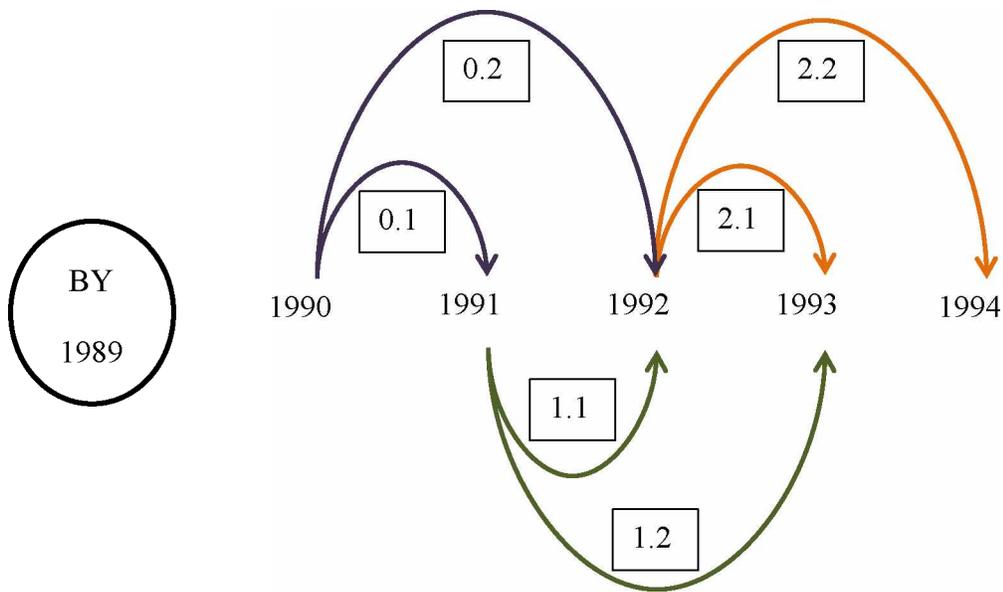
Figure 1.3 Diagram of the year of smolt ocean-entry linked to year of return for different age classes produced from the 1989 brood year (BY), as an example. Analyses were done on BY 1987-1992 of smolts that entered the ocean in 1990-1993. Freshwater and saltwater ages are shown in boxes in European notation where 0.1 fish out-migrated in their first year and spent one year at sea prior to returning to freshwater.
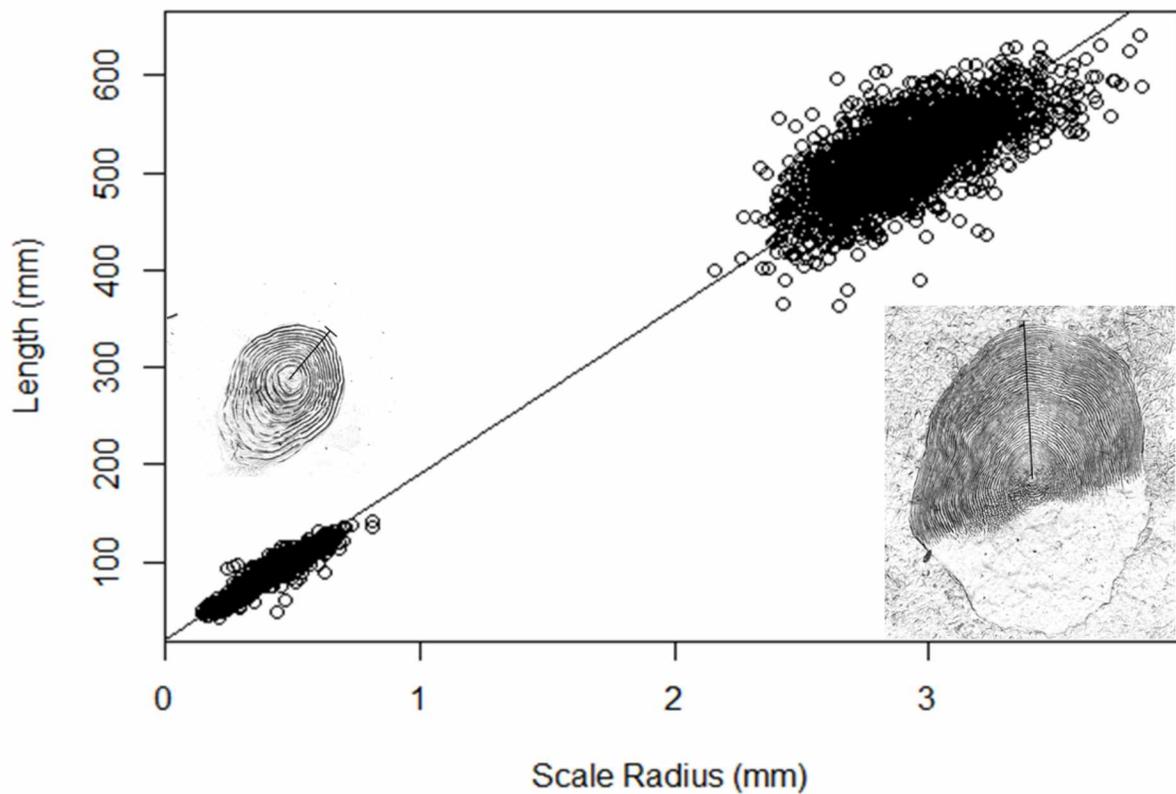
Figure 1.4 Relationship between length (mm) and scale radius (mm) based on scale and length measurements from juvenile and adult sockeye salmon *Oncorhynchus nerka* from Olga lakes, Kodiak, AK. The intercept c = 21 mm and represents the theoretical length of a sockeye salmon at the beginning of scale formation.
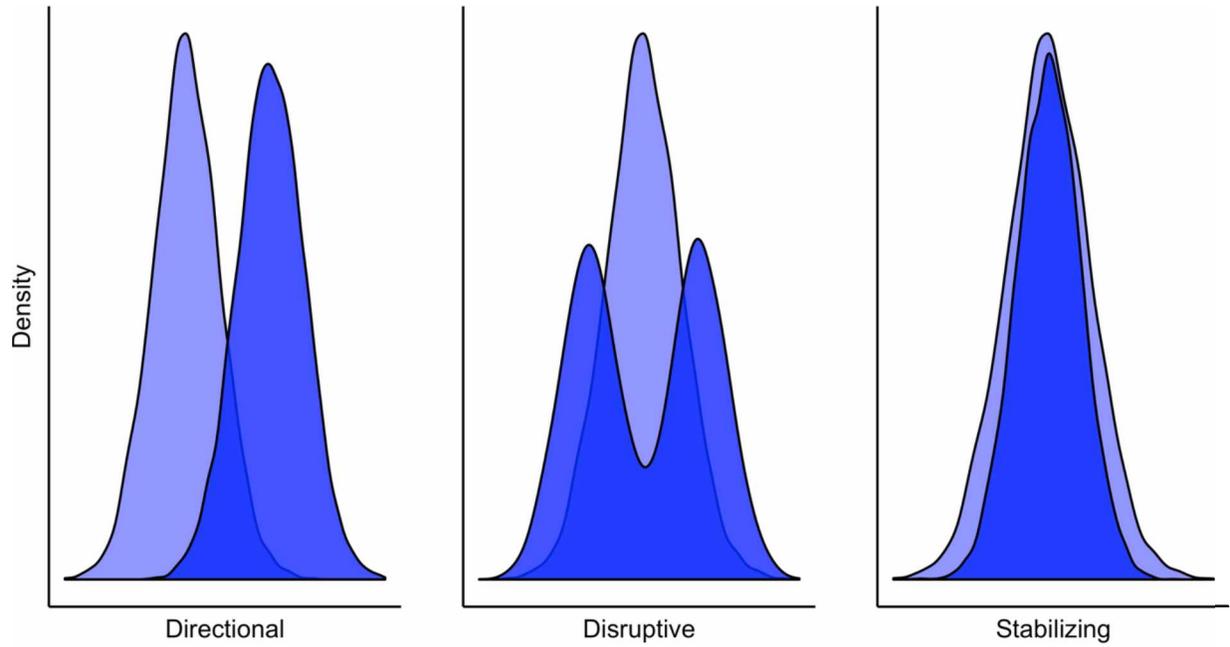
Figure 1.5 Conceptual diagram of forms of selection, where the distribution of a trait before selection is indicated by light shading and the distribution of a trait after directional, disruptive, or stabilizing selection is indicated by dark shading.
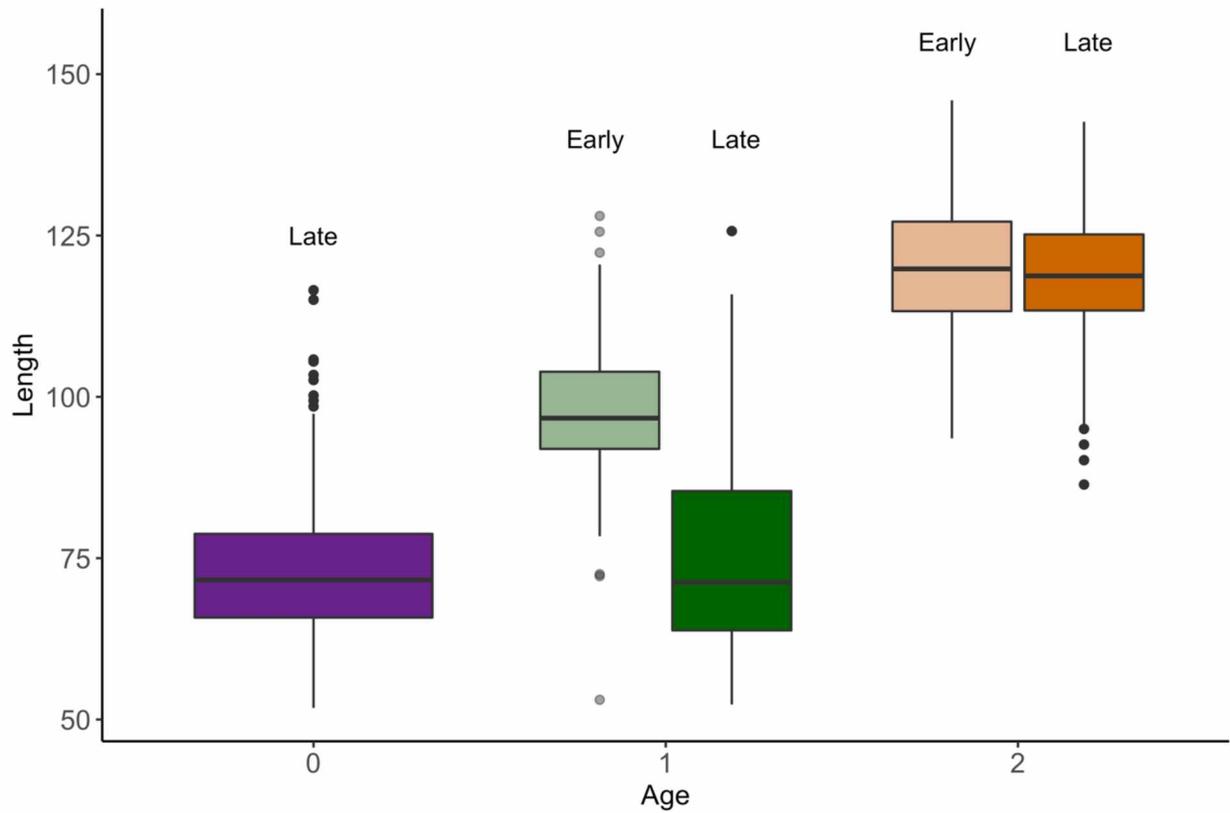
Figure 1.6 Mean back-calculated smolt length of Olga lakes returning adults among three freshwater ages of ocean entry years 1990 – 1993. Both the Early run (light) and Late run (dark) are shown here, where freshwater age 0 fish are only present in the Late run.
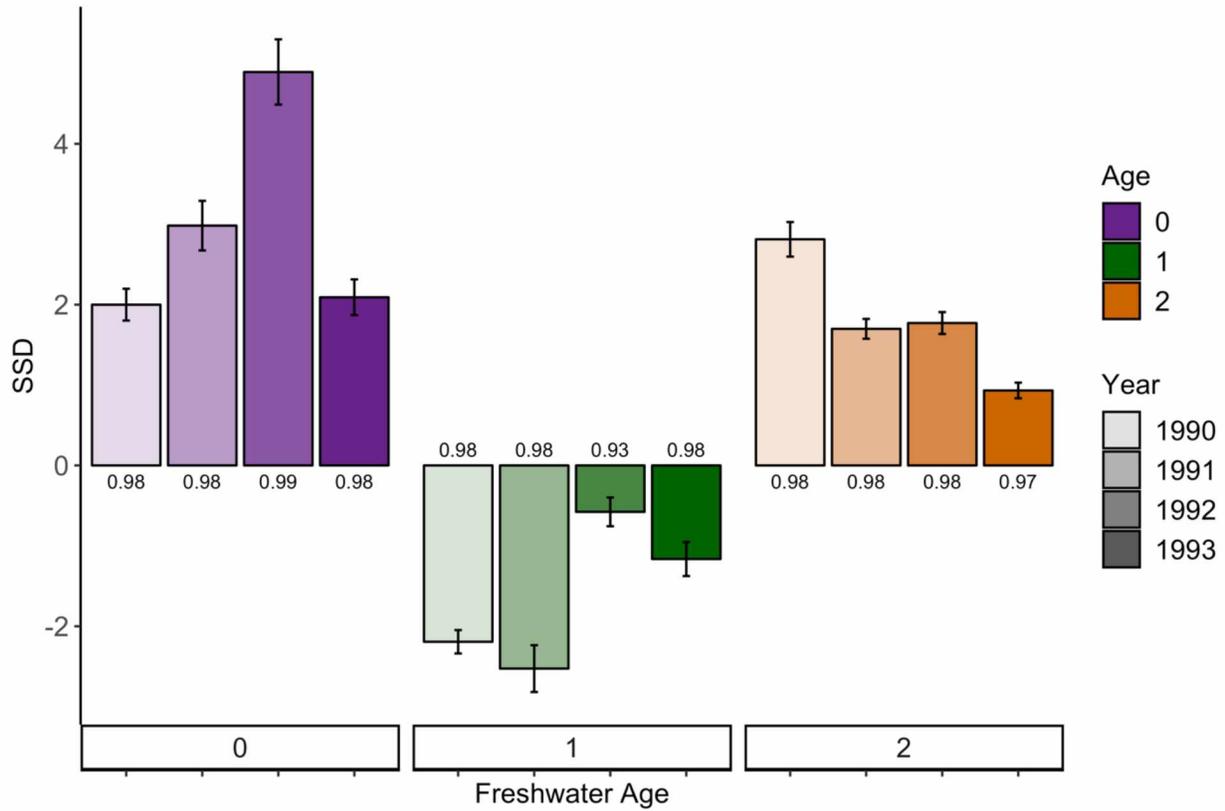
Figure 1.7 Standardized selection differentials (SSDs) measuring the magnitude of selection for smolts, where a positive SSD indicates that selection favored larger individuals and a negative SSD indicates that selection favored smaller individuals. Graph depicts SSDs of three different freshwater age classes across ocean entry years of 1990 – 1993. Error bars indicate standard deviation of boot-strapped (r = 1,000) mean and labels indicate percentile within a global database of selection differentials (Siepielski et al. 2017).
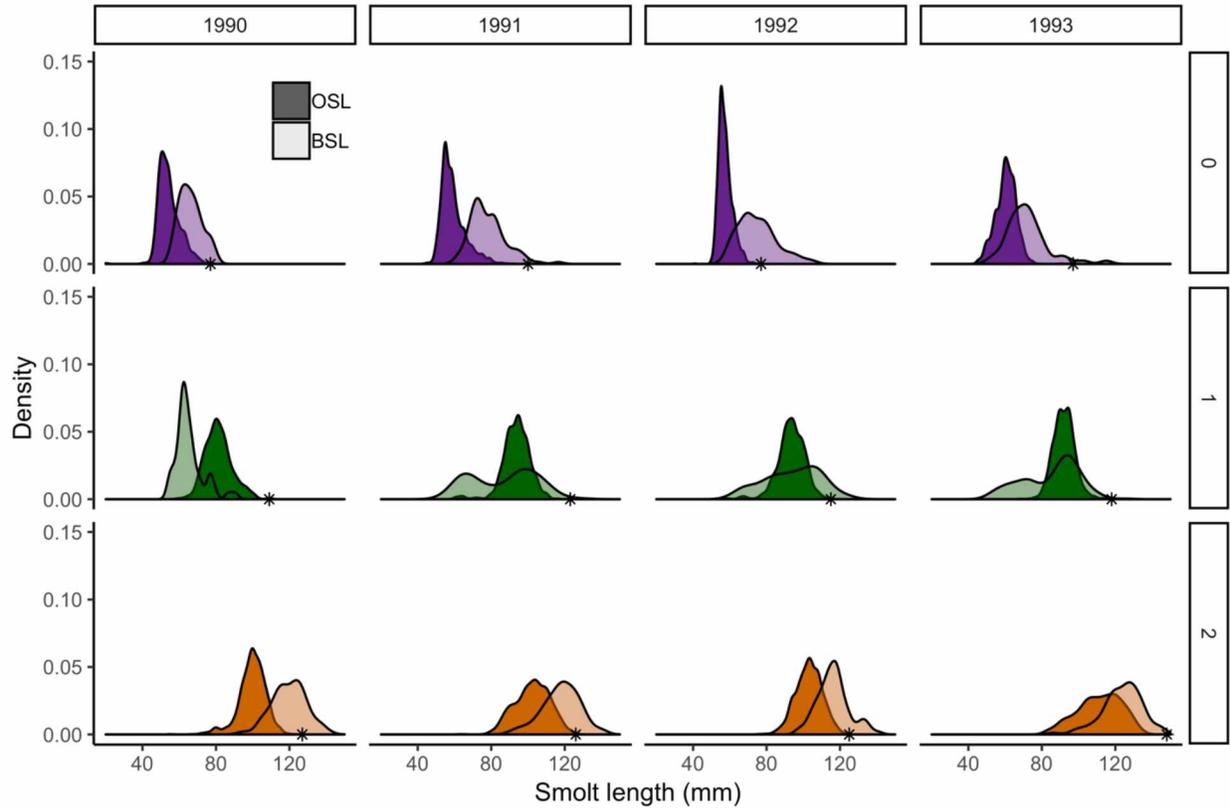
Figure 1.8 Probability density of observed smolt length (OSL) at ocean entry (dark) and back-calculated smolt length (BSL) of returning adults (light) for three different age classes from years 1990 – 1993 of ocean entry. Purple, green, and orange colors correspond to freshwater age 0, age 1, and age 2, respectively. Global difference in mean length of OSL and BSL was significant (ANOVA, $F_1 = 214.02$, $p < 0.001$). Star indicates the maximum observed smolt length for a given year and age.
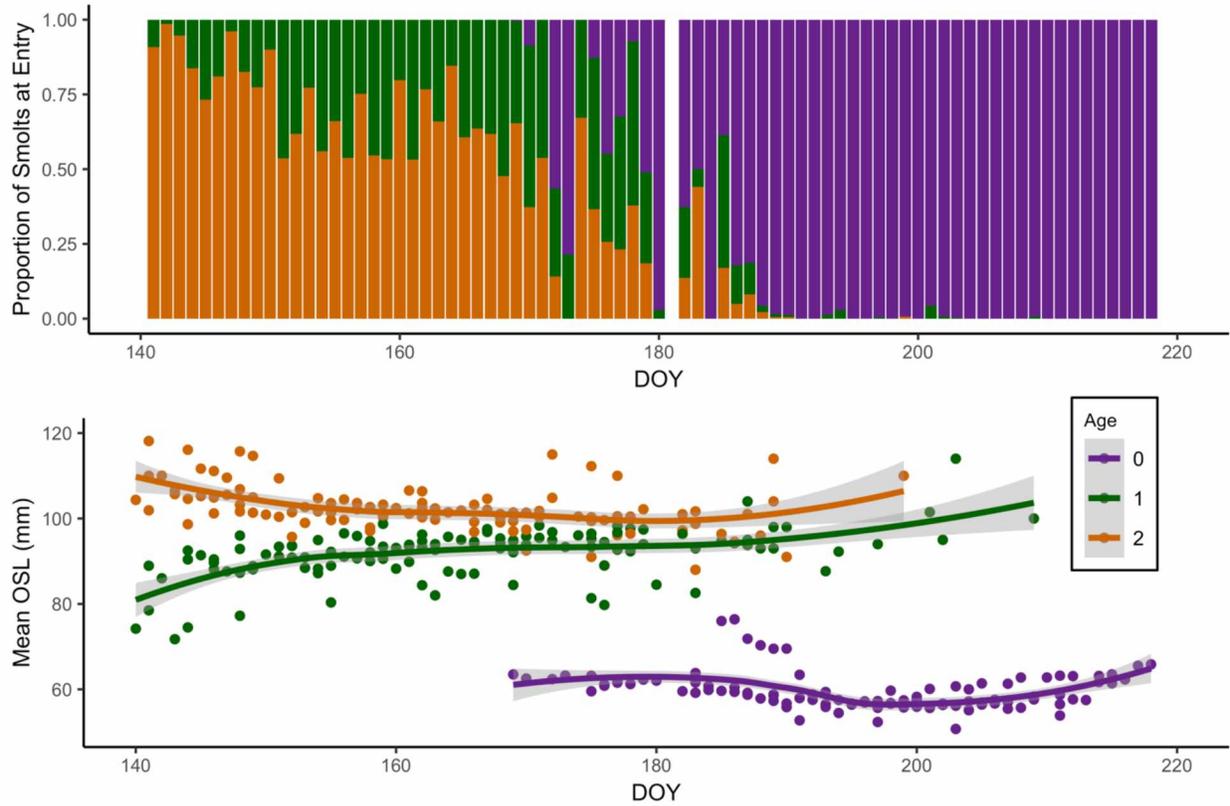
Figure 1.9 Proportion of age 0 – 2 smolts at ocean-entry according to day of year (DOY) pooled across 1990 – 1993 (top) and mean observed smolt length (OSL) at ocean-entry by DOY from 1990 – 1993 (bottom). Lines represent smooth relationship (LOESS) between mean OSL and DOY between 1990 – 1993.
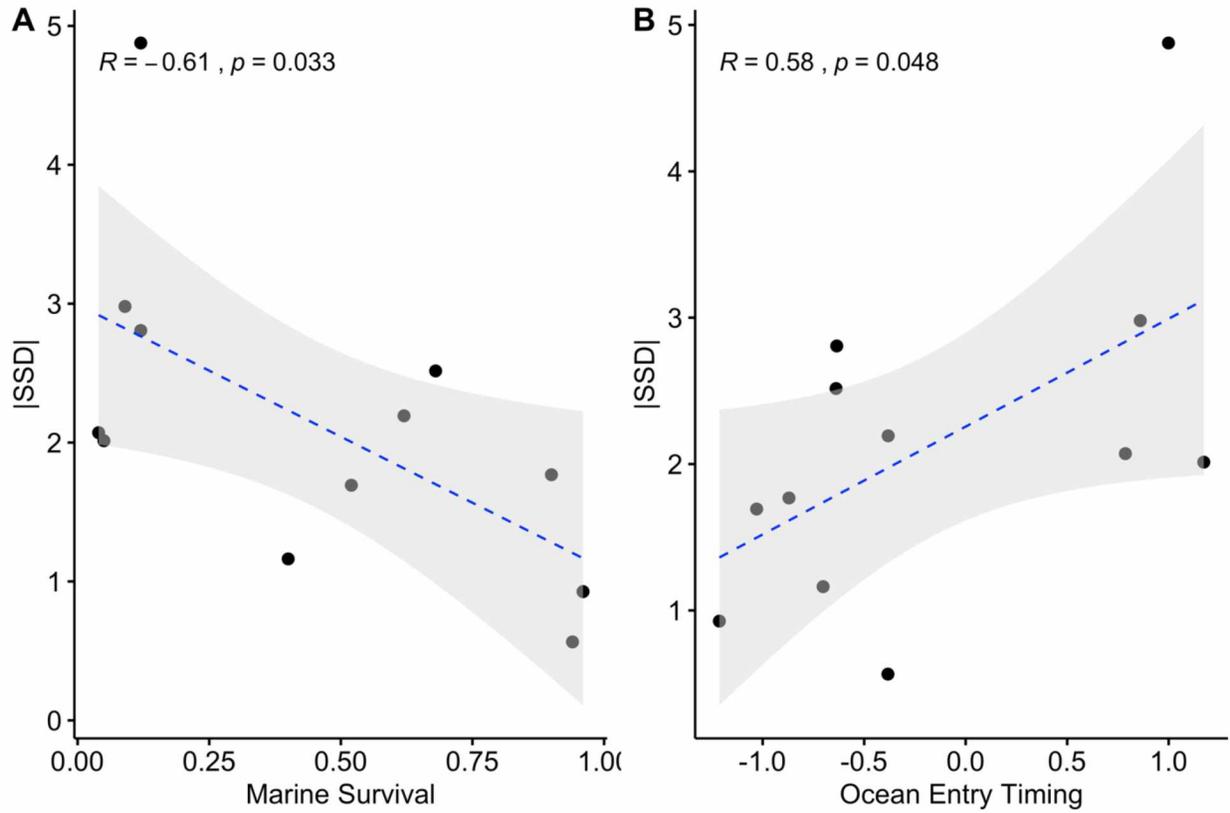
Figure 1.10 Significant correlation of the magnitude of selection on smolt size (|SSD|) with an index of apparent marine survival (A) and standardized ocean entry timing (B). Correlation of apparent marine survival and ocean entry timing was calculated using the Pearson and Spearman method respectively. Shaded areas indicate 95% confidence intervals.

Table 1.1 Summary of observed smolt length (OSL), back-calculated smolt length (BSL) of returning adults, selection on size, survival, and ocean entry timing of age 0 – 2 smolts of Olga lakes. Standardized selection differentials (SSD) compare the mean length before and after selection and are sd-standardized.

Age	Year	Sample size (OSL/BSL)	Mean OSL (mm)	Mean BSL (mm)	Difference in mean length (mm)	SSD	Index of marine survival	Mean day of ocean entry
0	1990	939/98	54.5(5.9)	66.2(6.2)	21.5	2.0(0.2)	0.05	July 17
	1991	1622/99	59.3(6.8)	78.2(9.8)	32.0	2.9(0.3)	0.09	July 21
	1992	1783/99	57.5(3.7)	75.0(10.5)	30.4	4.9(0.4)	0.12	July 17
	1993	2309/50	60.5(5.7)	72.1(11.5)	19.3	2.1(0.2)	0.04	July 15
1	1990	325/49	81.4(7.3)	65.4(7.6)	-19.6	-2.2(0.1)	0.62	June 15
	1991	658/97	93.7(7.6)	86.5(17.7)	-7.7	-2.5(0.3)	0.68	June 17
	1992	476/100	93.5(7.3)	94.0(15.2)	0.6	-0.6(0.2)	0.94	June 17
	1993	1113/197	92.0(5.8)	85.0(15.3)	-7.6	-1.1(0.2)	0.40	June 7
2	1990	1539/150	99.7(7.5)	119.8(9.4)	20.1	2.8(0.3)	0.12	June 10
	1991	947/99	102.3(9.4)	118.0(10.2)	15.3	1.7(0.1)	0.52	June 9
	1992	1837/99	103.1(7.2)	116.3(8.6)	12.8	1.8(0.1)	0.90	June 6
	1993	853/98	111.4(12.0)	123.8(10.8)	11.1	0.9(0.1)	0.96	May 26

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Chapter 2 Stock-specific responses of size at ocean entry to temperature and density in Alaska sockeye salmon (*Oncorhynchus nerka*) over four decades [2]

Abstract

The transition from freshwater to saltwater by migrating anadromous fishes such as Pacific salmon (genus *Oncorhynchus*) is thought to reflect a critical life history transition, where survival is mediated largely by the size of the migrating individuals. For salmon that spend extended periods rearing in freshwater, the size at ocean entry (i.e., smolt size) may be sensitive to changes in freshwater conditions shaped by biotic and abiotic factors. Due to differences in freshwater habitats that effectively integrate climate, trophic dynamics, and population traits, the response of specific populations is likely to be context dependent. To explore potential population specific responses, we back-calculated smolt size from returning adult scales to reconstruct a time-series of smolt length for two stocks within a small watershed on Kodiak Island, Alaska. Using a dynamic linear model framework, we found that temperature was important in explaining smolt length for one stock, while density influenced smolt length for both stocks utilizing the same lakes. Furthermore, forecasts of smolt length showed highly variable responses under scenarios of increasing temperature and high and low densities. Collectively, these results demonstrate the importance of stock-specific data and proactive management, as the outcomes of climate warming will not be the same for all systems.

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[2] Ree, M. E., P. A. H. Westley, H. Finkle, and A. Beaudreau. *In prep.* Stock-specific responses of size at ocean entry to temperature and density in Alaska sockeye salmon (*Oncorhynchus nerka*) over four decades. Canadian Journal of Fisheries and Aquatic Science.

Introduction

Body size can have a strong influence on the probability of starvation and risk of predation in fishes (Gliwicz 1990; Sogard 1997; Scharf et al. 2000). In some cases, a small decrease in fish size-at-age can result in a dramatic increase in predation mortality (Audzijonyte et al. 2013). For anadromous Pacific salmon (genus *Oncorhynchus*), the early period following ocean entry is a well-known survival bottleneck, presumably due to predation, (Parker 1971; Healey 1982). Body size at this life-history stage has been identified as a key trait in determining marine survival (Foerster 1954; Ward et al. 1989; Koenings and Geiger 1993). Moreover, the magnitude of selection on size can be fairly consistent across years but can differ across age classes within a population (Ree et al. *in prep*). Although the ecological agents of selection are not fully described, higher survivability of larger smolts is presumably linked to increased escape ability, faster growth, and a shorter time to attain a size less susceptible to predation and starvation (Sogard 1997; Heintz and Vollenweider 2010). Therefore, the conditions mediating growth that juvenile salmon experience in freshwater may have direct consequences for the number of adults that return to spawn.

For salmon species that reside for >1 year in freshwater, such as sockeye salmon *O. nerka*, the freshwater environment may have a greater effect on smolt size-at-age than for species that migrate to the ocean directly after emergence. Sockeye salmon freshwater growth is influenced by many different factors; however, conspecific density and temperature have consistently been identified as two major drivers of smolt size (Edmundson and Mazumder 2001; Schindler et al. 2005b; Rich et al. 2009). In some locations, juvenile sockeye salmon growth is negatively correlated with conspecific fry density, with the relative effects of air temperature and fry density varying between lakes (Rich et al. 2009). Fry density may have a stronger effect on fry growth when spawning capacity exceeds rearing capacity and a weaker effect in systems that

are spawning habitat limited (Kyle and Koenings 1988). Temperature has a direct effect on metabolic rate, translating into effects on somatic growth (Edmundson and Mazumder 2001). There may also be interactive effects of temperature and prey supply, where the optimal temperature for growth decreases with decreasing food availability (Brett et al. 1969). Increases in air temperature are also associated with earlier spring ice breakup on lakes, leading to increased zooplankton densities that bolster sockeye salmon growth in their first year (Schindler et al. 2005b).

Regions in the northern high latitudes are warming at over twice the global rate (IPCC 2014). The effects of climate change on freshwater habitats will likely include increases in water temperature and decreased dissolved oxygen levels (Ficke et al. 2007). Ecological responses to warming temperatures will vary among species and habitats due to trophic dynamics and species' thermal tolerances (Magnuson et al. 1990; O'Gorman et al. 2016). For example, in 24 lakes within regions of Europe experiencing increases in air temperature, changes in fish body size were both species and lake-dependent, due in part to differences in species' thermal tolerances and density dependent effects (Jeppesen et al. 2012). Air temperatures can also affect the onset, duration, and intensity of lake stratification, thereby affecting the growth of fish positively or negatively depending on where they are distributed in the water column (King et al. 1999). If rising temperatures do not exceed the physiological tolerance of a fish species, they may be favorable given sufficient availability and quality of prey to meet metabolic demands; however, decreases in growth rates would be expected if rising temperatures are coupled with food limitation (Magnuson et al. 1990; McDonald et al. 1996). Similarly, local differences in the density of competitors can cause asynchronous effects of climate on populations in close geographic proximity (Rogers and Schindler 2011).

Effects of climate change on growth and survival of juvenile salmon rearing in freshwater can depend on features of the landscape and local habitat. For example, for 18 populations of Chinook salmon in the same river basin, survival in some populations was negatively correlated with summer air temperature, where survival in others was positively correlated with minimum fall stream flow (Crozier and Zabel 2006). Stream width was also identified as a key habitat factor that shaped the response of individual populations to climate (Crozier and Zabel 2006). Similarly, in two morphometrically different lakes in the same small watershed, juvenile sockeye salmon growth had the opposite response to spring and fall air temperatures (Griffiths et al. 2014). It follows that the response of salmon smolt size to changing environmental conditions would be highly variable in space and time; therefore, population-specific predictions are necessary to determine the potential consequences of a warming climate for growth and marine survival. Yet, due to a lack of time-series data on smolt length for most salmon populations it is difficult to a) understand how smolt length has been historically related to factors such as temperature and density, and b) make specific predictions of how smolt size at age may change in the future for individual populations. In contrast, records of adult salmon returning to freshwater are abundant, including sex and length information. Scales of returning adults have been collected over long periods of time for many populations and individual growth of juveniles during freshwater residence can be inferred from scale patterns (Ruggerone et al. 2007). Therefore, smolt size-at-age can be determined using back-calculation methods to reconstruct time-series of smolt length, allowing for opportunities to understand the effect of climate and density on smolt size over time.

The purpose of this study was to use a long-term archive of adult scales to determine the relative effects of temperature and density on reconstructed smolt size for two sympatric, but distinct sockeye salmon populations. Our objectives were to: 1) quantify responses of

smolt size-at-age to climate and density effects for two populations that occupy the same watershed and 2) forecast smolt size-at-age responses to future scenarios of increasing temperature and escapement. We hypothesized that temperature and density would be important in predicting smolt size for both populations, though the relative effects of temperature may vary between populations. In addition, we hypothesized that smolt length would be forecasted to increase under scenarios of low escapement and higher temperature scenarios.

Methods

Model study system

The South Olga lakes system on the southern end of Kodiak Island, Alaska, USA supports one of the largest sockeye salmon runs in the Kodiak Archipelago and has a long-term average sockeye salmon total return of approximately half a million fish (Jackson et al. 2012; Finkle and Loewen 2015). The system is composed of two lakes: Upper Olga Lake, an oligotrophic lake with a maximum depth of 70 m, and Lower Olga Lake, a mesotrophic lake with a maximum depth of 2 m (Finkle and Loewen 2015; Figure 2.1). The South Olga lakes system has two temporally and genetically (Gomez-Uchida et al. 2012) distinct sockeye salmon populations that are managed as separate stocks. Early run fish return from late May through mid-July and spawn in tributaries of Upper Olga, while Late run fish return from mid-July through September and spawn in the shoals and creek between the two lakes (Finkle and Loewen 2015). The life history of sockeye salmon has been reviewed extensively elsewhere (Burgner 1991), but in brief, juvenile anadromous sockeye salmon rear in lakes for one to three years after emergence from the gravel, though some migrate to sea soon after emergence. After migrating to sea, adult sockeye salmon spend one to four years in the ocean before returning to fresh water, where they spawn and die in late summer and autumn (Quinn 2018). For South Olga lakes sockeye salmon, the

predominant age classes have historically been freshwater age 1 and freshwater age 2, though between 1978 and 1993 freshwater age 0 sockeye salmon made up a large portion of Late run returns during periods of high population productivity (Figure 2.2).

Time-series of smolt length at ocean entry for Olga lakes sockeye salmon

Adult sockeye salmon have been enumerated and sampled for age and length at the Upper Station weir since 1928. Based on stock-specific run timing with minimal overlap, fish returning through July 15 are considered Early run, where fish returning after July 15 are deemed to be part of the Late run (Gomez-Uchida et al. 2012). Run reconstructions based on escapement and scale pattern analysis are available beginning in 1970 for both the Early and Late run. As such, the collection of archived adult scales begins in 1970 and continues on an annual basis by the Alaska Department of Fish & Game (ADF&G). Archived scales sampled by ADF&G from returning adult fish during 1970 - 2012 were preserved as impressions in acetate cards and include corresponding information on length, age, and sex (based on physical examination of external characteristics). Seaward migrating sockeye salmon smolts were sampled at ocean entry by ADF&G using a Canadian fan trap 1.6 km downstream of Lower Olga Lake on the following dates: May 20 – July 30, 1990; May 11 – August 4, 1991; May 5 – July 31, 1992; and May 10 – August 6, 1993 (Finkle and Loewen 2015). A smear of scales was pulled from individuals and mounted on glass slides and age and length data were recorded (Finkle and Loewen 2015). Juvenile scales and adult scale impressions were included in the study based on the following criteria: 1) we agreed with ADF&G age determination, 2) annuli are clearly defined and not affected by regeneration or reabsorption of the scale, and 3) the shape of the scale indicates it was taken from the preferred area, which is immediately above the lateral line and slightly forward of the adipose fin (Koo 1962; Ruggerone et al. 2007). Smolt scales were randomly

sampled (n = 1300) for each age class (0 – 3) from when smolts were sampled (1990 – 1993) with stratified random sampling for each age and year (0 – 2). A random sample of age 3 smolts were sampled across all years due to a low number of available scales (n = 100). Following the approach of Ruggerone et al. (2007) a random sample of 25 scales from a single age class of adult females (age 2.2) was selected from each run (i.e., Early or Late) and each year of ocean entry between 1971 and 2010. Age 2.2 females were chosen because this age class was present in high abundance for both the Early and Late run return in most years; in addition, they spend the most time in freshwater and therefore may be more susceptible to changes in conditions during this life stage. Adult scales were not available for age 2.2 adults that entered the ocean in 1975, therefore this observation is missing from analyses. Acetate scale impressions were digitized using a Z-Scan 46-II microfiche reader attached to a 19.3 mm zoom lens and images were exported at high resolution (3352 x 4425 pixels) to Image-Pro software$^{®}$ for measurements of scale patterns.

To back-calculate smolt length from returning adult scales, we first measured the distance (mm) on the longest axis from the focus of the scale to the last circulus of the end of freshwater growth. In addition, we measured the total distance from the focus of the scale to the edge of the scale for both adult and smolt scales (Ruggerone et al. 2007). Random checks between two trained readers were done to assure consistency in measurements for adult scales (~5% of scales checked, as in Ree et al. *in prep*). We used the Fraser-Lee equation (Fraser 1915; Lee 1920) to back-calculate smolt length from scales of returning adults. The Fraser-Lee method has been widely used for many species of fish (Ward et al. 1989; Bond et al. 2008; Weitkamp et al. 2011) and is preferred because the intercept, c, has a biological interpretation as the length of a fish at the beginning of scale growth. In addition, the Fraser Lee method has been verified for sockeye salmon by comparing the length of fish and scale radius of tagged and recaptured sockeye salmon (Fukuwaka and Kaeriyama 1997). First, the constant c was obtained

by calculating the regression of length on scale radius from adult and smolt scales:

$$g(S) = c + dS, \tag{2.1}$$

where $g(S)$ is the mean body length for a fish with scale radius S. The intercept, c, represents the theoretical length of Olga lakes sockeye salmon at the time of scale formation. The back-calculated smolt length of returning sockeye salmon at the time of ocean-entry was then calculated using the following equation:

$$BSL = c + (L_c - c)\left(\frac{S_f}{S_c}\right), \tag{2.2}$$

where BSL is back-calculated smolt length, L_c is the length of the returning adult, S_f is the scale radius of the freshwater growth zone, S_c is the scale radius of the returning adult, and c is equivalent to c in Equation 2.1.

Potential predictors of smolt length at ocean entry

The first factor hypothesized to affect smolt size was the density of adult salmon that produced the smolts at ocean entry in year y (escapement lag-3; Figure 2.3) as a proxy for the density of juveniles of the same cohort. The second factor hypothesized to affect smolt size was the density of adult salmon that spawned in the system before their second summer of growth (escapement lag-2; Figure 2.3) as a proxy for the density of juveniles emerging that summer. The density of juvenile sockeye is likely to be non-linearly related to the number of spawning adults due to density-dependent effects (Rich et al. 2009) and, therefore, we used the natural log of escapement as a proxy for juvenile density. Escapement was pooled for both the Early and Late run as it is probable that juveniles have overlapping rearing habitat and mix with conspecifics of both stocks. The third factor hypothesized to affect smolt size was temperature. We used mean daily maximum air temperature in spring (March – June) as recorded by the Kodiak Airport, 130 km northeast of Olga lakes, as an index of temperature experienced by

juveniles during their second summer of growth. Air temperature has been shown to be a good predictor of water temperature (Stefan and Preud'homme 1993; Livingstone and Lotter 1998) though lake depth has a strong influence on thermal inertia (Toffolon et al. 2014). We explored model performance of several other combinations of temperature before our temperature index was selected including summer temperature (June – September) and spring/summer temperature (March – September).

Time-series analysis

We used dynamic linear models (DLM) to quantify the relative effects of three factors on smolt size at ocean entry of sockeye salmon: escapement lag-3, escapement lag-2, and temperature. This technique has been used effectively to identify abiotic and biotic drivers of growth and survival for salmon (Scheuerell and Williams 2005; Schindler et al. 2005b) while accounting for autocorrelation. A major advantage of a DLM approach is that the model structure allows regression coefficients of predictor variables to vary through time whereas more typical GLM or GAM approaches assume stationary (i.e., temporally static) relationships with predictor variables. Accounting for non-stationarity of regression parameters is important, as it is becoming increasingly clear that the processes linking climate and population parameters may not be static (Litzow et al. 2018). The DLM structure can be described by two equations. First, the observation equation can be written as the following:

$$Y_t = \mathbf{F}_t^{\mathrm{T}} \boldsymbol{\theta}_t + v_t \qquad\qquad v_t \sim N(0, r) \qquad\qquad (2.3)$$

where smolt size Y_t at time t is modeled as a function of $\mathbf{F}_t$, a column vector of potential predictor variables, $\boldsymbol{\theta}_t$ is a column vector of fitted regression parameters, and v_t is a vector of normally distributed observation errors with mean 0 and variance r. The second, the process equation, allows the regression parameters to vary over time through an autoregressive process

via a Kalman filter and smoother (Holmes et al. 2012):

$$\boldsymbol{\theta}_t = \boldsymbol{\theta}_{t-1} + \boldsymbol{w}_t \qquad \boldsymbol{w}_t \sim MVN(0, \boldsymbol{Q_t}) \qquad\qquad (2.4)$$

where w_t is a vector of process errors and $\boldsymbol{Q_t}$ is the system variance matrix where the variance

of w_t is stored in the diagonal with zeroes elsewhere. We began by fitting a reference model

such that the observation equation was written as follows:

$$Y_t = \boldsymbol{\theta}_t + v_t \qquad v_t \sim N(0, r) \qquad\qquad (2.5)$$

We used this random-walk model as a means to evaluate the relative performance of more

complicated models containing predictor variables (Rich et al. 2009). All models were fit using

the MARSS package (Holmes et al. 2012) in the R programming language (www.r-project.org).

Models were fit separately to smolt length data for the Early and Late runs. Alternative

models for each stock were compared using the Akaike Information Criterion, bias-corrected

for small sample sizes (AICc; Table 2.1). Models were ranked by AICc and the difference

between each model and the model with lowest AICc was determined according to:

$$\Delta\text{AICc} = AICc_i - AICc_{min} \qquad\qquad (2.6)$$

When ΔAICc equals $0 - 2$, the empirical support for model i is "substantial"; $4 - 7$ is

"considerably less"; and >10 is "essentially none" (Burnham and Anderson 2002).

To compare the relative effects of each predictor on smolt length, we calculated effect

sizes as the product of the regression coefficient and the value of the independent variable in

each year of the time series (Schindler et al. 2005b; Rich et al. 2009). Effect sizes were

expressed in the units of the response variable in order to provide a simple interpretation of the

effect of independent variables on smolt length of Olga lakes sockeye salmon.

Forecasting smolt length at ocean entry

Forecasts for smolt size at ocean entry were estimated under four different scenarios: 1) high increases in temperature and high escapement, 2) high increases in temperature and low escapement, 3) low temperature increases and high escapement, and 4) low temperature increases and low escapement. Forecasts were computed using observed escapement data from 1968 – 2018 and observed mean daily max air temperatures (March – June) from 1970 – 2016; after which temperature for each scenario was computed using down-scaled global climate models from Scenarios Network for Arctic Planning (SNAP; https://www.snap.uaf.edu). High emission forecasts were based on the highest emission scenario global climate model (i.e., rcp 8.5), where low emission scenarios were based on a low emission scenario global climate model (i.e., rcp 4.5; Walsh et al. 2018). High escapement forecasts were calculated from the maximum observed escapement and low escapement from the minimum observed. One step forecasts of the parameters at time t were calculated via the Kalman filter algorithm where the predictive distributions of the regression parameters are conditioned on previous observations ($\boldsymbol{\theta}_t | y_{1:t-1}$) and are updated as new information is incorporated into the model. MARSS estimates the states at $t = 0$ ($\boldsymbol{\theta}_0$), which allows us to compute a forecast for the first time point. Prediction intervals of forecasts are computed from the variance of parameter estimates calculated as part of the Kalman filter and observation variance (Holmes and Ward 2011).

Results

Time-series of smolt length at ocean entry for Olga lakes sockeye salmon

The intercept of the linear regression c of fish length on scale radius from smolt (n = 1300) and adult (n = 2361) scales was estimated as 21 mm. Smolt length for the Early run varied considerably over the 40-year time series (1971 – 2010) with an annual mean back-calculated smolt length ranging from 105 – 139 mm. Smolt length for the Late run also varied over the 40-

year time series, ranging from 106 – 135 mm (Figure 2.4). Smolt length of the Early and Late run were correlated (*cor* = 0.72) though the mean length of age 2.2 Early run smolts was 2.8 mm larger, on average, than their Late run counterparts (ANOVA, F_1 = 28.7, p < 0.001).

Predictors of smolt length at ocean entry

For the Early run, the top-performing model (ΔAICc < 2) included escapement lag-3 density, escapement lag-2, spring temperature, and an interaction between escapement lag-2 and temperature (Table 2.1). There was a good match between the observed data and the values fitted by the model (r^2 = 0.69) and the model performed substantially better than the reference model (ΔAICc = 33.2; Table 2.1). The regression parameter for escapement lag-3 was -2.10 ± 0.004 throughout the time-series, whereas the parameter for escapement lag-2 was dynamic through time with a mean of 5.01 ± 5.0 and only became significantly positive after 1990. The regression parameter for spring temperature was 1.2 ± 0.01, where the parameter for spring temperature*escapement lag-2 was -4.19 ± 0.002 (Figure 2.5). The mean effect of escapement lag-3 was 0 mm with a range of -4.00 to 5.32 mm and the mean effect of escapement lag-2 was 1.05 mm with a range of -9.96 to 17.65 mm. The mean effect of spring temperature was 0 mm with a range of -2.83 to 2.22 mm and the mean effect of the interaction between spring temperature and escapement lag-2 was 0.05 with a range of -12.47 to 19.00 mm (Figure 2.6).

The top-ranked model for the Late run only included escapement lag-3 and escapement lag-2 and it performed much better than the reference model (ΔAICc = 29.5; Table 2.1). The regression parameter for escapement lag-3 was -2.95 ± 0.01 and the parameter for escapement lag-2 was dynamic through time with a mean of 5.71 ± 4.7. Unlike the Early run, the parameter for escapement lag-2 was significantly positive from 1971 – 1973, significantly negative during the year 1979, and became increasingly positive from 1993 – 2010 (Figure 2.5). There was a

good match between the observed data and the values fitted by the model ($r^2 = 0.67$) and the mean effect of escapement lag-3 was 0.01 mm with a range of -5.6 to 7.50 mm; the mean effect of escapement lag-2 was 1.11 mm with a range of -9.33 to 6.69 mm (Figure 2.6).

Forecasting smolt length at ocean entry

One-step forecasts matched the observed trends from 1971 - 2010 reasonably well ($r^2 = 0.49$). Forecasts from 2011 - 2015 that were calculated using observed air temperature and escapement showed a small decrease and subsequent increase in smolt length at ocean entry (Figure 2.7). After 2015, forecasted smolt length varied among the four different climate and escapement scenarios. In general, both scenarios with high escapement showed decreases in smolt length with a mean length of 118 mm from 2016 - 2030 (Figure 2.7). With low escapement and reduced climate warming (rcp 4.5), smolt length is forecasted to increase to a mean of 134 mm; whereas if climate warming was more extreme (rcp 8.5) smolt length is forecasted to remain relatively stable at a mean of 125 mm through 2030 if escapement remained low (Figure 2.7).

Discussion

Consistent with the role of within-watershed climate filtering, we have shown stock-specific responses of smolt size to temperature and density for two distinct, sympatric populations of sockeye salmon within a small watershed. In addition, we have we demonstrated that smolt size can be forecasted with reasonable model certainty using a dynamic linear model framework and predictions indicated a varied response of smolt size to scenarios of increasing temperature and changes in density. Overall, our results demonstrate that population responses to climate and density can be variable which will complicate large scale predictions of population responses to global change.

Predictors of smolt length at ocean entry

We hypothesized that for both sockeye salmon stocks in Olga lakes (Early & Late run) temperature and conspecific density would be important factors explaining variation in smolt length, though the relative effects of each may vary among populations (Schindler et al. 2005b; Rich et al. 2009; Griffiths et al. 2014). Temperature and conspecific density appeared to be relatively important for Early run smolt length, providing support for this hypothesis, whereas the relative weight of evidence only identified conspecific density as an important predictor variable for Late run smolt length. Additionally, the effects of conspecific density on smolt length were similar in magnitude for both the Early and Late run. For both runs there was a consistent negative relationship between escapement lag-3 and smolt length, where high density resulted in decreased smolt length and vice versa. The regression parameter corresponding to escapement lag-2 was dynamic through time for both the Early and Late run and had a significant positive effect on smolt length in both stocks after 1990. For the Early run, the interaction between spring air temperature and escapement lag-2 was negative, thus smolt size is predicted to increase with density if temperatures are low, but in contrast smolt size would decrease with density if temperatures are high.

Consistent with previous findings, we have shown that two distinct populations occupying the same small watershed may have different responses to climate and competition. Griffiths et al. (2014) in particular found two populations of sockeye salmon at the sub-watershed scale had opposite growth responses to spring and fall air temperatures, likely due to climate drivers being mediated by differences in lake morphometry. Upper and Lower Olga lakes are morphometrically dissimilar; Lower Olga Lake is characterized as warm, with temperatures sometimes exceeding 15°C which may increase metabolic stress for juveniles (Griffiths and Schindler 2012; Finkle and Loewen 2015). Although the stock-specific distribution of juveniles

in Olga lakes is not well known, it is possible that juveniles from the Early and Late run would be somewhat segregated in this small watershed. If Early run fish are more commonly distributed in Lower Olga Lake, differences in lake morphometry may explain why Early run smolt size is slightly more sensitive to changes in air temperature. Another possibility for Olga lakes sockeye is that due to segregation in space and/or time of the two stocks, density dependent effects for Late run juveniles may overshadow temperature effects since they are more numerically abundant than the Early run stock. The mechanisms for these differences, however, remain unknown.

Overall, our findings corroborate the general understanding that conspecific density can negatively affect juvenile sockeye salmon freshwater growth in some systems (Schindler et al. 2005b; Rich et al. 2009). The overall effects of density on growth appear to be of a lower magnitude than in previous studies (Schindler et al. 2005b; Rich et al. 2009). These differences may be a result of several factors. For example, the present study relates conspecific density to the total accumulated freshwater growth of age 2 sockeye, whereas previous studies have quantified the growth of fry in the first summer. In addition, smolt length was back-calculated from returning adults in this study and is survivor-biased; significant size-selective mortality (Ree et al. *in prep*) of smolts after they enter the ocean could make strong density-dependent effects more difficult to detect.

Contrary to most findings, however, was the positive effect of escapement lag-2 on smolt length at ocean entry. The positive effect of escapement lag-2 became significant after 1990, when parent escapements were relatively low. Since we are not using a direct measure of juvenile density but rather the natural log of escapement to measure density, this positive effect may be evidence of nutrient subsidies introduced from parent carcasses. Though it has been shown that marine-derived nutrients (MDN) from salmon carcasses can lead to increases in algal

productivity in coastal lakes, the links between MDN and salmon population productivity are less clear (Schindler et al. 2005a). It is likely that over long time periods (>100 years) in systems that are spawning limited, the effect of nutrient supplementation is hard to detect (Schindler et al. 2005a). However, juvenile growth may be more sensitive to changes in MDN compared to survival, where an increase in MDN results in more available zooplankton prey that juveniles are able to consume. The input of pink salmon carcasses has been shown to increase juvenile coho *O. kisutch* growth in streams, where increasing the density of salmon carcasses increased growth up to a saturation point (Wipfli et al. 2003). The effect of MDN on juvenile salmon growth and survival in shallow lakes (i.e., mean depth < 10 m), such as Lower Olga Lake, that rely on a different prey base (i.e., aquatic insects) is poorly understood and may more closely resemble that of stream-dwelling salmonids (Richardson et al. 2017). In addition, as juveniles increase in size (> 60 mm) they undergo an ontogenetic shift in their diet to even higher compositions of aquatic insects compared to zooplankton (Richardson et al. 2017). Further investigation into the role of MDN in sockeye salmon systems with shallow nursery lakes and an older age structure (age 2) seems necessary to understand the role of nutrient input in similar systems.

There are a few limitations and caveats of the present study design in regard to quantifying smolt size at ocean entry. Back-calculation methods from returning adults can introduce inflated variance (Wilson et al. 2009) and, as previously mentioned, lengths are survivor-biased. However, back-calculated smolt length of the Early and Late run were highly correlated, suggesting that it is unlikely variation in mean smolt length is explained by spurious variation in sub-sampling methods. In addition, it appears that selection on size for age 2 smolts is relatively consistent among years (Ree et al. *in prep*); therefore, trends in smolt length should still be represented in growth patterns of surviving adults. We have demonstrated that despite the ecological noise of size-selective survival and a relatively small sample size per year, the effects

of climate and density on juvenile growth can still be detected and potentially used to inform management of these stocks. For example, as we continue to observe unprecedented climate warming, the interaction of temperature and density on growth may be important to consider when setting escapement goals that influence the levels of adult density in a system.

Forecasting smolt length at ocean entry

By using a dynamic linear model framework, we were able to forecast smolt length using real observed data of predictor variables up until 2015 and varying future climate and escapement scenarios from 2016 - 2030. We hypothesized that a future scenario of high escapement and greater increases of temperature (rcp 8.5) would result in a decrease of smolt length. However, the model for Early run smolt length forecasted that smolt length under the highest emission global climate model and minimum observed escapement would remain fairly stable with only a difference in mean smolt length of approximately -1 mm by 2030. This model had the highest level of uncertainty, where 95% prediction intervals were as large as ± 40 mm. We further hypothesized that a future scenario of high escapement and temperature increases under a lower emission global climate model (rcp 4.5) would result in a decrease in smolt length at ocean entry. As expected, both models with high escapement resulted in decreased smolt length, where the model under 'rcp 4.5' predicted smolt length to decrease by approximately 14 mm by 2030. In contrast, under a scenario of low escapement and temperatures under 'rcp 4.5', smolt length was forecasted to increase dramatically by 2030 with an increase in mean length of +15 mm. According to model forecasts it appears that smolt size for Early run sockeye is predominantly controlled by density dependent effects, though it is clear temperature can mediate the magnitude of those effects.

Though forecasting smolt length into the future using a dynamic linear model framework may be potentially useful for management, it is important to consider the limitations that arise from this approach. First, as the model predicts an increasing number of time-steps, the model uncertainty also increases. In addition, the model does not account for several factors that could affect smolt length over time. McDonald et al. (1996) predicted a decrease in young-of-the-year lake trout when zooplankton food resources did not increase with increasing temperatures. An earlier and more robust stratification of freshwater lakes could result in a reduced food supply due to an intense nutrient deficit in the epilimnion that results in lower plankton production; however, Upper Olga Lake appears to have consistent productivity in recent years (Healey 2011; Finkle and Loewen 2015). Although unknown in Olga Lakes, climate effects on predator structure and behavior may also have implications for sockeye salmon growth in freshwater (Petersen and Kitchell 2001). Inter-specific competition with three-spine stickleback *Gasterosteus aculeatus* may also increase as stickleback breeding frequency has been shown to increase with warm summer temperatures (Hovel et al. 2018). Dramatic changes in temperature and density could also partially result in shifts in age rather than size, where juvenile sockeye enter the ocean predominantly as age 0 or age 1 smolts (Finkle and Loewen 2015). Therefore, this framework may be useful to explore general trends in smolt length in response to warming temperatures or changes in escapement goals, but it does not represent a complete understanding of the various and inter-connected factors that determine mean smolt length at ocean entry for this system.

Conclusions

Salmon populations can have differential responses to climate and competition whether they are geographically proximate or otherwise; therefore, drivers of smolt size for many

populations are unknown. By utilizing archived scales from returning adult scales to reconstruct smolt size, there may be many more opportunities to understand the factors that influence freshwater growth and subsequent marine survival for salmon across their geographic range. As conditions for growth in freshwater continue to change from shifts in climate and anthropogenic disturbances (Hyatt et al. 2004; Schindler et al. 2005b; Finstad et al. 2007) it will become increasingly important to understand how salmon smolt size will respond. Since smolt size mediates the outcomes of marine survival (Henderson and Cass 1991; Koenings and Geiger 1993), the conditions that smolts experience in freshwater can have implications for overall population productivity and resilience. Moreover, stock-specific responses to climate and competition at the sub-watershed scale highlights the significance of collecting fishery-specific data in order to manage stocks appropriately in the face of continuing environmental change.
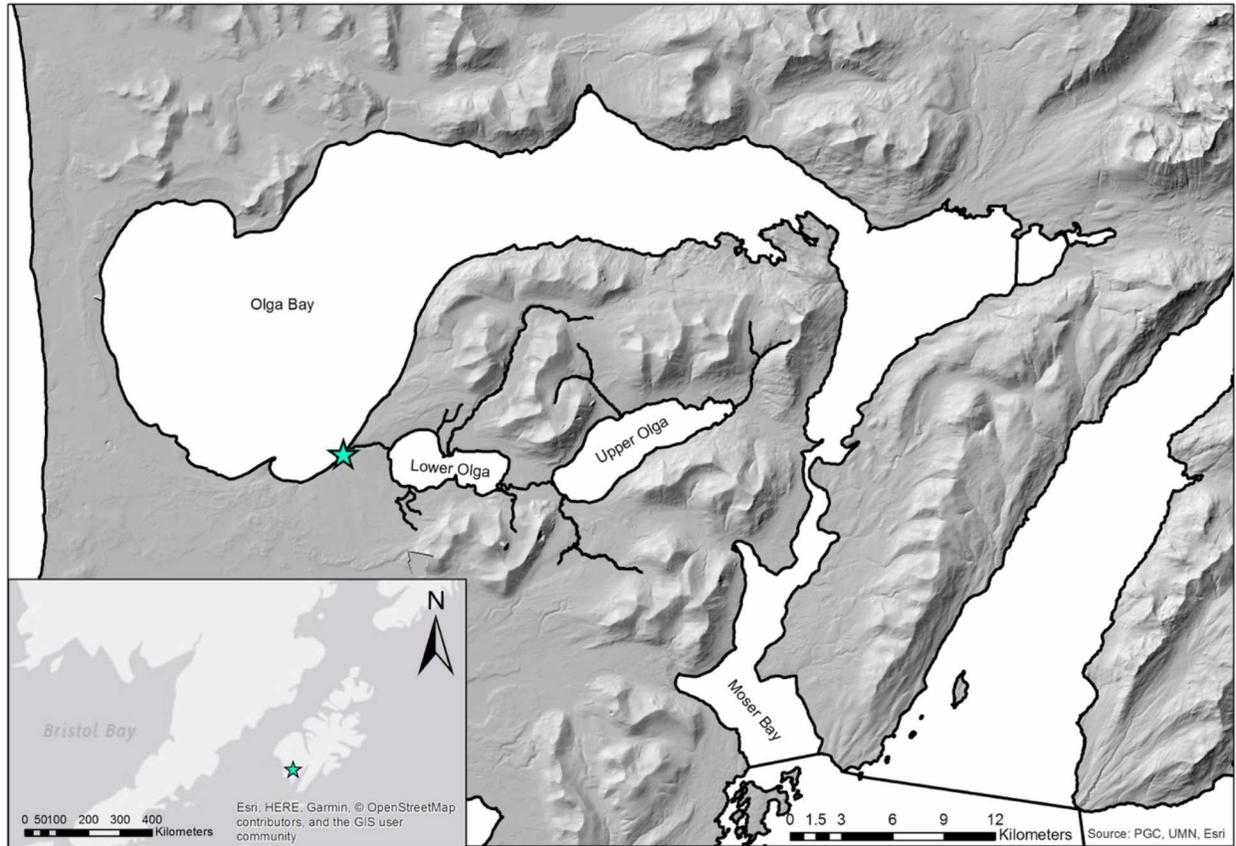
Figure 2.1 A map of Olga lakes, Kodiak, Alaska. The study area includes the Upper Station weir (colored star), and Lower and Upper Olga Lake.
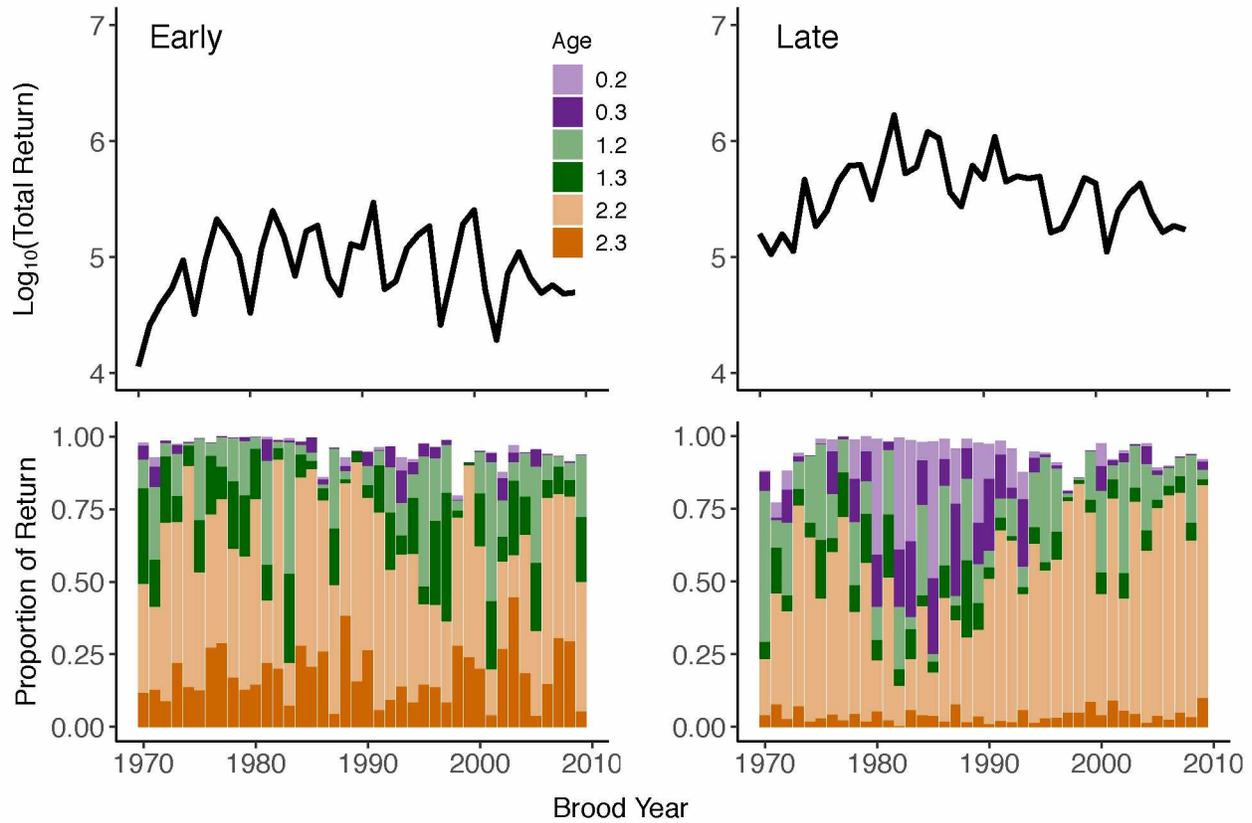
Figure 2.2 Estimated proportions of dominant age classes of Olga lakes Late run sockeye salmon (bottom panel) out of total return by brood year (top panel). Ages are represented in European notation where the number before the decimal denotes years spent in freshwater and the number after the decimal indicates the number of years spent at sea.
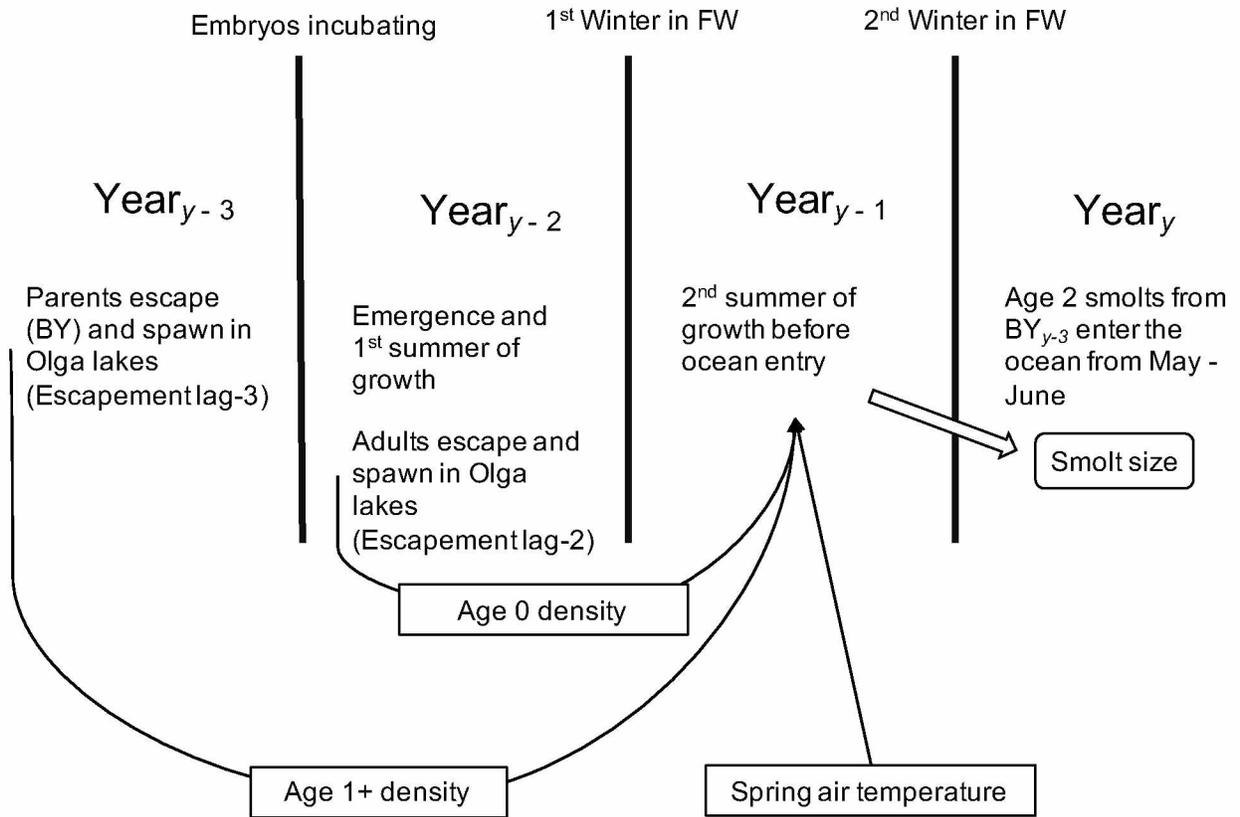
Figure 2.3 Diagram of freshwater life-history of age 2 smolts produced by brood year (BY) y - 3 in relation to timing of predictor variables in Olga lakes for smolts entering the ocean in year y.
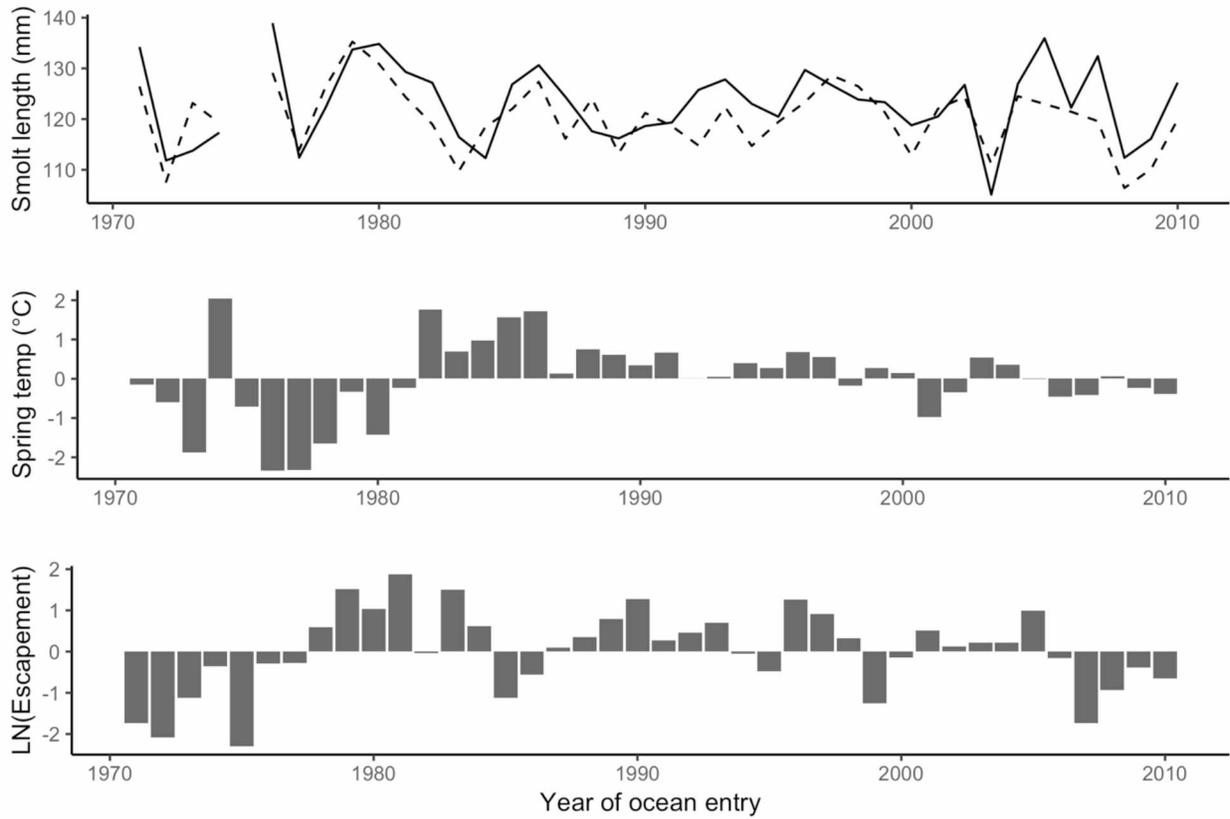
Figure 2.4 Time-series of back-calculated smolt length of age 2.2 females from the Early run (solid) and Late run (dashed) and predictor variables standardized to a mean of 0 and variance of 1.
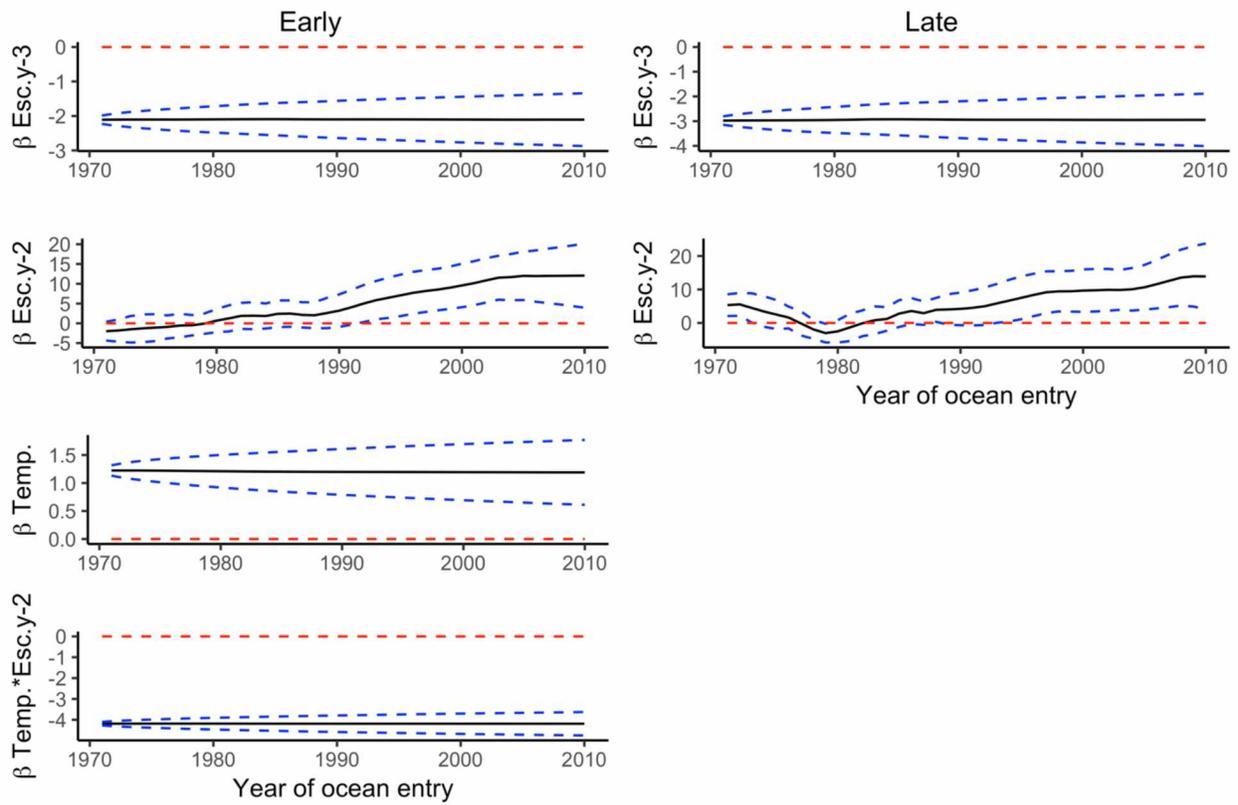
Figure 2.5 Regression coefficients of predictor variables (black line) at time *t* (i.e., year of ocean entry) for the Early (left panel) and Late (right panel) run models. Blue dashed lines denote 95% confidence intervals and red dashed line is located at zero.
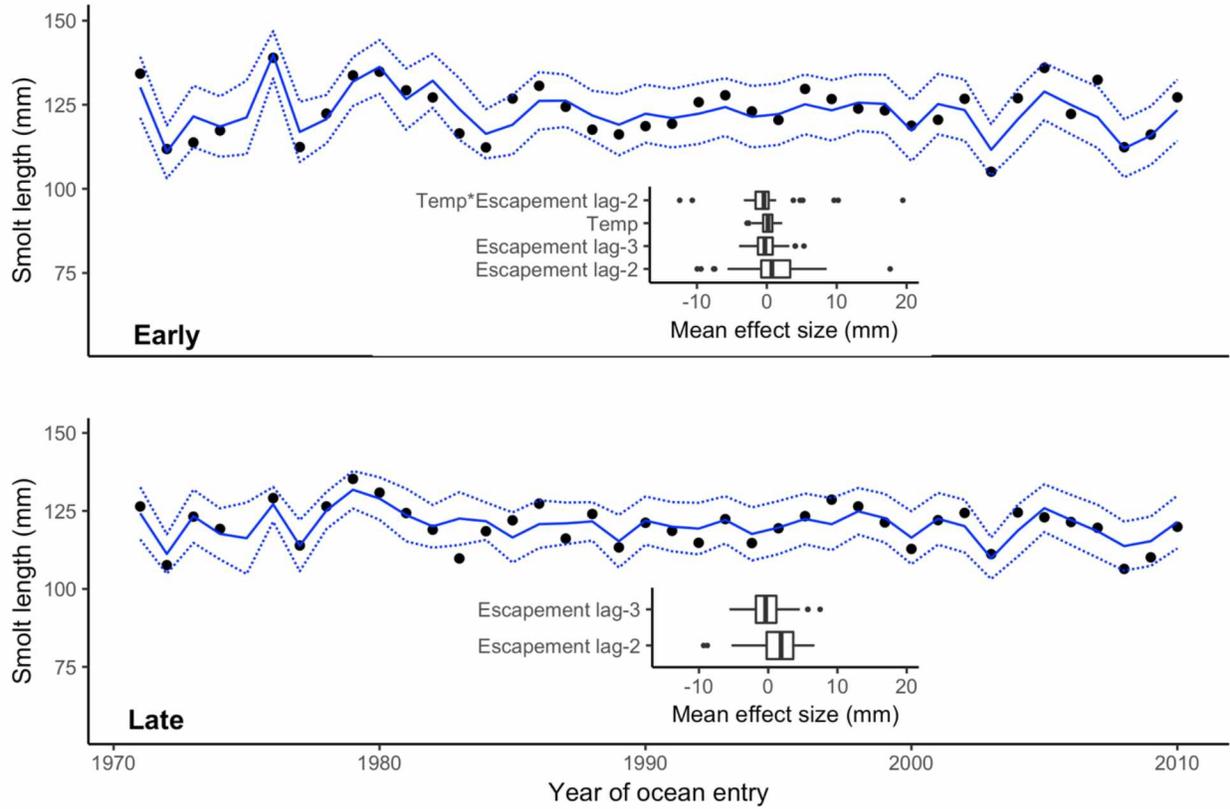
Figure 2.6 Top-ranked model fits for the Early (top) and Late (bottom) run back-calculated smolt length, where the blue line indicates fitted values and the dashed lines depicts 95% confidence intervals. Inset plots illustrate mean effect size (mm) for predictor variables.
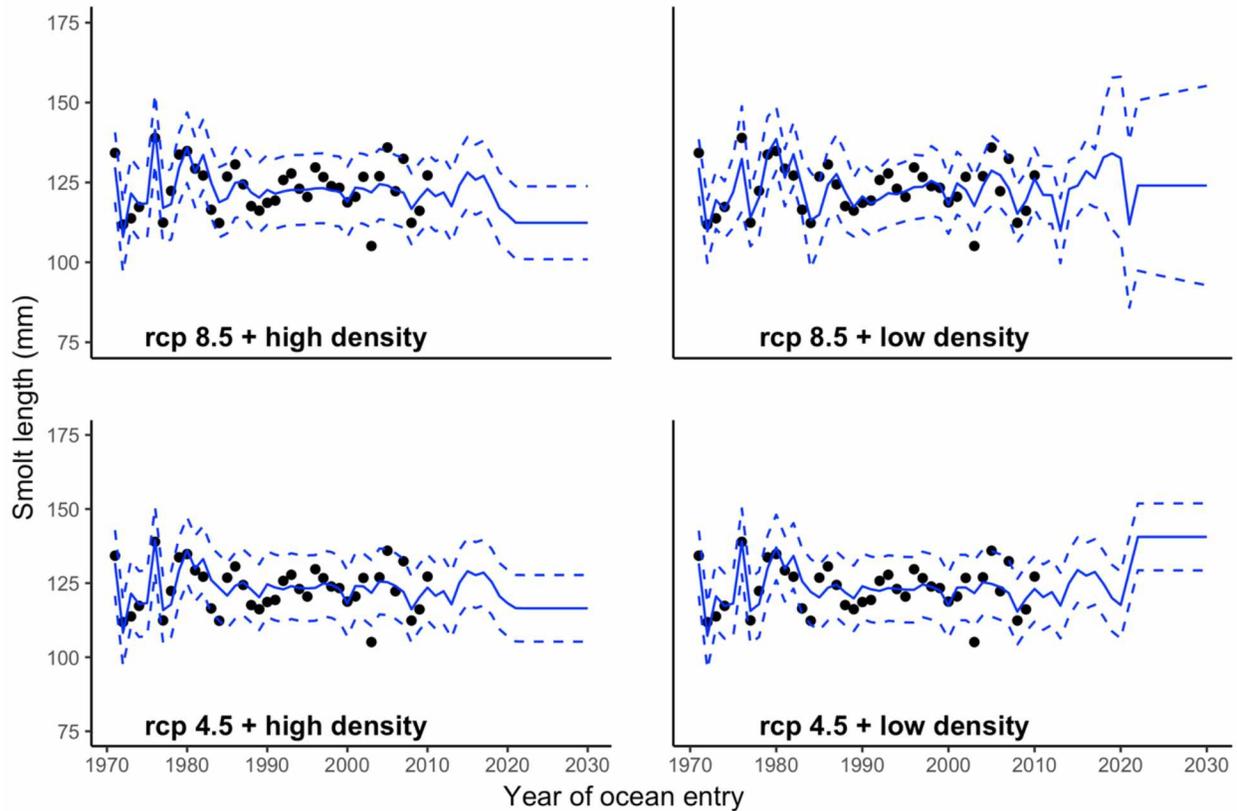
Figure 2.7 Forecasts of top-ranking models for Early run back-calculated smolt length, where the blue line indicates the model forecasts and the dashed lines depicts 95% confidence intervals. Model forecasts were determined using spring air temperatures from Kodiak Airport and ADF&G escapement counts from 1970 – 2015. Forecasts after 2015 were calculated using observed maximum and minimum escapement of Olga lakes. Temperatures after 2015 were predicted from two down-scaled global climate models of a low (rcp 4.5) and high (rcp 8.5) emission scenario from SNAP (https://www.snap.uaf.edu).

Table 2.1 Summary for dynamic linear models (DLM) to explain variation in age 2.2 female sockeye salmon *O. nerka* smolt length from Olga lakes, Alaska. Top-ranked models are in bold.

Rank	Model	AICc	ΔAICc
Early run			
1	**escapement lag-2:spring temp + escapement lag-3**	**270.3**	**0.0**
2	escapement lag-2 + escapement lag-3	272.7	2.4
3	escapement lag-2	273.3	3.0
4	escapement lag-3	275.9	5.6
5	escapement lag-2 + spring temperature	278.6	8.3
6	escapement lag-3 + spring temperature	279.4	9.1
7	spring temperature	297.9	9.6
8	escapement lag-2 + escapement lag-3 + spring temperature	284.1	13.7
9	reference	303.5	33.2
Late run			
1	**escapement lag-2 + escapement lag-3**	**255.6**	**0.0**
2	escapement lag-2	260.8	5.2
3	escapement lag-3 + spring temperature	260.9	5.4
4	escapement lag-2:spring temperature + escapement lag-3	261.7	6.1
5	escapement lag-3	262.3	6.7
6	spring temperature	263.9	8.3
7	escapement lag-2 + spring temperature	265.8	10.2
8	escapement lag-2 + escapement lag-3 + spring temperature	267.2	11.6
9	reference	285.0	29.5

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Conclusions

This thesis sought to contribute to our understanding of the linkages between climate, freshwater growth, and size-selective marine survival for sockeye salmon *O. nerka*. By using Olga lakes, Kodiak Island, AK as a study system, I explored the process of natural selection acting on smolt size of sockeye salmon within a small watershed with diverse age structure. In addition, by reconstructing a multi-decade time-series of smolt size, I gained new insights on stock-specific effects of temperature and conspecific density for sockeye salmon smolt size as well as possible future responses to a changing climate. The central findings of this thesis are as follows:

- Bigger is not always better in regard to sockeye salmon smolt survival; natural selection can either favor large or small smolts and the difference appears to relate to associations between body size and timing of smolt migration.

- Natural selection on smolt size in this system is relatively strong compared to documented examples of selection in other natural populations.

- The magnitude of selection on smolt size appears to be negatively associated with apparent marine survival and positively associated with earlier mean ocean entry timing.

- The relative effects of temperature and conspecific density on smolt size can vary among stocks coinhabiting a small watershed.

- Early run Olga lakes smolt size showed variable responses to scenarios of increasing temperature and high and low densities (e.g., smolt size increased with lower temperature increases and low escapement but decreased with higher temperature increases and high escapement).

Natural selection on smolt size and implications for management

Changes in escapement goals for Olga lakes sockeye, particularly for the early run, has been hypothesized by ADF&G to have had an effect on growth and survival of juvenile salmon (Finkle and Loewen 2015). The management of the two runs of sockeye salmon in Olga lakes has varied significantly over time with the first escapement goal set in 1978 at 100,000 to 180,000 fish; however, the Alitak District was managed for Frazer sockeye salmon, a nearby stock that mixes with Olga lakes stock in the Alitak district, up until 1988. Since 1988, several formal escapement goals have been established for both Early and Late run sockeye. Decreasing escapement goals could have an indirect effect on smolt length by decreasing adult density in the system causing a hypothetical increase in juvenile growth.

Although long used as a management and enhancement tool to increase survival, it is increasingly evident that simply increasing the size of smolts at ocean entry may not have the desired effects on population productivity as previously thought. I have demonstrated here that natural selection on smolt size can be positive *or* negative depending on smolt age. Although the ecological mechanisms behind this selection are unknown, this is likely due to a trade-off for age 1 smolts to migrate earlier in the season, but at a smaller size than they would be if they migrated later in the summer. Previous work has shown that the relationship of smolt size and survival is dependent on other factors such as ocean entry timing and smolt abundance (Bilton et al. 1982; Peterman 1982).

In some sockeye salmon lakes, the addition of nutrients (in particular phosphorus) to fertilize the system has been used as a means to increase smolt-size through bottom-up effects with the ultimate goal of increasing marine survival; though substantial increases in smolt size have been observed during lake fertilization, the evidence for increased marine survival is weak (Hyatt et al. 2004). It is probable that high variability in marine survival year-to-year makes the

effects of fertilization difficult to detect, and this is true of the effect of smolt size in unmanipulated systems as well (Holtby et al. 1990; Henderson and Cass 1991). Therefore, it is vital to test both site-specific selection on smolt size and the assumption fertilization will increase fry growth before pursuing efforts to manipulate a natural system by increasing nutrient input.

More importantly, recent evidence has shown that phenological diversity in smolt migration timing may be underappreciated and contribute to resiliency to climate change (Huber and Carlson 2015; Carr-Harris et al. 2018). The presence of age structure diversity is recognized to buffer populations from poor marine conditions by staggering the year of ocean entry (Moore et al. 2014). The effects of lake fertilization on age structure and smolt migration timing is not well understood; however, there may be potential long-term adverse effects if a) migration timing was compressed and b) age structure became more homogenized due to lower variation in growth rates. It seems that fundamental questions such as the effect of increased growth rates and size on smolt migration timing and age-at-maturation should be addressed as part of any environmental impact-type assessment prior to fertilization for enhancement purposes.

It is worth noting that though we have quantified the magnitude of selection on size in this system, the ecological mechanisms of selection remain unknown. Presumably selection on size is a function of size-biased predation that may be facilitated by other factors such as parasitism (Boyce and Clarke 1983; Wood 1987; Sturdevant et al. 2009; Tucker et al. 2016); alternatively, the relationship of smolt length with ocean entry timing may influence the magnitude and direction of selection that we have observed (Bilton et al. 1982; Quinn 2018). However, other sources of selection on smolt size should be considered. For example, late-stage predation or fishing mortality could potentially introduce bias in selection estimates especially if smolt size is significantly correlated with adult size (Hanson et al. 2010). Olga lakes sockeye

salmon are subject to both a purse seine and gillnet fishery and therefore adults that escape to spawn may be smaller than those caught by the fishery (Kendall et al. 2009; Kendall and Quinn 2012). Previous work has found that Pacific salmon that are large as smolts have a higher probability of maturing at an earlier age (Bilton 1971; Vøllestad et al. 2004) and therefore may have a higher probability of escaping the fishery. However, back-calculated smolt length was only significantly different by saltwater age for freshwater age 0 fish and larger smolts tended to be larger as adults. Thus, the fishery may slightly influence estimates of selection on size, but the trends we have observed do not appear to be directly introduced by this mechanism.

Sockeye salmon smolt size in a warming climate

One of the most salient findings from this work is the variability in predicted responses of sockeye smolt size to varying degrees of increasing temperature and densities. Under the low emission scenario (rcp 4.5) and low density, smolt size was predicted to increase; however, under a high emission scenario (rcp 8.5) and low density, predictions of smolt size were highly uncertain compared to the other three scenarios. Under low densities smolt size would be predicted to increase as conspecific grazing pressure on zooplankton and macroinvertebrate prey would be eased (Mazumder and Edmundson 2002). However, it appears that as temperatures increase to levels that have not been observed in this system, the future response of smolt size is uncertain. If increases in temperature increase metabolic demand of juvenile fish beyond what prey resources can sustain, then smolt size could decrease even with lowest observed densities. Alternatively, juvenile growth could increase if their prey base responds positively to climate warming and temperatures remain below stressful levels (Brett 1971; Magnuson et al. 1990; McDonald et al. 1996).

A management issue that may arise from warming temperatures is site-specific shifts in growth opportunities of freshwater lakes. For example, juveniles occupying large, deep lakes that rely on zooplankton as their main prey source, may have changes in freshwater growth as warming causes shifts in zooplankton density, phenology, or community composition (Winder and Schindler 2004; Schindler et al. 2005). Whereas, juvenile sockeye occupying small, shallow lakes that can consume high proportions of adult insects may not be affected in the same way as their prey base may respond differently to warming temperatures (Richardson et al. 2017). Smaller, shallow lakes may also be more susceptible to changes in air temperature and therefore have warmer and more variable thermal regimes than cold, deep lakes. In this way, the direct effect of temperature on metabolic rates via varying thermal habitats may result in differential responses of juvenile growth (Edmundson and Mazumder 2001). Since landscape filtering of climate may cause variation in metabolic demand (Griffiths et al. 2014) it would be beneficial to gather biological data such as long-term trends in smolt size and grazing pressure to monitor shifts in density dependence (i.e., rearing capacity). This is likely especially true in systems, such as the Olga lakes, with a diversity of habitats.

For Olga lakes sockeye salmon specifically, there does not appear to be any downward trends for size of age 2 smolts. With recent limnological work on zooplankton densities (Finkle and Loewen 2015) it appears that, currently, freshwater growth may not be a limiting factor for Olga lakes sockeye salmon survival. Furthermore, using observed spring air temperature and escapement data after 2010, age 2 smolt size is predicted to have increased. Further steps to better understand trends in Olga lakes stocks specifically would be to reconstruct smolt size for all ages (age 0 and age 1) in order to assess whether trends in age 2 smolt size reflect that of other age classes, and to understand linkages between growth and size-dependent migration decisions (Tillotson and Quinn 2016).

One caveat to consider from this work is the effect of selection on smolt size on detecting true trends of smolt size at ocean entry through time. By quantifying natural selection for several years of ocean entry (Ree et al. *in prep*) we found that though the magnitude of selection on size did not significantly vary among years, there was still some variation for selection on age 2 smolts (SSD = 1.80 ± 0.77). Therefore, we have assumed that the trends we observed in reconstructed smolt length is a result of freshwater conditions (i.e., temperature and density) and is not significantly biased by variation in the magnitude of selection on size. There is some evidence to support this assumption as observed smolt length was highly correlated with back-calculated smolt length (*cor* = 0.87, *p* < 0.001); therefore, trends in observed smolt length are likely preserved in the reconstructed time-series.

Comments for future work on retrospective scale analyses

Utilizing returning adult salmon scales to back-calculate size at age can be an extremely useful tool to gain insights on long-term growth trends. It should not be underestimated, however, the amount of processing time that this method requires. To put into perspective, the number of adult and smolt scales that were processed for this thesis was ~ 4,000 scales. The total time to process a scale (digitize and measure) is approximately 10 minutes. Therefore 4,000 scales would take *at minimum* four months to process if one was continuously working for 8-hours per day during a normal work week. Realistically, the processing time would take much longer once you take into account losses in maximum efficiency and QA/QC. Despite the laborious task of processing a large volume of salmon scales, new insights on population parameters can be gained in systems that may be relatively data poor. In addition, because retrospective scale analyses are so time-consuming, many archived scale collections remain underutilized. Therefore, there are many opportunities for the tenacious individual to determine

population-specific responses of Pacific salmon to multiple potential drivers throughout their geographic range.

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