Trends in juvenile sockeye salmon rearing capacity, stock specific growth performance, and estuarine habitat use in the Chignik watershed, Alaska

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Abstract

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Coastal watersheds provide a network of interconnected heterogeneous habitats accessible to mobile species. Multiple populations can exploit alternative habitats, buffering overall abundances against perturbations in climate and ecosystem processes. In the Chignik Lakes watershed, Alaska, sockeye salmon (*Oncorhynchus nerka)* populations exhibit a diversity of juvenile life history strategies, exploiting diverse freshwater and estuarine rearing habitats. In 2018, Chignik sockeye salmon stocks experienced a catastrophic collapse, threatening the viability of commercial and subsistence harvest. The overall goal of this thesis was to investigate how changes in juvenile sockeye salmon rearing capacity, growth performance, and habitat use within the Chignik watershed may have contributed to the 2018 fishery disaster.

We compiled and analyzed multiple decades of habitat quality data to explore long-term trends in the freshwater rearing capacity and growth performance of juvenile sockeye salmon in the years preceding the 2018 collapse. We identified increasing water temperatures in a shallow lake, and more stable conditions in a deeper lake. Zooplankton prey quality increased in response to both bottom-up and top-down food web dynamics. We observed strong effects of competition and density dependence in sockeye salmon populations throughout the watershed. Although we detected no evidence that freshwater habitat quality has declined, the data suggest that high early life stage mortality in brood years of the 2018 collapse likely contributed to poor adult returns.

Using Single Nucleotide Polymorphisms, we successfully assigned individual juvenile sockeye salmon to two distinct populations. We reenforced previous findings that body condition reflects the productivity of an individual's rearing habitat, regardless of stock of origin. Additionally, we observed multiple stocks exploiting estuarine habitat for juvenile rearing for the duration of the summer growing season.

Together, our results suggest habitat heterogeneity and population diversity buffer sockeye salmon populations in the Chignik watershed. By exploiting alternative habitats, multiple populations are able to achieve sufficient growth despite variability in local habitat quality.

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Chapter 1 : Long-term Changes in the Juvenile Sockeye Salmon Rearing Capacity of the Chignik Lakes Watershed

1.1 Abstract

Freshwater ecosystems respond rapidly to perturbations in climate, geomorphology, and population abundances. For migratory species in interconnected habitat networks, local habitat conditions can control the productivity of individual populations. Asynchronous variation in habitat quality can simultaneously stabilize ecological processes at broad scales but also complicate understanding of ecosystem dynamics. We investigated habitat-specific trends in indicators of the rearing capacity for juvenile sockeye salmon in a remote watershed in Alaska over the last ~60 years. The motivation of this effort was to understand if the collapse of the local salmon fishery in 2018 could be traced to changes in habitat quality within the nursery watershed. Our analyses describe high variability in the habitat conditions across both spatial and temporal scales, yet do not suggest a dramatic decline in the overall sockeye salmon rearing capacity of the watershed. We observed increasing maximum water temperatures in a shallow lake but more stable conditions in a deep lake, an improvement in zooplankton prey resources in the deep lake, and increased juvenile sockeye salmon growth rates throughout the watershed. Although we detected no long-term decline in rearing habitat quality, there was a decrease in juvenile sockeye salmon abundance from 2013-2016, suggesting high early life stage mortality during the period of juvenile rearing leading up to the fishery collapse.

1.2 Introduction

Lakes are inherently dynamic ecosystems, whose physical structure is controlled by interactions between climatic drivers and geomorphological characteristics of their watersheds (Griffiths et al., 2014). The system of chemical, physical, and biological processes which filter climate variables in aquatic ecosystems makes lakes respond in complex and often unpredictable ways to climate variation (Adrian et al., 2009; Woolway et al., 2020). The responses of lake biota to changing physical and chemical drivers can feed back to alter direct responses to changing climate through phenomenon such as recruitment variation of important species (Hovel et al., 2017) which can produce changes in the strength of trophic cascades (Post et al., 1997). As global climate change continues, understanding ecological responses to changing environmental conditions in lakes has utility for developing successful adaptive management strategies for key resources and the ecosystem services they provide.

Fisheries management is complicated by uncertainties in both density-dependent feedbacks within exploited populations, and in the dynamics of the habitat used by organisms to complete their life cycles. For migratory species, understanding changing ecological constraints on productivity is particularly difficult, as they use a variety of habitats over the course of their lives (Brennan et al., 2019). Because regional and local habitat conditions can respond asynchronously to climate forcing, habitat connectivity enables individuals to migrate among habitats to exploit changing growth and survival opportunities and avoid stressful conditions as habitats respond to regional climate forcing (Baguette et al., 2013). Thus, habitat complexity encountered by exploited species can simultaneously stabilize population dynamics and complicate understanding ecosystem responses to changing climate, thereby challenging the development of prescriptive management strategies (Chr, 1980; Schindler & Hilborn, 2015).

Pacific salmon (*Oncorhynchus.* spp) fisheries are supported by heterogeneous freshwater habitats, providing economic and cultural ecosystem services through subsistence and commercial harvest. Maintained by strong natal homing (Bodznick, 1978; Quinn & Dittman, 1990), salmon populations exhibit a wide range of life histories among genetically distinct populations within watersheds (Blair et al., 1993; Hilborn et al. 2003). Sockeye salmon (*Oncorhynchus nerka*) are particularly reliant on lakes and their watersheds for spawning and juvenile rearing habitat (Arostegui & Quinn, 2019). Marine survival of sockeye salmon is positively correlated to the size and body condition of out-migrating smolts (Groot & Margolis, 1991; Henderson & Cass, 1991; Koenings et al., 1993). If rearing habitat conditions are degraded juvenile sockeye salmon can experience poor growth performance, decreasing chances of ocean survival and ultimately population recruitment. Therefore, dynamics of exploited sockeye salmon populations are ultimately responsive to both freshwater and marine habitat conditions, as well as density-dependent responses to harvest (Quinn et al., 2009).

Situated on the Alaska Peninsula, the Chignik Lakes watershed provides spawning and rearing habitat for multiple genetically distinct populations of sockeye salmon (Creelman et al., 2011) which have supported a vibrant commercial fishery for over a century, and are a crucial subsistence resource for local communities (Dahlberg, 1979). Chignik sockeye salmon stocks are aggregated into early run (May-July) and late run (July-September) populations for management purposes. Commercial and subsistence harvest of both runs is managed by the Alaska Department of Fish & Game (ADF&G), who operate a weir on the lower Chignik River to enumerate and provide stock assignment of returning adult fish. Their management strategy seeks to maximize fishing opportunity while achieving escapement goals set to maximize long-term yield from the stocks (Finkle et al., 2022).

In 2018, Chignik sockeye salmon experienced a precipitous decline in the number of returning adults (Fig. 1), resulting in several years painful closures of the commercial fishery. Concern over the future sustainability of the Chignik sockeye salmon fishery motivated the ADF&G to propose implementing a new management strategy to account for a hypothesized regime shift within the freshwater rearing habitat of the system (Finkle et al., 2022). Citing geomorphological changes (Griffiths & Schindler, 2012; Westley et al., 2008) and climate as controls on habitat quality, ADF&G hypothesized that the watershed is no longer able to support historic abundances of juvenile sockeye salmon. While the proposed management strategy was not implemented due to a lack of empirical evidence of declining habitat quality, a clear consensus on the cause of the 2018 collapse has not yet been reached. Without a comprehensive analysis of temporal trends in the habitat quality of the Chignik watershed, it remains unclear how freshwater rearing capacity has changed, and whether potential changes justify altering management strategies to accommodate degrading freshwater habitat conditions.

We used several decadal-scale datasets to characterize long-term trends in lake thermal conditions, zooplankton community, planktivorous fish community, and juvenile sockeye salmon growth performance to quantify evidence for changes in the rearing capacity of the Chignik lakes watershed. In particular, we focused on ecosystem shifts during the juvenile sockeye salmon rearing years (2013-2016) preceding the (2018-2021) stock collapse. We organized our analyses of historical data collected over the last several decades to assess the evidence that the growth and rearing conditions experienced by juvenile sockeye salmon in this ecosystem have declined in recent years. In particular, we asked the following questions:

1) How have summer thermal conditions changed within the two dominant nursery lakes of the Chignik watershed?
2) Has the zooplankton community structure of Chignik and Black lakes changed, and do these changes reflect responses to top-down predation effects or bottom-up environmental effects?
3) How have abundances of resident planktivorous fishes that compete with juvenile sockeye salmon changed in ways that would affect the growth and survival of juvenile sockeye salmon?
4) What were the lake-specific growth responses of juvenile sockeye salmon to habitat change?

1.3 Methods

1.3.1 Study Area

The Chignik Lakes watershed (N56°16' W158°50') on the Alaska Peninsula drains southward through two lakes and a large semi-enclosed estuary into the Gulf of Alaska. Situated in the upper watershed, Black Lake is large (35 km^2) and shallow ($\bar{X}$= 1.5 m), sitting in a low tundra depression on the northern slope of the Alaska Peninsula. Black Lake is relatively warm and turbid, with high primary and secondary production during the summer growing season. Chignik Lake, located downstream in a glacial valley, is smaller (22 km^2) and deeper ($\bar{X}$= 64 m). Persistent winds keep both lakes well mixed during the ice-free seasons and thermal stratification is rare in both lakes. Black Lake is fed by a primary tributary, the Alec River, and drains into Chignik Lake via the Black River. Chignik Lake empties into the Chignik Lagoon through the short Chignik River (Fig. 1a).

Anadromous sockeye salmon return to spawn in the watershed in two distinct periods. From May- mid-July, 'early run' adults enter the watershed, migrating to tributaries of Black Lake to spawn. Early run juveniles rear primarily in Black Lake, growing rapidly before emigrating to sea as smolts after one year of growth. From mid-July - September, 'late run' adults spawn in tributaries and beaches of Chignik Lake and the Chignik River. Offspring of late run populations grow slower in Chignik Lake, typically rearing for two years before leaving the watershed as smolts. The collapse of the Chignik sockeye salmon fisheries in 2018 and subsequent years was particularly acute for the early run stocks that spawn in Black Lake, though the number of recruits-per-spawner for both stocks have declined notably since the 2014 brood year (Fig.1c).

Natural geomorphological and hydrological shifts during the 1970's resulted in notable changes to the habitat structure of the watershed. Downstream movement of the confluence of the dynamic West Fork River and the Black River, eliminated a key source of sediments that had maintained the elevation of the outlet of Black Lake. Subsequent erosion resulted in a ~40% decline in the volume of Black Lake (Elhakeem & Papanicolaou, 2008; Ruggerone, 2003), reducing the per capita volume of rearing habitat available to juvenile sockeye salmon. Black Lake volume has remained stable since the 1980's (Griffiths et al., 2011: UW Alaska Salmon Program, unpublished data).

LAKE TEMPERATURE

Water temperatures in Chignik and Black Lakes were compiled from multiple sources and summarized into monthly summer averages spanning 1929-2023. Data from 1929-1932 were obtained from historic logbooks from the Federal Fish and Wildlife commission Chignik Field Station, accessible via the University of Washington (UW), School of Aquatic and Fishery Sciences archives. Methods and site locations from this period were unavailable. Surface water temperatures from 1955-1967 and 1989-2023 were recorded by the UW Alaska Salmon Program (ASP) from routine limnological surveys. Sampling occurred approximately every 10 days from June-September at two sites in Chignik Lake and three sites in Black Lake. Between 1995-2023, Yellow Springs Incorporated and CastAway sondes were deployed during limnological sampling at two sites in Chignik Lake to create vertical temperature profiles of the water column. As Black Lake is shallow and well mixed, depth profiles were not collected and we simply summarized surface temperature measurements. From 2013-2023, Onset Computers pressure transducers were deployed year-round at two sites in Black Lake, recording hourly water temperature and lake levels. Loggers were anchored to the lake bottom, and recovered and redeployed annually.

Lake level data were corrected for changes in atmospheric pressure monitored by parallel pressure transducers at the lake edge.

Temperature measurements were compiled into a single dataset, and mean monthly temperatures were calculated for each year data was collected. In Black Lake, all temperature readings were used in our analysis. In Chignik Lake, stratification is rare due to sustained high winds. To reduce effects of occasional weak stratification events, only measurements take at 10m depth or less were used in analysis.

Maximum and mean monthly water temperatures were calculated for both Black and Chignik Lakes in all available years. Only June, July, and August temperatures were used in analysis to represent the summer growing season. Data were separated into three periods, 1955-1967, 1989-2023, 1995-2023, and plotted by lake. Due to variation in sampling methodology and relatively few samples during the first two periods, a linear regression of trends in monthly temperatures was applied only to the most recent period. Significance of the slope was assessed using a two-tailed t-test with $\alpha = 0.05$. All statistical analyses were performed in R (R Core Team, 2024).

ATMOSPHERIC TEMPERATURE

Mean monthly atmospheric temperatures were used to reflect local climate variation in the watershed. Mean monthly air temperatures were obtained from the Scenarios Network for Alaska Planning (SNAP, <www.snap.uaf.edu/>). These data are derived from Climate Research Unit (CRU) dataset CRU TS 4.08, downscaled to 2km grid cells. Temperature data are available from 1901-2023. A single grid cell (56°45′88″N, 158°99′77″W) centered on Black Lake was used to represent thermal conditions of the watershed following Griffiths et al. 2014 methodology (Griffiths et al., 2014).

ZOOPLANKTON

Zooplankton samples were collected from Chignik Lake and Black Lake approximately every 10 days from June-September from 1961-2023. Plankton were sampled with 40m vertical tows from two sites in Chignik Lake and 20m horizontal surface tows from three sites in Black Lake. The net was retrieved at approximately 0.5 m/s by hand. To ensure vertical tows in windy conditions in Chignik Lake, a 6.8kg weight was attached to the bottom of the net. In Black Lake, a float was attached to the mouth of to maintain surface contact. Over the course of the dataset, net mesh size and mouth opening size varied. Beginning in 2006, a conical net with 0.5 m wide mouth opening and 247 µm mesh size was used. Because net efficiencies of historical sampling gear were not estimated, we focus our analyses entirely on plankton community composition in this paper when comparing recent data to those collected before 2006. The same net was used after 2006 enabling the quantification of changes in estimated zooplankton densities from 2006-2023. Zooplankton were preserved in 50-70% ethanol. Consecutive sub-samples were obtained with a Gilson pipette and enumerated under a dissecting microscope until approximately 500 individual zooplankters were counted. Zooplankton were identified as taxa-specific densities, and we do not have species-specific counts or data on the life stage of the organisms.

Because of unrecorded changes in net size and incomplete density units in historical datasets, we were unable to directly compare zooplankton densities among all periods. Analysis of zooplankton community composition was conducted in two steps on the four dominant taxa present in the watershed (*Daphnia, Bosmina,* calanoid copepods, cyclopoid copepods). A proportional composition plot was used to assess changes in zooplankton community composition over time. A non-metric multidimensional scaling analysis (NMDS) analysis was used to assess the pairwise similarities in monthly (June, July, August) zooplankton community composition for each lake (Oksanen et al., 2022). Monthly averages of dominant zooplankton taxa were analyzed using a ranked similarity matrix based on Bray-Curtis similarity measures. Average monthly atmospheric temperatures from the UAF SNAP model were used to add environmental vectors to ordination plots to determine whether changes in zooplankton community composition were associated with warming climate conditions.

JUVENILE SOCKEYE SALMON AND RESIDENT FISH

Juvenile sockeye salmon and their freshwater competitors ('resident fish') were sampled annually between 10 August – 10 September via townet in Chignik Lake and Black Lake from 1961-2023. Nets were towed between two boats at the lake surface at a constant speed of approximately 3 km h^{-1}. Sampling was conducted at night to reduce net avoidance and capture fish during vertical diel migration (Narver, 1966). Tow durations varied from 5 – 10 minutes. Since 1992, tow duration has been standardized to 10 min. In Chignik Lake, a net with a 2 x 2 m opening was used. Declining lake volume made areas of Black Lake inaccessible to gear in 2003 (Griffiths et al., 2011). Prior to 2003, a net with a 1.8 x 1.8 m opening was used, while a net with 1.2 x 1.2m opening has been used since. Five sites were sampled in each lake, although the outlet site of Black Lake was abandoned in 2003 due to dense macrophyte growth. Since 2003, an additional site in the deeper portion of Black Lake was added to annual surveys.

Prior to 2005, fish were preserved in 10% formalin or 50-70% ethanol and measured at least 24hrs after capture. Since 2005, fish were euthanized in a buffered MS-222 solution, held on ice, and measured within 24hrs. Length measurements of preserved samples were not corrected following recommendations of Shields and Carlson (Shields & Carlson, 1996). If catches were large, a subsample containing at least 100 sockeye salmon was retained for measurement and the sample fraction recorded. Fork length measurements, to the nearest millimeter, were taken from up to 50 individuals of each species from each tow. If a sample contained more than 50 individuals of a species, remaining individuals were enumerated. Juvenile sockeye salmon lengths were standardized to 1 September assuming a growth rate of 0.3mm per day (Schindler et al., 2005).For years where multiple nights of towing were conducted, all data was included for analysis. Catch rates of juvenile sockeye salmon and three species of resident fish (pond smelt *Hypomesus olidus*, three-spine stickleback *Gasterosteus aculeatus*, and nine-spine stickleback *Pungitius pungitius*) were calculated as number of individuals per m^2 of net per min.

Analysis of fish community composition in Chignik and Black Lakes was conducted using townet sampling between 10 August and 10 September, from 1961-2023. Catch per unit effort (CPUE) for each tow was calculated for juvenile sockeye salmon and three dominant species of resident planktivorous fishes (pond smelt, three-spine stickleback, nine-spine stickleback) as number of fish per m^2 of net per min. Rare species (comprising <1% of total catch) such as juvenile coho salmon (*Oncorhynchus kisutch*), coastrange sculpin (*Cottus aleuticus*), and dolly varden (*Salvelinus malma*) were removed prior to analysis. Annual mean CPUE was calculated for two groups, juvenile sockeye salmon and combined resident fish species. These data were converted to log space to normalize residuals. Anomaly plots were used to highlight temporal trends in CPUE for juvenile sockeye salmon and resident fish in both lakes.

Mean annual lengths were calculated for juvenile sockeye salmon retained during townet sampling. In Black Lake, fish larger than 100mm were removed from the sample as these were rare and assumed to be smolts from earlier spawning events. These fish represent occasional 2+ parr which did not emigrate downstream after their first summer of growth, and comprised less than 0.01% of our sample. In Chignik Lake, multiple stocks and age classes of juvenile sockeye salmon are present. These include two age classes from the late run stock, and one age class from the early run stock which migrate from Black Lake into Chignik Lake during mid-summer (Westley et al., 2010). Without available genetic stock identification data, we were unable to definitively assign individuals to known stocks. Visual inspection of annual length distributions, two modes were visible at approximately 50mm and 70mm in most years. A hierarchical mixture model was unsuccessful at accurately identifying multiple distributions in years where distributions overlapped or where there was insufficient data. Based upon the known life histories, the smaller mode was assumed to represent Chignik Lake 0+ individuals, while the larger was comprised of both Chignik Lake 1+ and Black Lake 0+ emigrant sockeye salmon (Griffiths et al., 2013). We separated Chignik Lake samples accordingly, calculating annual means for individuals between 45-59mm and for 60-90mm. While we cannot assess stock-specific growth rates from this aggregation of the data, we can assess growth performance of the stock aggregates during their freshwater residency. We applied a generalized additive model (GAM) to each sample group to characterize trends in juvenile sockeye salmon length between 1960-2024. For each sample group, we modeled standard length as a smooth function of year. Models were fit using the `mgcv` package in R (Wood, 2001).

1.4 Results

1.4.1 Trends in lake temperature

Mean monthly summer water temperatures have remained relatively stable in Black (Fig. 2a) and Chignik (Fig. 2b) lakes from the 1920s to 2023. Black Lake is slightly warmer (mean temp °C = 11.3, 13.0, 13.0 for June, July and August) than Chignik Lake (mean temp °C = 8.2, 10.7, 12.1). In all years, the average monthly lake temperature in Black Lake and Chignik Lake never exceeded 17.0 C. The three warmest years on record were 1967, 2019, 2002 in Black Lake and 2020, 2016, 2005 in Chignik Lake. In Black Lake, visual trends suggest mean monthly temperatures have increased minimally since 1995, yet these trends were not statistically significant ($p > 0.05$). Chignik Lake mean summer temperatures did increase significantly from 1995-2003 ($p < 0.05$) but these changes were modest (slope = 0.052 °C/year). No significant trends were found in mean monthly temperatures of Chignik Lake ($p > 0.2$). During the freshwater rearing years of the 2018 stock collapse (2013-2016) mean water temperatures were marginally warmer than average in both lakes (mean anomalies were 1.0°C in Black Lake & 1.3°C in Chignik Lake), though were within the range of variation observed earlier in the time series.

Maximum observed monthly water temperatures have increased significantly in Black Lake since 1990 in June ($p < 0.05$), July ($p < 0.05$), and August ($p < 0.05$) (Fig. 3a). Since 2005, 10 years have experienced temperatures above 18°C. In 2013, temperatures exceeded 18°C in all three summer months. Chignik Lake maximum observed temperatures have increased significantly in June ($p < 0.05$), July ($p < 0.05$), although substantially less rapidly than Black Lake (Fig. 3b). Temperatures above 18°C were observed only in August 2011.

1.4.2 Zooplankton community composition, abundance, and climate covariates

The zooplankton community of Black Lake (Fig. 4a) is numerically dominated by *Bosmina*, with cyclopoid copepods being the second most abundant taxa. Calanoid copepods comprise a small proportion of catches, and *Daphnia* are virtually absent. Total zooplankton abundances showed a slight increasing trend from 2006-2015, with an anomalous increase during 2022 (Fig. 5a). In Chignik Lake (Fig. 4b), Cyclopoid copepods have historically dominated the zooplankton community. Since the early 1990's, *Daphnia*, *Bosmina*, and calanoid copepod contributions have all increased. Between 2013-2020, increasing *Daphnia* abundances contributed to high zooplankton densities in Chignik Lake (Fig. 5b) and their proportional contributions to the community were exceptionally high.

NMDS analysis accurately represented the zooplankton community composition in both Black and Chignik lakes during each month of the summer growing season (Table 1) (stress val. <0.1). In Chignik Lake, *Daphnia* relative abundance was positively correlated with warmer temperatures throughout the summer growing season in all three months considered. In contrast, cyclopoid copepod abundance was correlated with cooler temperatures. In Black Lake, atmospheric temperatures were significantly correlated with the zooplankton community composition during July, with *Bosmina* dominance associated with warmer conditions and cyclopoid copepod with cooler conditions (Fig. 6).

Since the freshwater rearing years of the stock collapse (2014-2023), zooplankton abundances in both lakes were on average 230 and 56 individuals/m^2 above average in Black and Chignik Lakes respectively. In Chignik Lake *Daphnia* contributions and abundances were notably high between 2016-2020.

1.4.3 Fish community composition

Juvenile sockeye salmon (42% annual mean composition, 1960-2013) and threespine stickleback (28% annual mean composition, 1960-2013) have historically dominated the fish community of Black Lake (Fig. 7a). Between 1992-2024, pond smelt and ninespine stickleback contributions increased, while threespine stickleback and sockeye salmon contributions were more variable. A notable decrease in sockeye salmon dominance occurred between 2013-2020, during the period of time when the 2018 and subsequent adult returns would have been rearing in the lake. In Chignik Lake, juvenile sockeye salmon historically dominated the resident fish community (78% annual mean composition, 1960-2013) (Fig. 7b). Concurrent with the observations in Black Lake, sockeye salmon contributions were notably low between 2014-2021. Threespine sticklebacks remained the dominant resident species observed in Chignik Lake across the time series.

CPUE anomalies depict an inverse relationship between resident species and juvenile sockeye salmon abundances. Sockeye salmon catches declined sharply between 2017-2021 and 2014-2020 in Black and Chignik Lakes respectively, while resident fish catches increased concurrently (Fig. 8).

1.4.4 Juvenile Sockeye Salmon Body Size

In Black Lake, mean juvenile sockeye salmon lengths in late August increased between 1978-2020 (Fig. 9a). During the freshwater rearing years of the 2018 stock collapse (2014-2016), individuals were on average 9 mm longer than the long-term average. In Chignik Lake, lengths of fish between 45-59mm have remained relatively consistent, although showed greater interannual variability after 2000 (Fig. 9b). Lengths for this group did not appear to decline between 2013-2020. Average lengths of the larger size group (60-90mm) increased between 2000-2021 (Fig. 9c). From 2013-2016, individuals where on average 1.7 mm shorter for the small group and 1.6 mm longer in the large group.

1.5 Discussion

We provide a case study of the long-term changes in the limnological conditions and ecological responses in two lakes that serve as the spawning and nursery habitats for sockeye salmon which have supported valuable commercial and subsistence fisheries for over a century. Our primary goal was to investigate changes in habitat quality which may have contributed to a collapse in the adult returns of sockeye salmon to the watershed in 2018 and beyond. In particular, we ask whether rearing conditions for juvenile sockeye salmon were favorable or not during their freshwater residency for the cohorts that returned to the watershed as adults starting in 2018.

1.5.1 Water temperature

We identified only subtle trends of increasing water temperatures in both Black and Chignik Lakes since 1995. While changing field methodology precluded us from making quantitative assessment of long-term changes in thermal conditions in Black and Chignik lakes, the data we have compiled show no large magnitude changes in monthly average water temperatures from the 1920s to the present. It is well documented that climate warming is occurring most rapidly at high latitudes, with similar lakes showing trends of earlier ice-out dates lengthening growing seasons and increasing summer water temperatures (Carter & Schindler, 2012; Schindler et al., 2005). In the Chignik watershed however, consistently strong winds drive mixing of the water column and prevent thermal stratification, thereby buffering against dramatic interannual lake temperature variability (Schindler & Smol, 2006). However, we did find a significant increase in maximum observed summer temperatures in the shallow Black Lake. Although convective cooling buffers average temperatures, even short periods of low wind can produce rapid warming in Black Lake due to its shallow depth and turbid water efficiently absorbing solar radiation.

The distinct geomorphological characteristics of both lakes control local thermal dynamics, resulting in Black Lake remaining consistently warmer than Chignik Lake throughout the summer growing season. Additionally, the shallow depth of Black Lake results in greater temperature variability than Chignik Lake. Chignik Lake has experienced the greatest temperature increase during August, likely enhanced by occasional stratification events during the late summer. Stratification of the water column in Chignik Lake remains a rare occurrence, requiring sustained periods of high solar radiation and low wind. As atmospheric temperatures continue to increase, stratification may become more frequent (Woolway et al., 2021). If the physical structure of Chignik Lake were to stabilize for a significant period of the summer growing season, it is likely new zooplankton communities would emerge producing bottom up behavioral and growth changes for juvenile sockeye salmon (Berger et al., 2010; Carter & Schindler, 2012).

As ectotherms, juvenile sockeye salmon bioenergetics are directly controlled by thermal conditions (Elliott, 1982; Jobling, 1997). Previous research shows juvenile sockeye salmon experience optimal growth in water temperatures of approximately 15°C, while actively avoiding temperatures >18°C (Brett, 1971). Based upon our results, both lakes remain on average near or below the thermal optima for juvenile sockeye salmon growth. In Black Lake, occasional spikes in temperatures exceed 18°C (average n = 6.7 days/year with a maximum temperature > 18°C, 1995-2023), producing stressful thermal conditions for juvenile sockeye salmon. Typically occurring in the late summer, these events have been hypothesized drivers behind a trend of earlier downstream emigration of poor body condition Black Lake individuals (Griffiths et al., 2013; Westley et al., 2008). Not only are smaller sockeye salmon at a competitive foraging disadvantage, they may also be less resilient to stressful thermal regimes. Conversely, Chignik Lake rarely exceeds 18°C in the epilimnion, and hypolimnetic thermal refugia typically used by vertically migrating juvenile sockeye salmon (Scheuerell & Schindler, 2003). persists throughout even the warmest periods, though the degree of vertical stratification is typically less than 2°C. The stock specific juvenile life history differences exemplify these lake specific thermal discrepancies as Chignik Lake juveniles exhibit two years of freshwater growth, while their Black Lake counterparts typically require only one. While our data suggest average temperatures are slowly increasing, the thermal habitat conditions of Chignik Lakes watershed remain conducive for productive juvenile sockeye salmon growth.

During the freshwater rearing years of individuals returning during the 2018 stock collapse, average water temperatures were only slightly warmer in both lakes. In Black Lake however, maximum observed water temperatures exceeded the thermal tolerance for juvenile sockeye salmon at least once in all rearing years of the collapse. While it is likely these episodic stressful thermal conditions contribute to downstream emigration choices of juvenile sockeye salmon in Black Lake, it is unlikely they had a substantial influence on juvenile mortality during the rearing years of the stock collapse because downstream Chignik Lake remains a hospitable and productive rearing habitat prior to their migration to the ocean (Griffiths et al., 2013; Walsworth et al., 2015).

1.5.2 Zooplankton community

Our analysis of long-term changes in the zooplankton community found an increase in *Bosmina* dominance in Black Lake beginning in the 1990's, and increasing *Daphnia* contributions in Chignik Lake since 1992 with notably high contributions between 2013-2023 when the fish that returned in 2018 were rearing in the lakes. Additionally, we identified temperature as a control on zooplankton community structure, particularly in Chignik Lake where *Daphnia* dominance was significantly correlated with warmer air temperatures. The four dominant taxa of crustacean zooplankton in the Chignik watershed provide integral ecosystem services as consumers of phytoplankton and as prey resources for planktivorous fish communities. With distinct life histories, zooplankton community structure fluctuates throughout the growing season in response to both bottom-up environmental effects and top-down predator controls. Our results provide evidence of both processes occurring within the watershed.

In Black Lake, *Bosmina* dominance emerged following the decline in lake volume of the 1970's. We found *Daphnia* to be rare within Black Lake comprising < 0.077% of catches. As large bodied zooplankters, *Daphnia* are a highly preferred prey resource for planktivores, particularly by juvenile sockeye salmon (Scheuerell et al., 2005). With high planktivorous fish abundances in Black Lake and no deep-water predation refuge, size selective predation likely exerts strong top-down controls, limiting *Daphnia* populations(Amsinck et al., 2006; Jeppesen et al., 1997). Diet studies in Black Lake have shown juvenile sockeye salmon are able to achieve rapid growth without access to *Daphnia* by exploiting abundant invertebrate prey resources, primarily chironomid larvae (Narver, 1966) .

With a deeper water column, cooler temperatures, and lower densities of planktivorous fish, the zooplankton community of Chignik Lake is not only more diverse, but also more dynamic than Black Lake. Since 1992, *Daphnia* composition has tended to increase. Employing a NMDS analysis, we were able to test for correlation between climate variables and zooplankton community composition. We observed a significant correlation between atmospheric temperatures and zooplankton community composition across the growing season within Chignik Lake. Notably, years with warmer temperatures were associated with greater *Daphnia* contributions. As *Daphnia* have a competitive and reproductive advantage at higher temperatures, this result was expected and supports the hypothesis that climate variables exert control on zooplankton communities through bottom-up processes (Carter & Schindler, 2012; Edmondson & Litt, 1982). Additionally, cyclopoid copepods, which experience peak abundances in early spring, were more dominant during cooler years.

The distinct increase in *Daphnia* contributions between 2013-2023 also provides evidence of top-down predation controls on the zooplankton community within Chignik Lake. Beginning in 2013, low sockeye salmon catch rates correlate temporally with the increased *Daphnia* contributions we observed. Released from high levels of sockeye salmon predation, *Daphnia* were likely able to exploit their competitive advantages resulting in increased abundance. Thus, the increase in *Daphnia* contributions to the zooplankton community in Chignik Lake suggest they were subject to lower predation pressure from juvenile sockeye salmon and other planktivores. This response suggests that juvenile sockeye abundances were reduced for these year classes, earlier in their life cycles; for example, either from failed adult spawning or from reduced egg-to-fry survival rates.

1.5.3 Planktivorous fish community

In the planktivorous fish communities of both Black and Chignik Lakes, we observed a dramatic decline in juvenile sockeye salmon dominance since 2013 and 2014, respectively. Additionally, our results suggest an inverse relationship of sockeye salmon and resident species abundances throughout the watershed. Considering thermal conditions and prey resources remain conducive for freshwater sockeye salmon growth, it is unlikely that poor habitat conditions for juvenile rearing drove the trends we observed. The recruit/spawner ratio shows a strong decline in sockeye recruitment beginning in 2013. This suggests either failed adult spawning or reduced egg maturation during the 2013-2016 brood years resulted in a period of low sockeye abundances in freshwater rearing habitat. Collectively, our observations of low sockeye recruitment and freshwater abundance correlate temporally with adults returning during the 2018 collapse. This supports an alternate, yet untested, hypothesis that low early life survival contributed to the collapse observed in 2018 and beyond.

Previous studies have shown sockeye salmon and resident fish populations can effectively coexist within Black Lake due to high prey densities and discrete habitat preferences (Parr, 1972). Black Lake sockeye rely heavily on invertebrate prey, allowing gape limited stickleback to exploit abundant zooplankton populations without significant interspecific competitive pressures (Narver, 1966). While sockeye salmon have historically dominated the fish community of Black Lake, Westley et al. (2008) documented an increase in resident fish abundances following the geomorphological shifts of the 1970's. They concluded lower lake levels had improved climate mediated stickleback recruitment, increasing competitive pressures on small sockeye unable to target invertebrate prey. Facing intra- and interspecific competitive pressures, and increased thermal stress, poor condition individuals were observed to migrate downstream earlier in the season seeking habitat refugia. The declines in sockeye dominance and catch rates we observed suggest this process has continued and intensified. While the thermal conditions and prey resources of Black Lake enable rapid growth of fit individuals, it is likely poor condition sockeye continue to emigrate downstream earlier in the season. This helps explain the high resident fish abundances and low juvenile sockeye salmon catch rates of the last decade.

With cooler water temperatures, lower productivity, and minimal littoral spawning habitat, resident fish species are at a competitive disadvantage to sockeye salmon in Chignik Lake. Historically, juvenile sockeye salmon have successfully exploited these favorable habitat conditions and strongly dominated the fish community. As downstream emigration of Black Lake sockeye salmon intensifies, we would expect to see a corresponding juvenile sockeye salmon densities in Chignik Lake. Our results contradict this hypothesis, showing juvenile sockeye salmon dominance and catch rates fell sharply between 2014-2021. While climate mediated recruitment is likely increasing resident fish abundances in Chignik Lake (Hovel et al., 2017), there is limited littoral rearing habitat compared to Black Lake. Additionally, warming temperatures and higher *Daphnia* abundance during this period suggest the pelagic habitat quality of Chignik Lake has improved for juvenile sockeye salmon since 2013. These observations support the hypothesis of high early life stage mortality, observed in the poor recruitment of 2012-2016 sockeye brood years. With low sockeye salmon abundance, resident fish were relieved from historically high competitive pressures, enabling rapid population growth.

1.5.4 Juvenile sockeye salmon growth

Juvenile salmon body length reflects the habitat mediated growth performance of individuals during freshwater residence (Brett et al., 1969). Our analysis of juvenile sockeye salmon lengths showed increasing growth trends in Black Lake, and stable growth trends in multiple Chignik Lake size classes. These observations refute the hypothesis of significant declines in habitat quality across the watershed, yet alone do not directly reflect lake specific rearing capacity. While habitat conditions remain conducive for juvenile sockeye salmon growth, changing emigration patterns resulting in increased population mixing complicate our interpretation of lake specific rearing capacity (Griffiths et al., 2013).

For mobile species in interconnected ecosystems, source-sink dynamics emerge as individuals experience stressors in source habitats (Westley et al., 2010). The ability of individuals to migrate in search of habitat refugia can buffer total species abundances from localized habitat change, leading to decreased abundances in source habitats and novel population interactions in sink habitats (Walsworth et al., 2015). As we have described, Black Lake is shown to act as a source habitat for juvenile sockeye within the Chignik watershed. A trend of poor condition individuals emigrating downstream earlier in the summer has likely decreased interspecific competitive pressures on sockeye salmon remaining in Black Lake for the entire growing season. With access to high quality habitat and less competition, our results of increasing length trends suggest individuals remaining in Black Lake have experienced improved rearing conditions since the 1980's. Notably, this trend continued through the collapse rearing years of 2014-2016, refuting the hypothesis that a decline in Black Lake habitat quality contributed to the 2018 stock collapse.

Behaving as a potential sink habitat, Chignik Lake supports both natal and emigrant sockeye populations. Juvenile sockeye salmon exhibit strong density dependence, suggesting population mixing likely drives asynchronous growth responses for individual age classes and stocks (Kyle et al., 1988; Schindler et al., 2005). With multiple mixed stocks and age classes, a cumulative length analysis of all Chignik Lake catches does not specifically reflect population specific growth performance. Previous research has successfully solved this issue by employed genetic stock identification techniques to assign individuals to either Black or Chignik Lake populations (Griffiths et al., 2013; Simmons et al., 2013). Without available genetics data for our entire time series, our analysis was limited to describing growth performance of two stock aggregates, both of which showed stable growth trends. These results suggest that any changes in the habitat quality of Chignik Lake have not had a negative effect on juvenile sockeye salmon growth. Additionally, juvenile sockeye salmon growth during the brood years of the 2018 collapse remained consistent with growth during historic periods of high adult returns.

Relying on the coarse stock aggregation methodology we employed has several drawbacks. Crucially, it does not account for stock specific responses to evolving density dependent pressures, driven by the climate mediated downstream migration of Black Lake individuals (Westley et al., 2008). However, Griffiths et al. (2013) observed that Black Lake emigrants did not exhibit significantly different body condition to natal Chignik Lake juveniles (Griffiths et al., 2013). This suggests that while there may be more Black Lake origin individuals rearing in Chignik Lake, the emigrants are not at a significant competitive advantage over their Chignik Lake counterparts. In the decade since these studies were conducted, it remains unknown if increased Black Lake emigration has influenced natal Chignik Lake juvenile sockeye salmon growth performance.

1.5.5 Conclusion

Variation in habitat conditions withing and among watersheds supports reliable and sustainable salmon fisheries in Alaska where ecosystems remain largely unperturbed from development (Hilborn et al., 2003; Schindler et al., 2010). Long term changes in geomorphology and climate drive shifts in habitat structure, organism interactions, and population performance (Griffiths et al., 2011). Here we have shown that multiple components of the Chignik lakes meta-ecosystem are highly variable, reflecting the dynamic nature of interconnected heterogeneous watersheds. Black and Chignik lakes exhibit divergent habitat characteristics, with asynchronous responses by juvenile sockeye salmon stocks to habitat change. Despite high variability, our assessment of rearing conditions between 2013-2016 found no evidence that freshwater habitat was less profitable for juvenile sockeye salmon during the rearing years that led to the 2018 stock collapse. Notably we observed abundant zooplankton resources throughout the watershed, and an increase in more profitable prey species in Chignik Lake. Juvenile sockeye salmon growth performance was above average, despite increasing resident fish populations. It is likely lower sockeye salmon abundances have decreased density-dependent pressures, enabling individuals to exploit improved prey resources and achieve faster growth. Additionally, the low juvenile sockeye salmon abundances we observed between 2013-2014 suggest a population bottleneck during the early life stages that likely contributed to the disastrous returns of 2018.

While our hydrologic data are incomplete, several winter floods that occurred in 2013 and onwards may have resulted in poor egg survival in the major spawning tributary of Black Lake due to gravel scour. Such poor recruitment of sockeye salmon fry into Black and Chignik lakes is apparent both in our estimates of abundance, in indirect indicators of their predation pressure (i.e., the zooplankton community composition), and may have propagated to produce failed year classes that led to the fishery collapses in 2018 and beyond.

Our analysis focused exclusively on the freshwater habitat conditions of juvenile sockeye salmon, yet changes in marine habitat may have also contributed to the 2018 stock collapse. From 2013-2017, anomalously high sea surface temperatures in the North Pacific resulted in dramatic changes to marine food webs (Bond et al., 2015; Cavole et al., 2016). Increasing marine temperatures resulted in a higher diversity of lower quality zooplankton prey species available to adult salmon (Fergusson et al., 2020). Cary et al. (2021) observed a decline in sockeye salmon spawning success correlated with the marine heatwave, suggesting poor marine prey resources reduced the number of viable eggs deposited (Carey et al., 2021). Last, declining body sizes of sockeye salmon as has been documented in other parts of Alaska (Cline et al., 2019; Oke et al., 2020) may also be contributing to reduced 'spawner quality' which may need to be incorporated into revising escapement goals to improve sockeye salmon yield from the Chignik watershed (Ohlberger et al., 2025). These other hypotheses should be considered as alternative explanations for the recent collapse of Chignik sockeye salmon fisheries, which would appropriately inform management actions designed to recover this fishery.

1.6 Figures

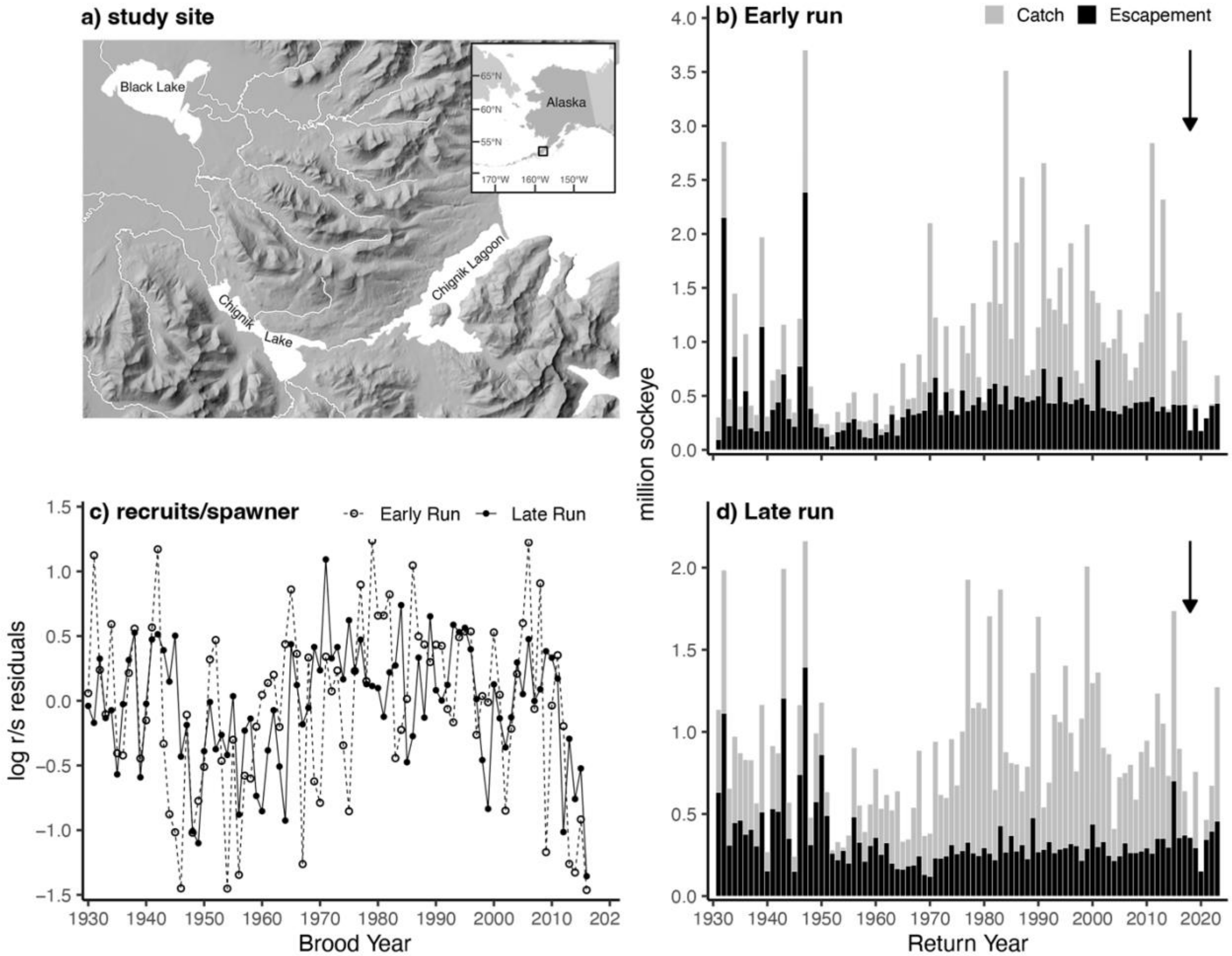

Figure 1.1. Map of the Chignik lakes watershed (a). Adult sockeye salmon returns to the Chignik lakes watershed by return year, for both early (b) and late runs (d). Log recruit/spawner residuals by brood year, for both the early and late runs (c). Data provided by the Alaska Department of Fish & Game.

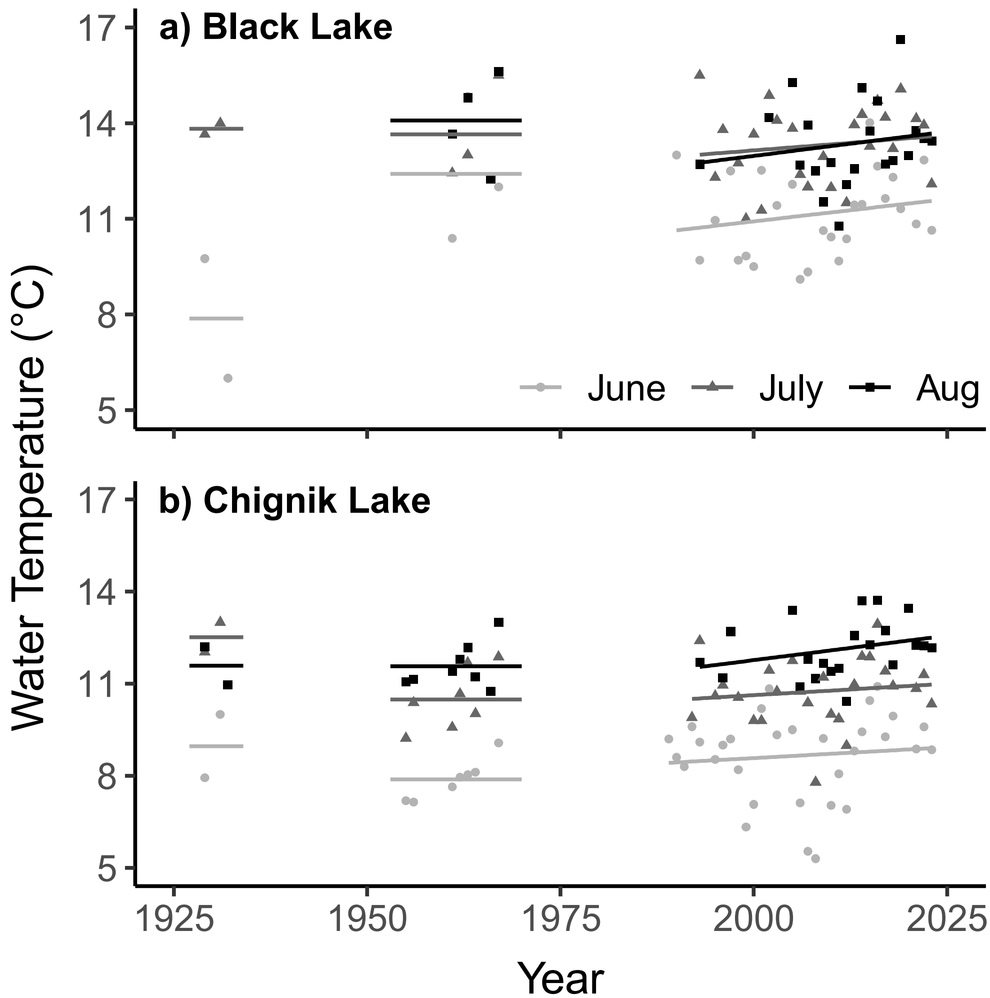

Figure 1.2. Mean monthly water temperatures during the summer in Black Lake (a) and Chignik Lake (b) from 1929-2024.

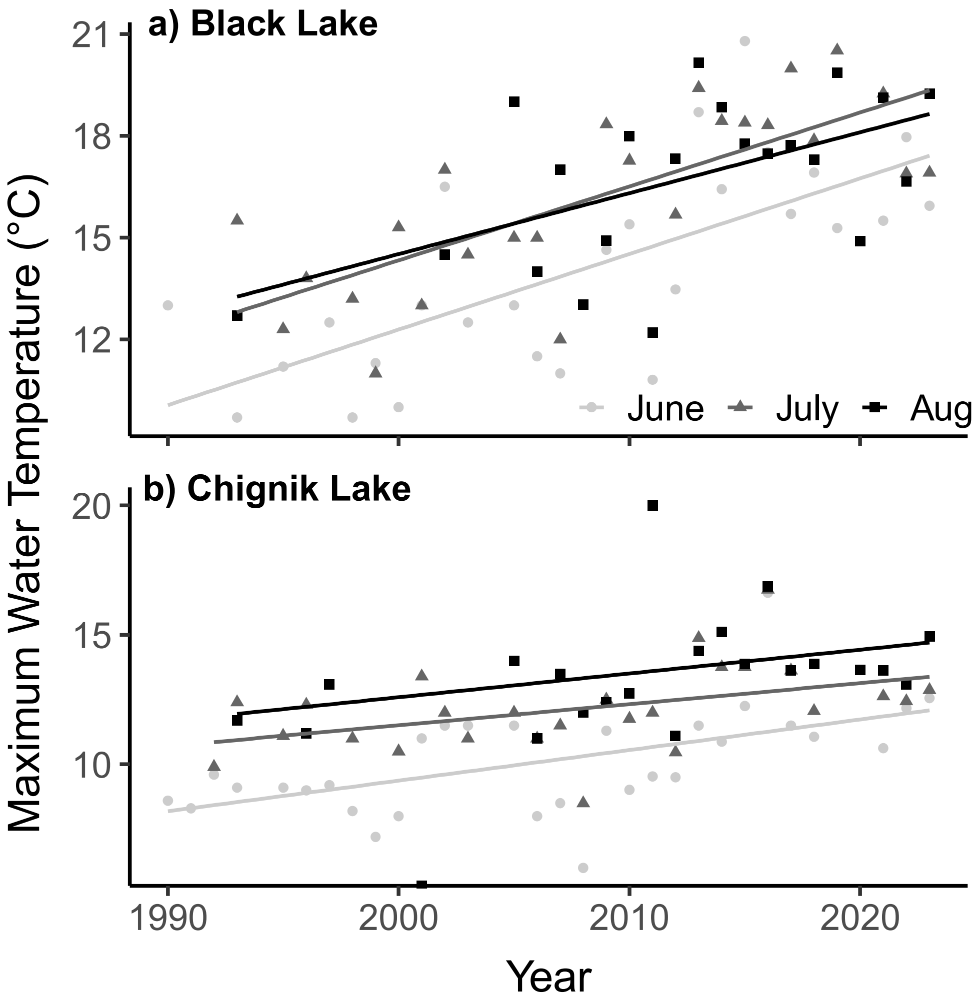

Figure 1.3 Maximum observed water temperatures during three summer months in Black Lake (a) and Chignik Lake (b) from 1990-2024.

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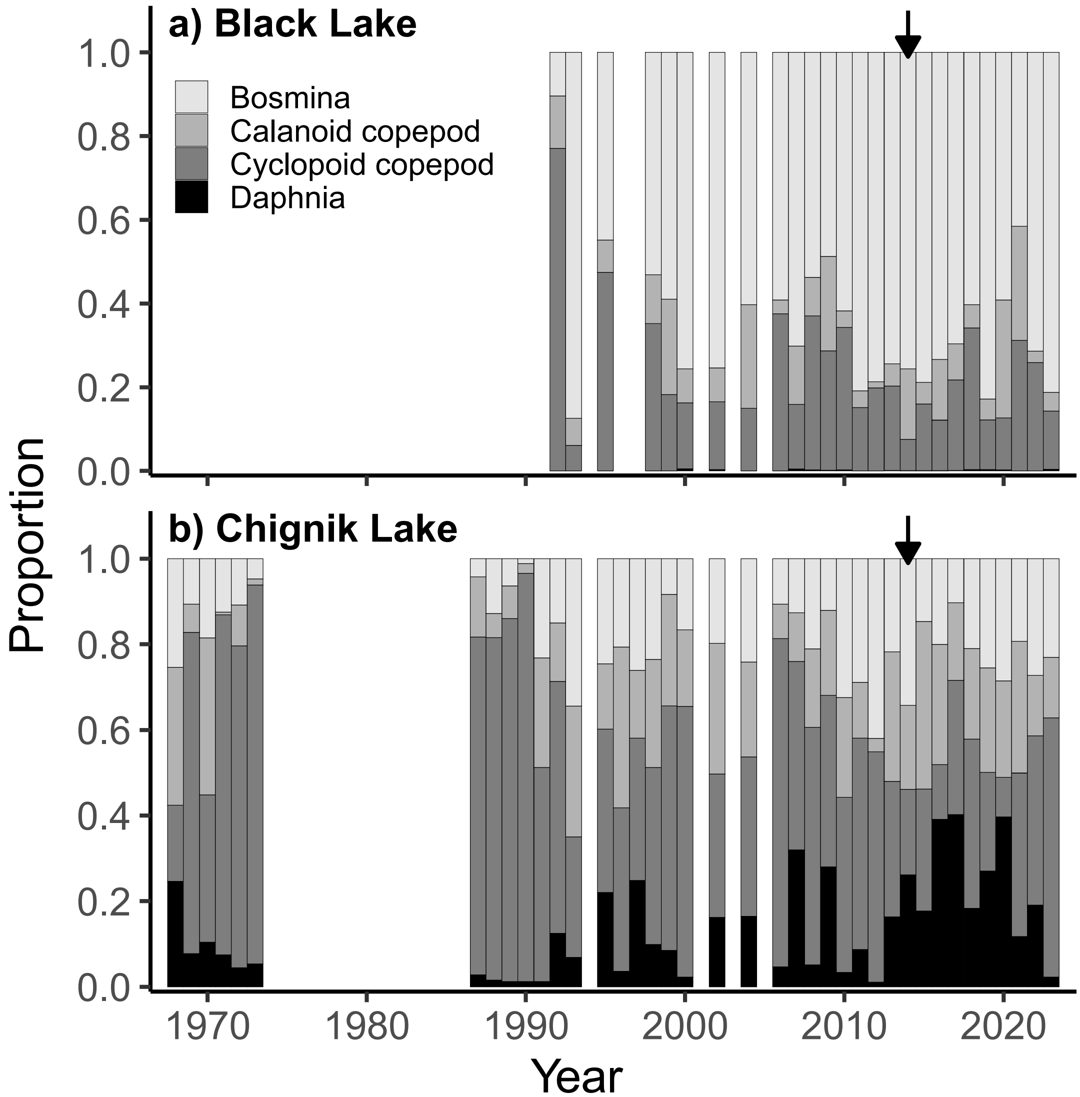

Figure 1.4 Annual zooplankton community composition in Black and Chignik lakes. Black arrows show 1st rearing year of fish that returned as adults during the 2018 sockeye salmon stock collapse.

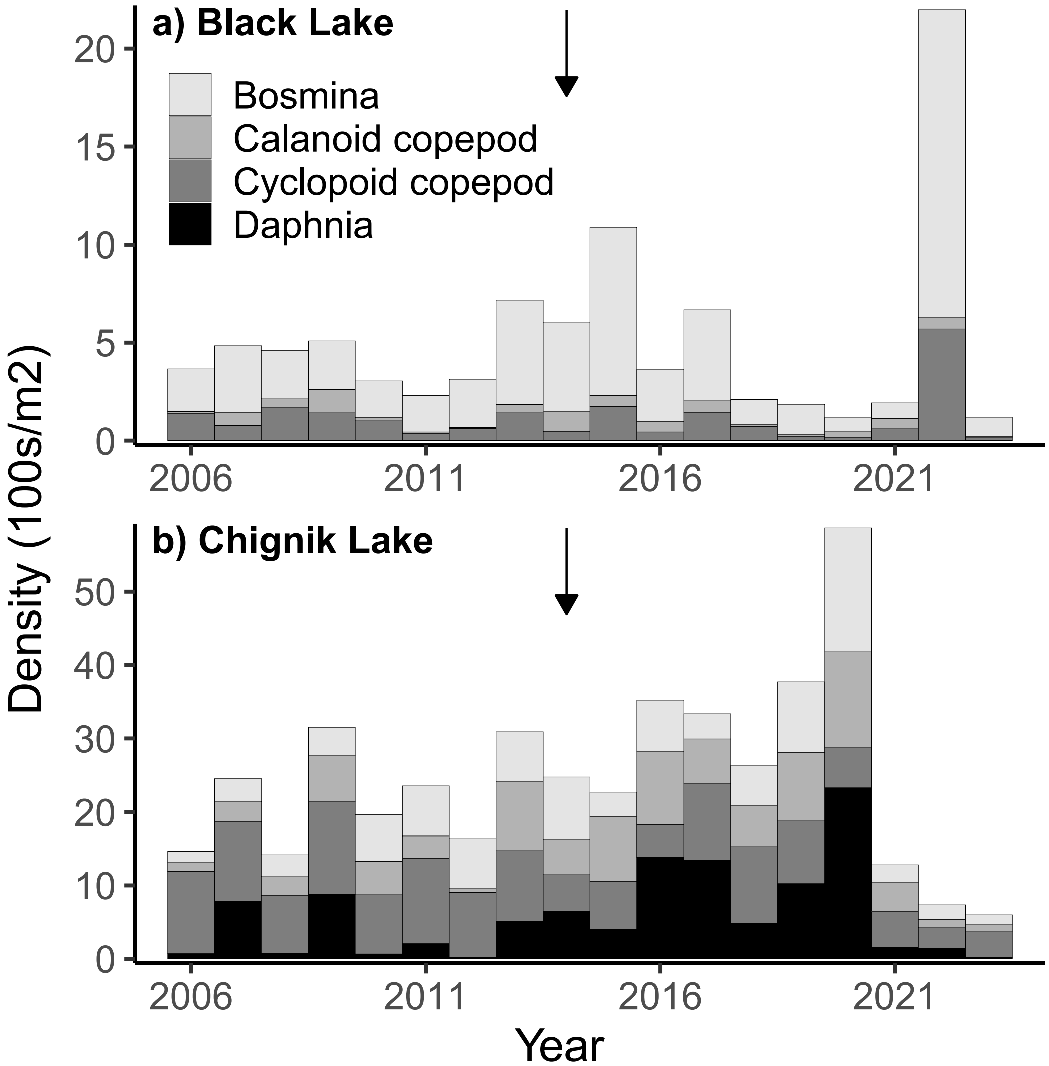

Figure 1.5 Annual mean zooplankton densities in Black and Chignik lakes. Black arrows show 1st rearing year for fish that returned as adults during the 2018 sockeye salmon stock collapse.

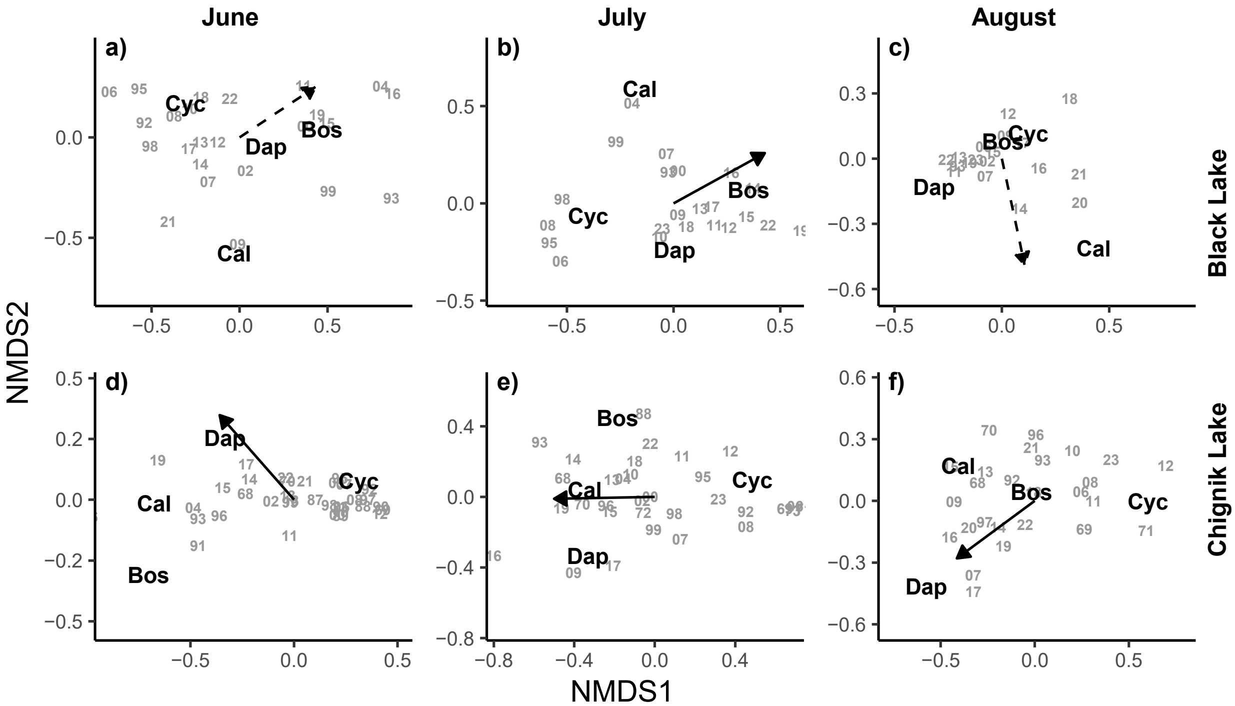

Figure 1.6 NMDS plot of dominant zooplankton taxa in Black Lake(a, b, c) and Chignik Lake (a, b, c) by month. Vectors represent influence of atmospheric temperatures on community composition. Stress values for all models were <0.1. Solid vectors show months when temperature had a significant effect ($p < 0.05$) on species composition.

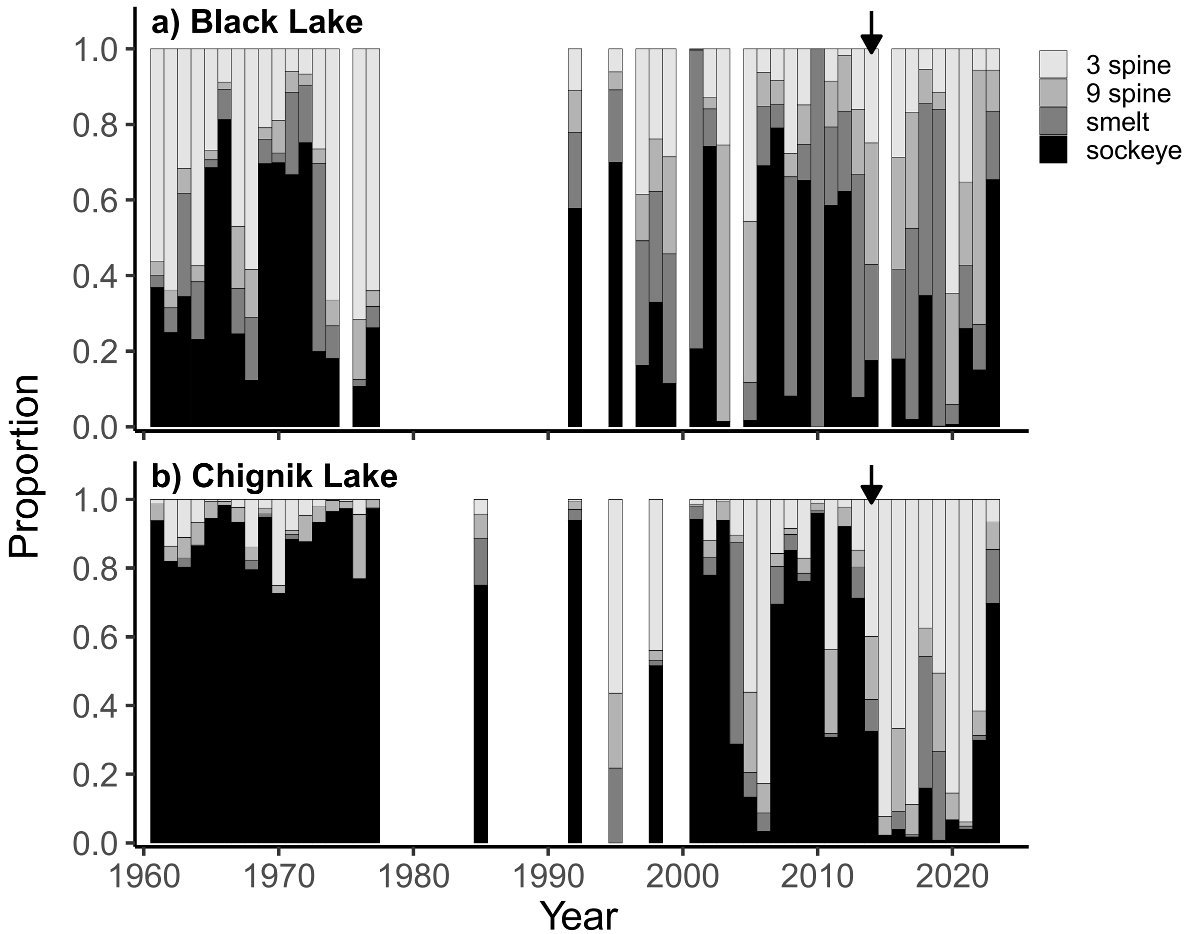

Figure 1.7Annual community composition of dominant planktivorous fish species (threespine stickleback, ninespine stickleback, pond smelt, sockeye salmon) in Black (**a**) and Chignik (**b**) Lakes. Black arrows show 2014, 1st rearing year for fish that returned as adults during the 2018 collapse.

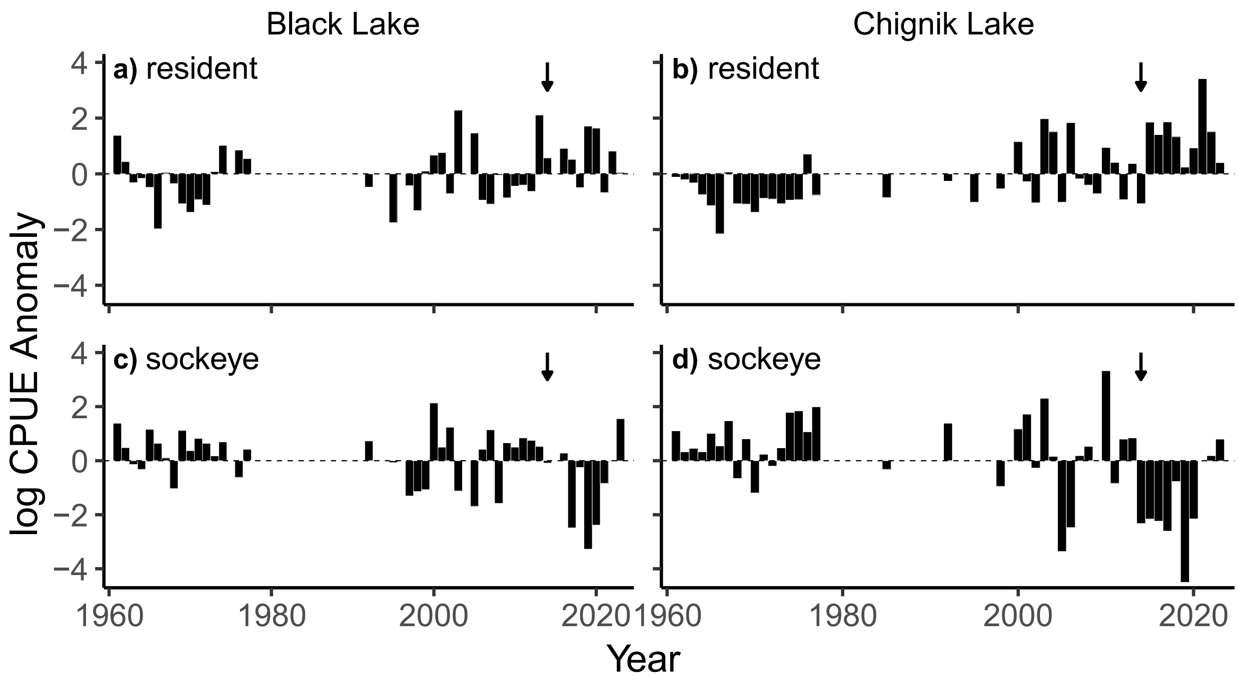

Figure 1.8 Log catch per unit effort (CPUE) anomalies for juvenile sockeye salmon and resident fish in Black Lake (a, c) and Chignik Lake (b, d). Black arrows show 2014, 1st rearing year for fish that returned as adults during the 2018 collapse.

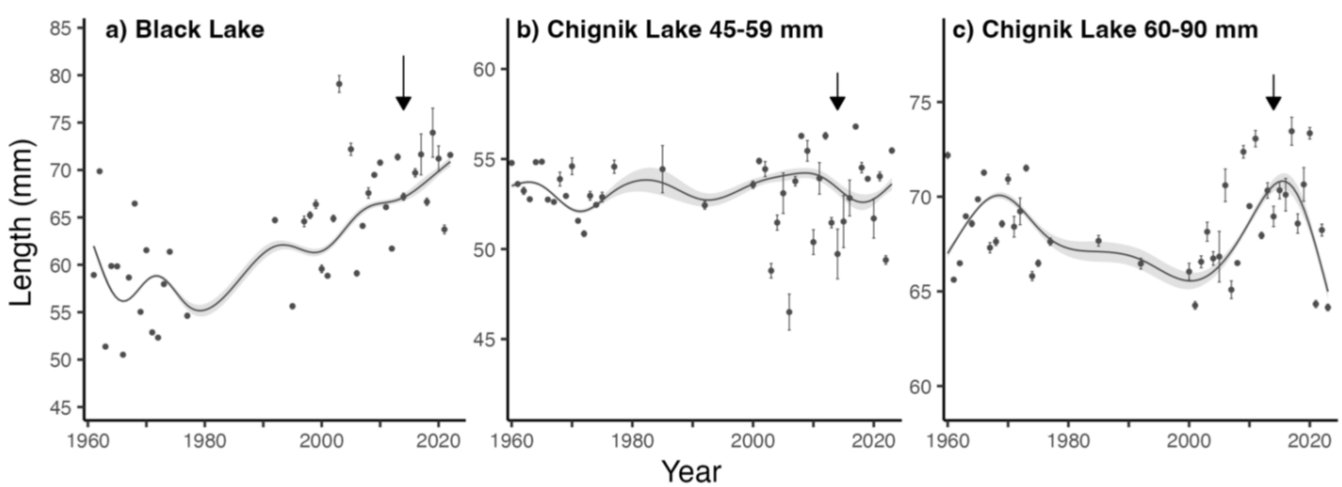

Figure 1.9 Juvenile sockeye lengths from townet sampling for Black Lake (a), Chignik Lake 45 – 60 mm (b), and Chignik Lake 60 – 90 mm (c). GAM fit to mean annual lengths, with shaded 95% CI's. Black arrows show 2014, 1st rearing year for fish that returned as adults during the 2018 collapse.

1.8 Tables

Table 1.1 Comparative summary of zooplankton community NMDS statistics

Lake	Month	NMDS Stress value	*Atmospheric temperature R^2	*Atmospheric temperature P – value
Chignik Lake	June	0.0340	0.385	0.001**
	July	0.0964	0.268	0.016**
	August	0.0995	0.444	0.001**
Black Lake	June	0.0255	0.230	0.055
	July	0.0237	0.299	0.042**
	August	0.0261	0.121	0.379

NMDS, Non-Metric Dimensional Scaling analysis
* Environmental vector
** statistically significant ($p < 0.05$)

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Chapter 2 : Stock Specific Growth Performance of Juvenile Sockeye Salmon Across Lake and Estuarine Rearing Habitat

2.1 Abstract

Watersheds provide interconnected habitat networks accessible to mobile species, buffering populations from environmental change and improving the reliability of ecosystem services. Temporal population stability is derived from the growth and survival benefits gained by an individual's ability to move among habitats which comprise meta-ecosystems. Here we expand spatially and temporally upon previous work using fine scale stock identification in the Chignik watershed to investigate how rearing habitat and stock of origin influence juvenile growth performance and distributions of fish from different genetically distinct populations. Our analyses shows that body size of juvenile sockeye salmon rearing in lakes is correlated with the productivity of the rearing habitat, regardless of and individuals' stock of origin. We also observed juvenile sockeye salmon from multiple stocks rearing in estuarine habitat throughout the entire summer growing season, with fish from a more productive natal lake having higher body condition than those from lower productivity natal habitat. These data demonstrate a complex interaction between stock of origin and habitat-specific growing conditions in regulating the growth performance of juvenile fish throughout watershed habitat networks.

2.2 Introduction

Habitat complexity promotes species and population diversity, stabilizing ecosystem function and improving the reliability of ecosystem services (Luck et al., 2003). Ecosystems filter climate variables through unique physical habitat characteristics, resulting in higher or lower quality habitat depending upon prevailing climate conditions and local geomorphology (Griffiths et al., 2014). Habitat conditions may vary asynchronously across a range of spatial and temporal scales, producing a mosaic of connected habitats which can be conceptualized as meta-ecosystems (Loreau et al., 2003). Individuals, material, and energy can move within component habitats, enabling the redistribution of resources and organisms. Mobile species exploit habitat heterogeneity, resulting in spatially variable population dynamics and life histories (Brennan et al., 2019). Highly diverse habitat networks with asynchronous productivity buffer populations, resulting in a more stable meta-ecosystem over time (Schindler et al., 2010).

Habitat mosaics are only effective at promoting population stability of migratory species if individual habitats are connected with one another (Runge et al., 2014). For example, pronghorn antelope in the Red Desert, Wyoming, experienced higher winter mortality when excluded from migration corridors by anthropogenic barriers such as fences and highways (Aikens et al., 2025). Dependance upon multiple habitats is usually appreciated for populations which migrate long distances for feeding, breeding, or seasonal refugia (Iwamura et al., 2013). However, at smaller spatial scales habitat connectivity enables individuals to exploit short-term benefits in prey resources, predator refugia, and environmental conditions (Flitcroft et al., 2019). Life history diversity between populations enables individuals to move within meta-ecosystems, seeking profitable habitat as local conditions change (Walsworth et al., 2015). For stressed individuals, emigrating to a new habitat can improve access to prey resources and relief from competition or predation. Natural barriers (topological, hydrological) can also restrict movement between habitats. If these barriers are unidirectional, source-sink habitat dynamics emerge where emigrants are prevented from returning to their natal habitats. In such scenarios, the flow of emigrants increase organism density and population diversity in sink habitats, potentially altering food web dynamics (Westley et al., 2010). Additionally, migration corridors themselves can provide valuable opportunities for rest, feeding, and adaptation to new environments (Buler et al., 2007; Moore et al., 2016).

Pacific salmon (*Oncorhynchus spp.*) are well known for their large-scale migrations between freshwater spawning and rearing habitats and marine growth habitat (Quinn et al., 2009). Salmon require connected habitat networks at fine and large spatial scales. It is well documented that anthropogenic barriers have degraded many salmon ecosystems by reducing connectivity between freshwater and marine environments (Thorstad et al., 2008). However, at smaller spatial scales habitat connectivity is also critical for maintaining productive salmon populations. During freshwater rearing, juvenile salmon migrate extensively within individual habitats and watersheds (Armstrong et al., 2013; Scheuerell & Schindler, 2003; Simmons et al., 2013). Exploiting heterogenous habitat networks, multiple locally adapted populations of juvenile salmon grow successfully within the same watershed (Griffiths et al., 2013; Walsworth et al., 2015). Movement within habitats may reflect seasonal variation in productivity, climate variables, predation, and competition (Westley et al., 2008). For example, juvenile sockeye salmon (*O. nerka*) rearing in lakes move from littoral to pelagic habitats as they grow, eventually exhibiting diel vertical migrations between the hypolimnion and epilimnion of lakes to maximize feeding efficiency and avoid predation (Scheuerell & Schindler, 2003). Within populations, individuals may exhibit alternative movement strategies during the same life stage. Coho salmon (*O. kisutch*) which feed in productive cold water habitat, migrating to digest food in warmer water, grow faster than individuals which do not move (Armstrong et al., 2013).

Heterogeneous coastal watersheds provide access to highly diverse lake, stream, and estuarine habitats. Balancing energetic tradeoffs, higher or lower performance individuals may choose to migrate to new habitats offering improved growth performance and survivability (Griffiths et al., 2013; Munsch et al., 2025; Westley et al., 2008). Multiple salmon species have been shown to exploit estuarine habitats for juvenile growth before ocean entry, sometimes returning upriver after their first summer of growth and overwinter in freshwater habitats (Hayes et al., 2011; Koski, 2009; Simmons et al., 2013).

When individuals move within a system with multiple populations, it can be challenging to identify and assess the relative ecological performance of individuals from different populations. Source habitat emigrants can have direct and indirect impacts on sink habitat resident populations (Westley et al., 2010). If source habitat conditions are stressful, individuals must balance energetic trade-offs of remaining versus emigrating. While lower population densities can reduce competition, stressful habitat conditions may limit growth potential. Assessing the success of movement strategies requires assigning individuals to populations of known origin. Genetic techniques provide an efficient solution, especially when sampling large numbers of concentrated individuals with little phenotypic variation (Seeb et al., 2011).

The Chignik watershed, Alaska Peninsula, USA, is comprised of two lakes and a large semi-enclosed estuary draining into the Gulf of Alaska. Each habitat is used by multiple genetically distinct populations of sockeye salmon, which exhibit a variety of juvenile life history strategies (Creelman et al., 2011; Griffiths et al., 2013; Walsworth et al., 2015). Juvenile sockeye salmon from the stock that spawns in the upper watershed (Black Lake) typically rear in the highly productive Black Lake for most of their first summer before migrating downstream. Juveniles of the population which spawns in the lower watershed (Chignik Lake) typically rear for two years, as lower productivity and thermal constraints restrict growth rates. Chignik Lagoon, a large estuary (~ 3 miles downstream of Chignik Lake) provides a third major rearing and transition habitat for individuals from all populations of sockeye salmon exiting the watershed into the Gulf of Alaska.

Previous studies have identified a variety of movement strategies within juvenile sockeye salmon populations in the Chignik watershed (Walsworth et al., 2015). While most Black Lake individuals emigrate downstream at the end of their first summer, a subset of the population has been observed emigrating earlier in the season (Westley et al., 2008). These emigrants have been described as having poorer body condition than individuals which remained in Black Lake, and similar condition to Chignik Lake residents(Griffiths et al., 2013; Westley et al., 2008).

Although multiple size and age classes of juvenile sockeye have been observed in the Chignik Lagoon (Simmons et al., 2013), it is unknown how individuals from different populations use estuarine habitat. Evidence suggests a proportion of individuals of Chignik River origin rear within Chignik Lagoon during their first summer, returning upriver to overwinter in Chignik Lake (Simmons et al., 2013). Juvenile sockeye salmon are common throughout the estuary during the summer, suggesting spatial and temporal variation in estuarine habitat use by out-migrating smolts. Differences in lagoon residence and timing among stocks may explain stock-specific population dynamics that currently characterize the Chignik system (Finkle et al., 2020) or salmon populations more generally (Hilborn et al., 2003).

In this study, we use single nucleotide polymorphisms (SNPs) to assess the stock specific growth performance of juvenile sockeye salmon in the three dominant rearing habitats of the Chignik watershed. Using improved genetic methods and six more years of sampling, we expand upon the scope of Griffiths et al., 2013 who showed that juvenile sockeye salmon body condition is related to the productivity of alternate rearing habitats. Incorporating samples from the Chignik Lagoon, we describe spatial and temporal variety in estuarine rearing by multiple populations of juvenile sockeye salmon and demonstrate an interaction between stock of origin and specific habitats in determining growth performance in juvenile sockeye salmon.

2.3 Methods

2.3.1 Study Site

The Chignik watershed, located on the southern coast of the Alaska Peninsula (Fig. 1), drains through two lakes and a large semi-enclosed estuary into the Gulf of Alaska. Sockeye salmon (*O. nerka*) are the dominant anadromous species, supporting a valuable commercial fishery and subsistence harvest. Multiple genetically distinct sockeye salmon populations (Creelman et al., 2011) migrate to the watershed from June – September to spawn in tributaries of Black and Chignik Lakes, and in Chignik Lake. Sockeye salmon typically rear for 1-2 years in freshwater as juveniles, before migrating to the Gulf of Alaska for 2-3 years of ocean growth and ultimately returning to natal habitat to spawn. Sockeye salmon harvest is managed by the Alaska Department of Fish and Game (ADF&G), which operates a weir on the lower Chignik River to enumerate escapement in the watershed. Scale pattern analysis and genetic stock identification is used to assign returning adults to either Black Lake (early run) or Chignik Lake (late run) populations. From 2019-2023, annual adult sockeye salmon escapement averaged 341,000 to Black Lake and 329,000 to Chignik Lake.

The physical characteristics of juvenile rearing habitat in the Chignik watershed are highly diverse. Black Lake is shallow (4m max. depth), warm, and highly productive. Geomorphic shifts in the watershed during the 1970’s resulted in a ~40% decrease in the volume of Black Lake (Griffiths et al., 2011; Ruggerone, 2003). In the lower watershed, Chignik Lake is deep (60m max. depth) and colder, with lower productivity than Black Lake. Average summer water temperatures during our study were 13.2 °C in Black Lake and 10.8 °C in Chignik Lake.

Connected to Chignik Lake by the Chignik River, Chignik Lagoon is a large estuary which provides both rearing and transition habitat for juvenile sockeye salmon. With strong tidal influence, temperature and salinity vary greatly between the mouth of the Chignik River and the outlet of the Chignik Lagoon. During our study, salinity averaged 1.6 ‰ in upper sites, and 25.3 ‰ in lower sites, and water temperatures averaged 11.7 °C in upper sites and 10.7 °C in lower sites).

2.3.2 Sample Collection

Juvenile sockeye salmon rearing in Chignik Lake and Black Lake were sampled annually between 26 July – 3 September via townet in 2010, 2011, and from 2019-2024. Nets were towed between two boats at the lake surface at a constant speed of approximately 3 km h^{-1} for 10 minutes. Sampling was conducted at night to reduce net avoidance and capture fish during vertical diel migration. In Chignik Lake, a net with a 2 x 2 m opening was used while in Black Lake a net with 1.2 x 1.2m. Five sites were sampled in each lake. If samples were large, a subsample of at least 100 fish per site was retained and the fraction recorded. Fish were euthanized in a buffered MS-222 solution and measured within 24hrs.

In the Chignik Lagoon, juvenile sockeye salmon were sampled using beach seines at four sites every 10 days from June 6 – September 6 in 2023 and 2024. If samples were large, a subsample of at least 20 fish per site was retained and the fraction recorded. Fish were euthanized in a buffered MS-222 solution and measured within 24hrs.

Sockeye salmon fork lengths were measured to the nearest millimeter, and weights were measured to the nearest 0.1 gram. Genetic samples from Chignik Lake and Chignik Lagoon were collected by removing the entire caudal fin. Tissue samples were placed or stapled onto gridded filter paper and air dried for later DNA extraction. The associated sample site, length, and weight were retained with each tissue sample.

2.3.3 Sample Selection for Genetic Stock Identification

A subset of individuals sampled from Chignik Lake were genotyped in 2023 and 2024. All fish ≤ 40mm were assumed to be Chignik Lake origin young of year and were removed from analysis. The majority of fish captured were between ≥ 50mm and ≤ 70mm. To capture fine scale patterns in stock variation, all samples within this range were genotyped. Fish > 40mm and < 50mm, and those >70mm were randomly sampled to reach a total of 200 individuals per year. From 2019-2022, townet catches in Chignik Lake were all below 200, and thus all fish were genotyped. For details of sampling in Chignik and Black Lake in 2010 and 2011 see Griffiths et al., (2013) who followed similar protocols.

In Chignik Lagoon, a subset of individuals was genotyped in both 2023 (n = 612) and 2024 (n = 547). All fish > 99mm (n = 30) were assumed to be out-migrating smolts (St. Saviour & Shedd, 2014) and were genotyped. Remaining fish were proportionally sampled by total catch, across sample location, year, and month to ensure spatial and temporal representation. Remaining samples were then either randomly added or removed from each group to select 200 individuals per month. In August 2024 only 130 individuals were captured, and all were genotyped.

2.3.4 Baseline Evaluation for Individual Assignment

We evaluated the current genetic baseline for its individual assignment (IA) ability and to determine appropriate assignment thresholds. The current genetic baseline for Chignik River sockeye salmon was constructed in 2020. It is composed of 1,691 individuals from 16 populations genotyped for 24 SNPs (Dann and Hsu, 2024). We applied the methods of Barclay et al. (2024) to assess the usefulness of the baseline for individual assignment. Leave-one out self-assignment tests conducted in *rubias* (Moran & Anderson, 2019) were used to calculate the numbers of true positives, false positives, and false negatives for a range of assignment likelihood thresholds greater than or equal to 0.50. These were summarized to construct precision-recall curves (Cook & Ramadas, 2020) to assess IA performance at different assignment thresholds. Our guidelines for considering a group adequate for IA were if recall was greater than or equal to 0.80 and precision was greater than or equal to 0.95 for assignment likelihoods greater than or equal to 0.50. Both Black Lake (Early) and Chignik Lake (Late) groups were tested for IA.

2.3.5 DNA Extraction and Genotyping

Genomic DNA was extracted using a NucleoSpin® 96 Tissue Kit by Macherey-Nagel (Düren, Germany). Genetic data were collected from the samples as individual, multilocus genotypes by assaying 24 loci common to the genetic baseline (Dann and Hsu 2024). Samples were genotyped using Taqman® assays (Applied Biosystems, Foster City, CA, USA) with multiple parallel reactions using Biomark™ 192.24 Dynamic Arrays (Fluidigm® platform, Standard Biotools https://www.standardbio.com/area-of-interest/genomics-analysis/pcr-applications/genotyping-with-microfluidics). The Dynamic Arrays were read on a BioMark™ or EP1™ System after amplification and scored using BioMark™ Genotyping Analysis software (Standard Biotools). For quality control purposes, ~8% of tissue samples were re-extracted and genotyped to check for genotyping errors. Any major genotyping errors were corrected.

2.3.6 Data Retrieval and Quality Control

All subsequent analyses were performed in *R*, unless otherwise noted. Genotypes were retrieved from the Gene Conservation Lab database and imported into *R* (R Core Team, 2024) with the *RJDBC* package (Urbanek, 2022). Two quality assurance analyses were performed to confirm the quality of the data. First, individuals missing substantial genotypic data (20% or more of loci; Dann et al. 2009) likely had poor quality DNA and were removed from further analyses. The second quality assurance analysis identified individuals with duplicate genotypes due to sampling or extracting the same individual twice. Duplicates were defined as pairs of individuals sharing the same alleles in 99% of screened loci, and the individual with the most missing genotypic data from each duplicate pair was removed from further analyses. If both had the same amount of genotypic data, the first individual was removed from further analyses.

2.3.7 Individual Assignment

Individual assignments were produced by summing the *rubias* individual posterior mean population assignment likelihoods to produce individual assignment likelihoods for each individual by reporting group. The likelihoods were filtered for the top reporting group assignment for each individual, then individuals that had top assignment likelihoods less than the threshold identified as the most appropriate from the previously described baseline evaluation based upon precision-recall curves were removed.

2.3.8 Dataset Compilation

Griffiths et al. (2013) conducted a similar genetics analysis of juvenile sockeye salmon rearing in the Chignik watershed, using samples collected in August of 2010 and 2011. Our sample collection methods remained the same to this study, but our data selection, laboratory analysis, genetic analysis, and mixture analysis differed slightly. Notably, their study used a baseline of 96 SNP's to assign individuals as opposed to our baseline of 103 SNP's. For mixture analysis, Griffiths et al., 2013 used a Bayesian approach BAYES (Pella & Masuda, 2001). Similar to our study, individuals were assigned to stock of origin at an 80% threshold. To expand the temporal scale of our study, Griffiths et al., 2013 data were combined with our 2019-2024 samples into a single dataset (n = 4868). A log-linear regression was used to identify extreme outliers produced from measurement or data entry errors. Individual samples that had extreme residuals from a log-mass vs log-length regression were removed from further analysis (n=28, 0.006% of the sample).

Sockeye salmon sampled in Chignik Lagoon and assigned to stock of origin were separated by size group as either parr (< 70mm) or smolts (≥ 70mm). The arbitrary length cutoff was informed by mean lengths of smolts sampled by ADF&G in the lower Chignik River (Loewen & Baechler, 2015; Loewen & Henslee, 2017; St. Saviour & Shedd, 2014). This enabled assessing stock specific body condition of parr rearing in estuarine habitat separately to individuals transiting through the Chignik Lagoon to sea.

2.3.9 Length and Body Condition Analysis

For individuals assigned to either Black Lake or Chignik Lake stock of origin, we tested for differences in body length between five combinations of stock of origin, location of capture, and size group for each year: 1) different stocks in natal rearing habitat (Black Lake residents and Chignik Lake residents), 2) same stock in natal/downstream habitats (Black Lake residents and Black Lake emigrants), 3) different stocks in the same habitat (Chignik Lake residents and Black Lake emigrants), 4) parr of different stocks in estuarine habitat (Black Lake and Chignik Lake parr), and 5) smolts of different stocks in estuarine habitat (Black Lake and Chignik Lake smolts). Sample sizes in most comparisons were highly unequal, and any stocks with <10 samples were not tested. A non-parametric Kruskal-Wallis test was used to test for differences in body length among stock groups (Zar, 1999).

To explore differences in the relative body condition of the three sockeye salmon stock groups rearing in freshwater habitat (Black Lake residents, Black Lake emigrants, Chignik Lake residents), we used a linear mixed effects regression to predict individual log-mass as a function of log-length. Natural log transformed length-mass relationships correct for allometric growth and are a reliable method for evaluating fish condition and its relationship with growth rate (Bentley & Schindler, 2013; Cone, 1989). This methodology is consistent with previous studies in the watershed (Griffiths et al., 2013;Simmons et al., 2013). The model included a global intercept (β_0) and a common slope (β_1) for log length across all groups. A fixed effect of stock (β_{2i}) represented the group specific deviations from the global intercept. Each stock-year interaction (u_{ij}) was included as a random deviation of the intercept to account for interannual variability in the body condition of each stock.

$$\log(\text{Mass}_{ijk}) = \beta_0 + \beta_1 \log\left(\text{Length}_{ijk}\right) + \beta_{2i} + u_{ij} + \varepsilon_{ijk}$$

A second linear mixed effects regression was used to explore differences in relative body condition for four juvenile sockeye salmon stock groups (Black Lake parr, Black Lake smolts, Chignik Lake parr, Chignik Lake smolts) in the Chignik Lagoon. The only change in the model being the definition of stock as an interaction between lake of origin and size group (smolts or parr).

Intercepts and 95% confidence intervals for random effects were calculated for each stock group in each year. Higher intercepts reflected greater body condition which we assumed was correlated with higher somatic growth rates (Bentley & Schindler, 2013).

2.3.10 Spatiotemporal Estuarine Habitat Use

Sampling sites within the Chignik Lagoon were grouped into zones as either upper lagoon (n=3) or lower lagoon (n=1) which typically have salinities of 1.6 ‰ and 25.3 ‰, respectively. The lower lagoon site is located directly adjacent to the outlet of the estuary, and likely samples smolts as they are leaving this habitat for the Gulf of Alaska (Fig. 1). Catch per unit effort (CPUE) was calculated as the number of individuals per beach seine haul.

Stock assignments from genetics samples were expanded to the total catch by proportionally scaling the observed stock composition within each zone, date, and size group. The proportion of each stock within genetic samples was calculated for each date-zone-size group combination. These proportions were then applied to the size-specific CPUE values, assigning a portion of the total catch to each stock based on its relative frequency in the genetic dataset. Final stock-specific catch estimates were obtained by multiplying the proportions by CPUE and rounding down to the nearest whole number.

2.4 Results

2.4.1 Sample Collection

From 2019-2024, a total of 2144 juvenile sockeye salmon from Chignik Lake were sampled for length, mass, and fin clip. After sub-sampling, a total of 859 fish from Chignik Lake were genotyped. During the same period, total of 1093 fish from Black Lake were sampled for length and mass. In 2023 and 2024, a total of 1744 fish were sampled for length, mass, and fin clip from the Chignik Lagoon. After sub-sampling, a total of 1159 fish from the Chignik Lagoon were genotyped.

2.4.2 Mixture Allocations and Individual Assignment

Across all years and sample habitats, the average stock composition of our genetics samples was 74.8% (63.5 – 84.2) for individuals of Chignik Lake origin, and 25.2% (15.8 – 36.5) for individuals of Black Lake origin. A total of 626 fish sampled in Chignik Lake from 2019-2024, and 894 fish sampled in Chignik Lagoon in 2023 and 2024, were assigned at the 80% threshold to stock of origin. Fewer individuals of Black Lake origin were successfully assigned at the 80% threshold (n = 271, 57% success) than individuals of Chignik Lake origin (n = 1249, 85% success) (Table. 1).

2.4.3 Length and Body Condition by Stock in Lake Habitat

In freshwater habitat, juvenile sockeye salmon body condition was highly dependent upon an individual's primary rearing habitat, regardless of stock of origin (Fig. 2). Black Lake residents were of significantly higher body condition in all years than either Chignik Lake residents or Black Lake emigrants. Chignik Lake residents and Black Lake emigrants had similar body conditions in most years, with Black Lake emigrants being of significantly higher condition only in 2022. There were no trends in body condition for any stock-habitat combination between 2010 and 2024 (Fig. 2).

A residuals versus fitted plot showed that residuals were approximately centered around zero with no clear evidence of nonlinearity. There was greater variation in residuals at lower fitted values suggesting some heteroscedasticity (Supplemental Fig. 1). A Q-Q plot of model residuals showed overall normality, although slight deviations in the tails of the distribution (Supplemental Fig. 2).

Juvenile sockeye salmon body length was variable between stocks and years (Fig. 3). Black Lake residents were significantly longer than either Black Lake emigrants (Table 2) and Chignik Lake residents (Table 3) in 2021, 2022, and 2024. Chignik Lake residents were significantly longer than Black Lake emigrants in 2011 and 2021, while the reverse was true in 2024 (Table 4). There were insufficient sample sizes in 2019, 2020, and 2023 to effectively compare stocks (Table 8). Black Lake emigrants had a wide variety of body lengths (38-84mm) (Supplemental Fig. 5).

2.4.4 Length and Body Condition by Stock in Estuarine Habitat

In the estuarine habitat, individuals of Black Lake origin were of higher body condition than those of Chignik Lake origin for both parr and smolts size classes (Fig. 4). While this trend was only significant for smolts in 2024, it was consistent among all years and size classes. Parr were of significantly higher body condition than smolts in all years, regardless of stock of origin.

A residuals versus fitted plot showed that residuals were approximately centered around zero with no clear evidence of nonlinearity. There was large variation in residuals at lower fitted values suggesting heteroscedasticity (Supplemental Fig. 3). A Q-Q plot of model residuals showed overall normality, although slight deviations in the lower tail of the distribution (Supplemental Fig. 4).

Sockeye salmon parr and smolts body lengths differed between stocks of origin (Fig. 5). Parr of Black Lake origin were significantly longer than parr of Chignik Lake origin (Table 5). Smolts of Chignik Lake origin were consistently, though not significantly, longer than Black Lake smolts (Table 6).

2.4.5 Estuarine Habitat Use

Sockeye salmon parr of both Black and Chignik Lake origin were observed rearing in the upper estuary throughout the summer growing season (Fig. 6). Chignik Lake parr were dominant in both years, and parr of both stocks were rare in the lower estuary.

Sockeye salmon smolts abundances peaked during early June in the upper estuary, and 1-2 weeks later the lower estuary (Fig. 7). Both Chignik and Black Lake smolts were abundant in 2023, while Chignik Lake smolts were strongly dominant in 2024. Smolts emigration timing in the upper estuary was similar between stocks, but varied between 2023 and 2024 (Fig. 8). In the lower estuary, Black Lake smolts emigrated slightly later in the season than Chignik Lake smolts.

2.5 Discussion

Our results demonstrate that the juvenile sockeye salmon body condition in lakes reflects the conditions experienced in the habitat of sampling, regardless of stock of origin. Fish rearing for the entire growing season in Black Lake had the highest relative body condition of all stocks rearing in lake habitats. This reflects the comparatively higher productivity habitat provided by Black Lake. With warmer water temperatures and high-density prey resources (Griffiths et al., 2013, 2014), individuals which remain in Black Lake can exploit higher metabolic rates to achieve faster growth and a higher body condition.

Within Chignik Lake, body condition of Black Lake emigrant and Chignik Lake residents did not differ significantly in most years. This suggests that despite originating from higher quality habitat, Black Lake emigrants do not retain a competitive advantage once in Chignik Lake. This is consistent with previous research describing poor condition fish emigrating from Black Lake through the Black River to disperse to Chignik Lake (Westley et al., 2008). An increasing trend in earlier emigration has been associated with declining habitat availability and higher water temperatures in Black Lake (Griffiths & Schindler, 2012; Westley et al., 2008).

Notably, in 2022 Black Lake emigrants had significantly higher body condition than Chignik Lake residents, suggesting that annual variation in climate and habitat productivity may influence emigration timing. This is consistent with previous work in the Chignik watershed which described Black Lake individuals exhibiting a diversity of movement strategies both within and among rearing years (Walsworth et al., 2015, 2020). While it is estimated that emigrants typically spend a month rearing in Chignik Lake before August sampling (Griffiths et al., 2013; Simmons et al., 2013), the high body condition of Black Lake emigrants in 2022 suggests emigration timing was delayed. In Black Lake, habitat capacity limits the number of individuals which can remain and feed competitively in the highly productive but crowded lake. Lower performance individuals who cannot attain a critical size threshold early in the season must move to attain sufficient energy storage for overwinter survival (Biro et al., 2005). As habitat quality and availability fluctuates, so does the time lower performance individuals can remain in Black Lake. During 2022, extremely high zooplankton densities in Black Lake likely provided sufficient prey resources for juvenile sockeye salmon (Chapter 1; Gammelin et al. in review). Thus, emigrants likely delayed downstream migration, achieving greater energy allocation during their extended residency in Black Lake.

Black Lake emigrants rearing in Chignik Lake comprised a variable proportion of the juvenile sockeye salmon population. Townet catch rates during 2019 were dramatically low across the watershed, which may explain why no Black Lake emigrants were observed, and reflect the uncharacteristically high-water temperatures in Black Lake that summer. This supports the existing hypothesis that stressful thermal conditions may contribute to early emigration of less fit Black Lake individuals (Griffiths & Schindler, 2012; Westley et al., 2008). Low body condition is correlated with decreased fitness (Henderson & Cass, 1991). Size at ocean entry is correlated with ocean survival (Koenings et al., 1993). If emigrant populations are more susceptible to habitat variation they must recuperate lost growth opportunities by exploiting longer freshwater residency or multiple rearing habitats.

In the Chignik Lagoon, sockeye salmon smolts and parr of Black Lake origin had higher relative body condition than those of Chignik Lake origin. Black Lake parr were significantly longer than Chignik Lake parr, while Chignik Lake smolts were slightly longer than Black Lake smolts. Additionally, parr had higher body condition than smolts for both stocks. Considering all parr in the estuary are emigrants from distinct natal habitats, the differences in body size between stocks suggest natal habitat productivity may influence early life stage growth performance, and that stock-specific body condition may develop in suitably productive habitats. With a shallow water column, Black Lake experiences earlier and more rapid early spring warming than Chignik Lake. For sockeye salmon fry entering their natal lakes in the spring, Black Lake provides higher quality habitat than Chignik Lake. The differences in estuarine body condition suggest habitat productivity influences early life growth rates, even for individuals which emigrate to estuarine habitat.

Sockeye salmon smolts sampled in the Chignik Lagoon represent two age classes. With higher habitat mediated growth rates, Black Lake individuals typically smolts after 1 year while Chignik Lake individuals smolts after 2 years of freshwater growth (Narver, 1966). Although we were not able to identify the rearing habitat exploited by each Black Lake smolts, we did observe that the majority of Black Lake individuals rear in their natal habitat which is consistent with previous studies in the watershed (Walsworth et al., 2020). Our results suggest Black Lake smolts achieved higher body condition in a single year than two year old Chignik Lake smolts. This may reflect stock specific variation in behavior, where successful Black Lake residents allocate more energy to storage rather than growth in length (Biro et al., 2005).

During smoltification, juvenile salmon undergo developmental changes adaptive for ocean survival and growth (Björnsson et al., 2011), including morphological changes for improved pelagic swimming (Winans & Nishioka, 1987). This likely explains why out-migrating smolts were of apparently lower body condition than parr rearing in estuarine habitat. However, the differences noted here may also simply reflect a change in body morphological associated with transitioning to the marine component of their life cycle.

Existing studies show a variety of estuarine habitat use patterns by juvenile sockeye salmon, associated with local watershed characteristics and life history strategies (Moore et al., 2016;Simmons et al., 2013). While Simmons et al., (2013) reported Chignik Lake parr rearing in the Chignik Lagoon, there have been no in-situ observations of Black Lake individuals rearing in the Chignik Lagoon. Analysis of otolith microchemical signatures suggest a small proportion of Black Lake juveniles enter estuarine habitat before returning upriver to Chignik Lake to overwinter, yet the spatial and temporal distribution of these individuals has remained undescribed (Walsworth et al., 2015). Our analysis confirms the presence of emigrant Black Lake individuals rearing in the upper Chignik Lagoon, and shows that they remain in estuarine habitat for the duration of the summer growing season. This provides evidence that emigrants from Black Lake exploit multiple alternative rearing habitats. With high competitor density in Chignik Lake, the opportunity to continue downstream migration provides access to greater diversity in available rearing habitat for juvenile sockeye salmon. In the high salinity lower estuary, parr of both stocks were less common. This likely reflects the high energetic costs associated with early osmoregulatory development and increased predation risk limiting parr use of marine habitat.

Our analysis found Chignik Lake smolts were abundant in the lower estuary in June and July, with declining catches in late summer. Although Black Lake smolts were observed, their low abundances in our catches showed no strong patterns in estuarine habitat use. Black Lake smolts must travel further than their Chignik Lake counterparts, which may result in later ocean entry as observed in 2024. This would only be true for the few smolts that overwinter in Black

Lake as most smolts of this stock overwinter in Chignik Lake. Alternatively, the low abundances of Black Lake smolts in our samples may reflect the tail end of an earlier peak in migration timing. In the Chignik watershed, peak emigration of sockeye salmon smolts has been shown to occur between late April and early June (Loewen & Baechler, 2015, p. 20; Loewen & Henslee, 2017, p. 20). Considering our earliest sampling occurred in early June, we missed observing the early components of the smolt migration into the lagoon. Assuming our results represent an unknown fraction of the migration, it is possible stocks exhibit greater variation in migration timing than described here.

Our results highlight the diversity of juvenile sockeye salmon life history strategies in the Chignik watershed, and the importance of interconnected habitat networks for juvenile salmon populations. While Black Lake provides highly productive rearing habitat, it is clear that it can become less favorable for some individuals as the growing season progresses. The ability for individuals to exhibit variable migration strategies as juveniles buffers population abundances against asynchrony in habitat productivity. Accessing estuarine habitat as parr, multiple stocks of sockeye salmon exploit all available rearing habitat within the watershed. Together this highlights the value of maintaining connectivity between alternate habitats with variable productivity for sustaining overall population abundances.

2.6 Figures

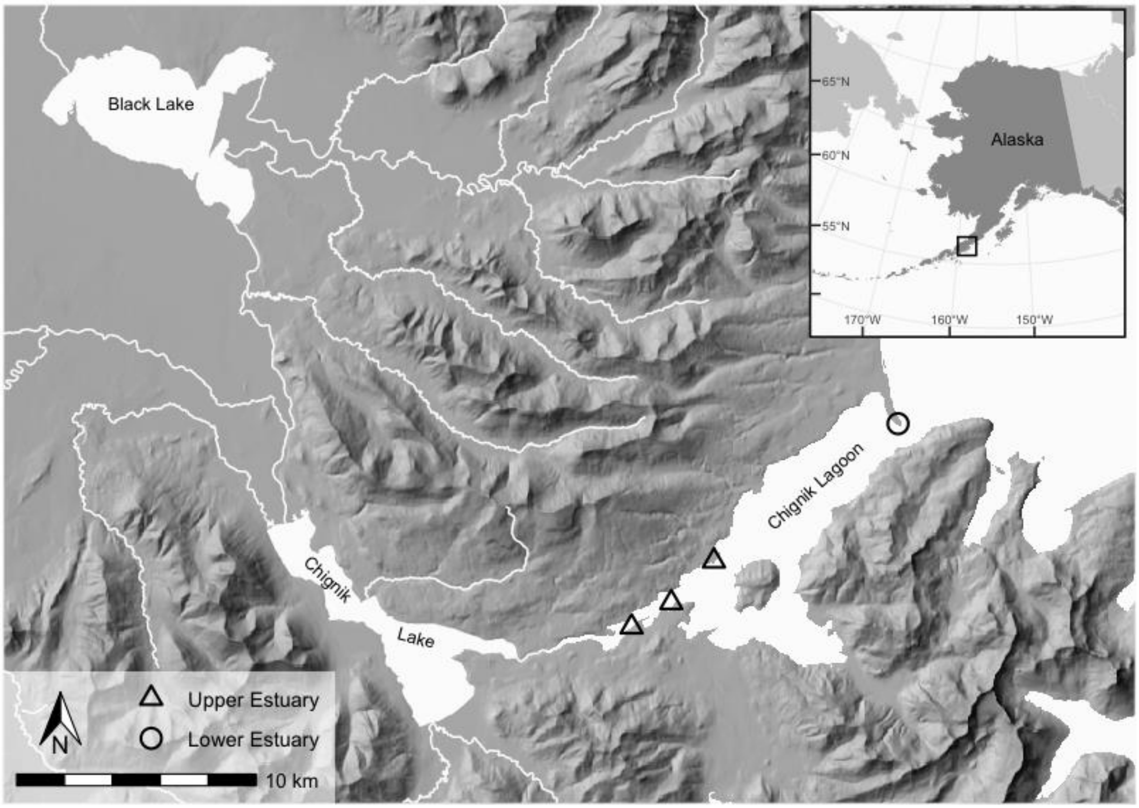


Figure 2.1 Chignik watershed, Alaska, USA. Beach sein sample locations in the Upper (triangles) and Lower (circle) estuary.

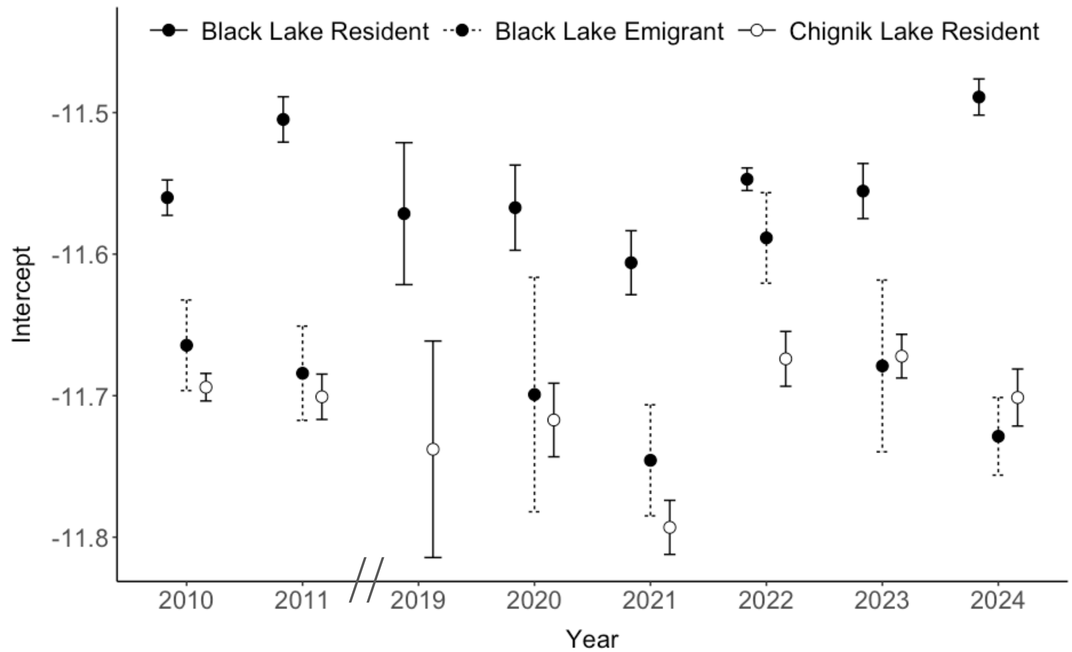


Figure 2.2 Relative body condition in lake habitats. Estimated model intercepts, and 95% CI's, for three juvenile sockeye salmon groups (Black Lake emigrants, Black Lake residents, and Chignik Lake residents) sampled in Black and Chignik Lakes.

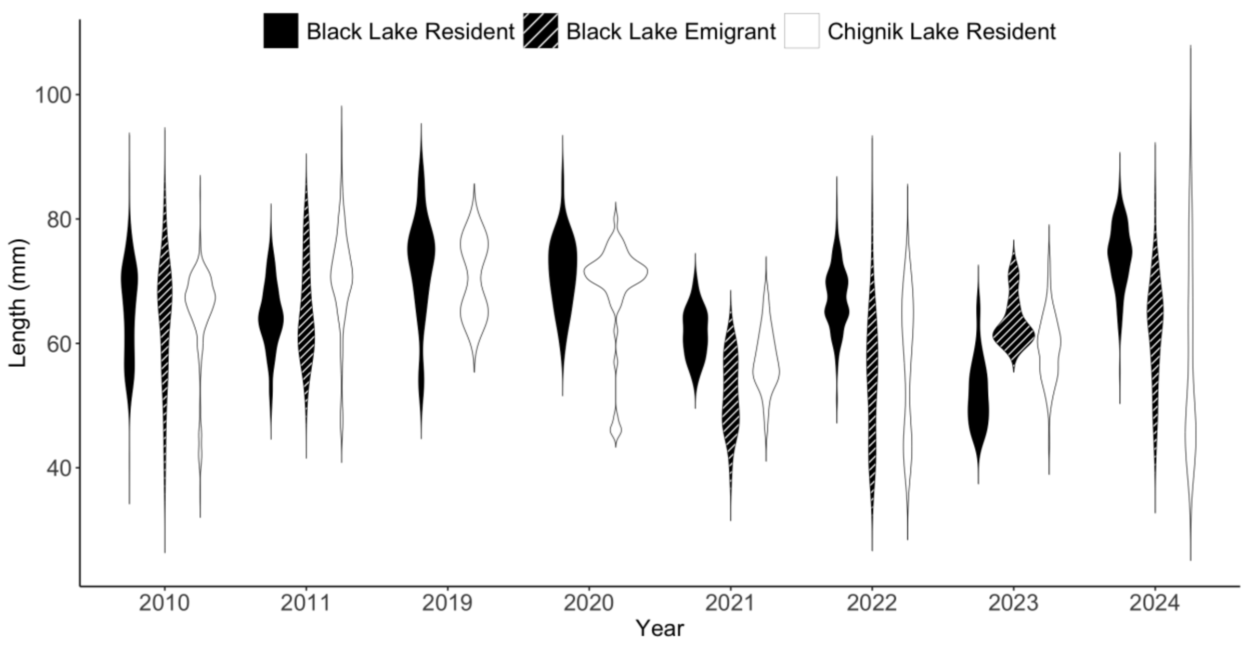


Figure 2.3 Length distributions for three juvenile sockeye salmon groups rearing in Black Lake (Black Lake residents) and Chignik Lake (Black Lake emigrants, Chignik Lake residents).

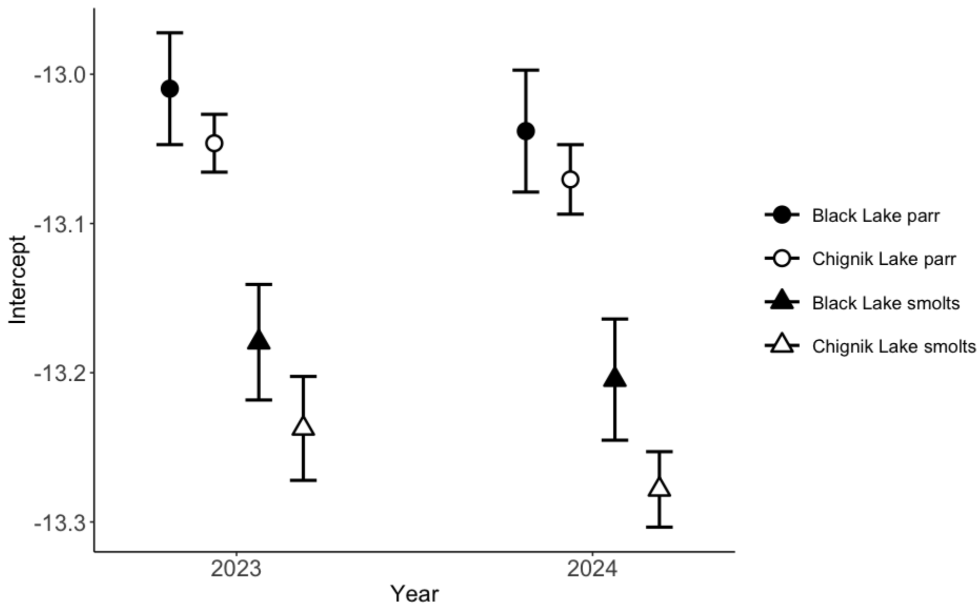


Figure 2.4 Relative body condition in estuarine habitat. Estimated linear model intercepts, and 95% CI's, for juvenile sockeye salmon smolts (triangles) and parr (circles) sampled in the Chignik Lagoon.

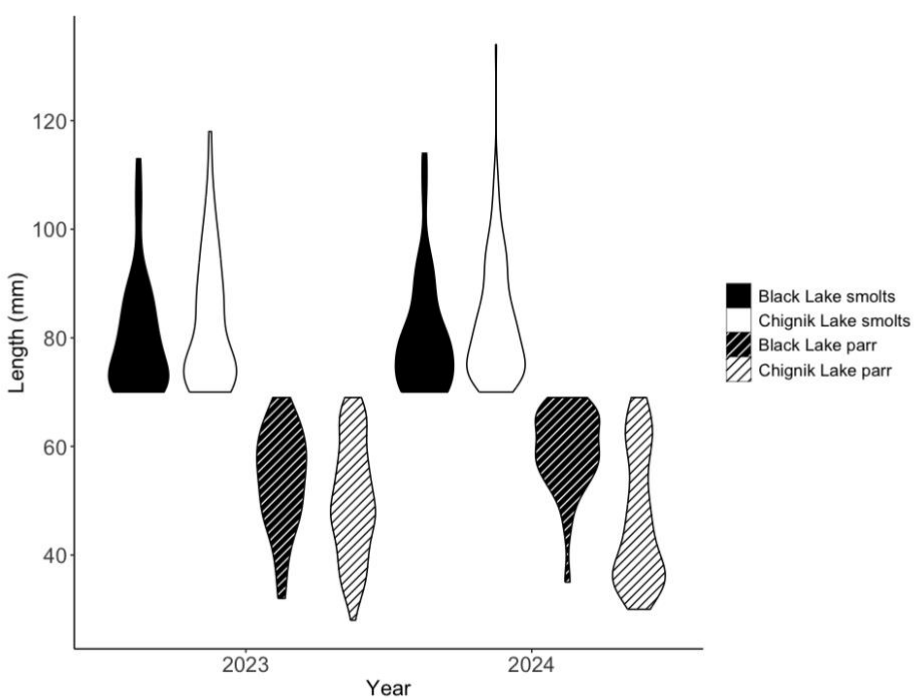


Figure 2.5 Length distributions of sockeye salmon smolts (solid) and parr (dashed) in the Chignik Lagoon.

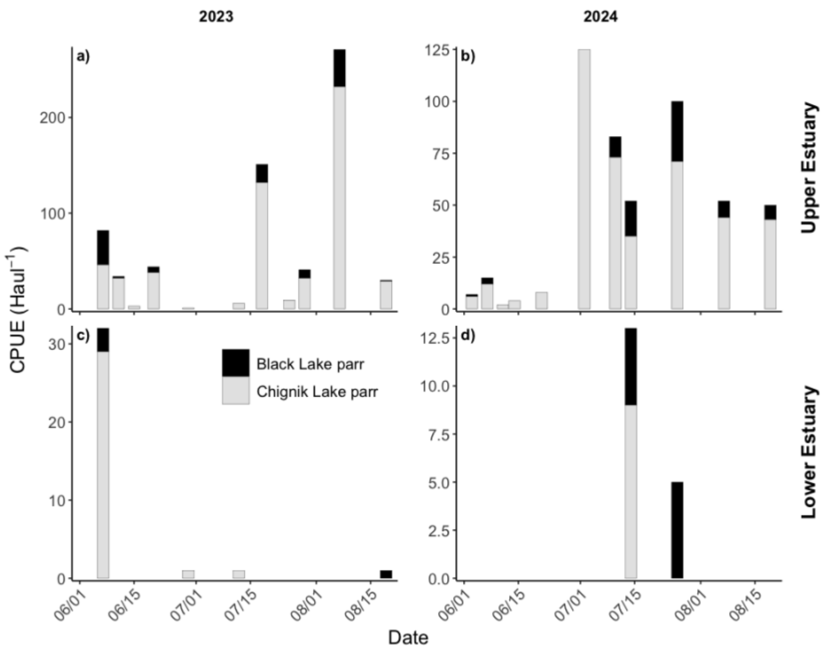


Figure 2.6 Sockeye salmon parr catch per unit effort (CPUE) in the upper (a, c) and lower (b, d) Chignik Lagoon from June 1- Sept. 6 in 2023 and 2024.

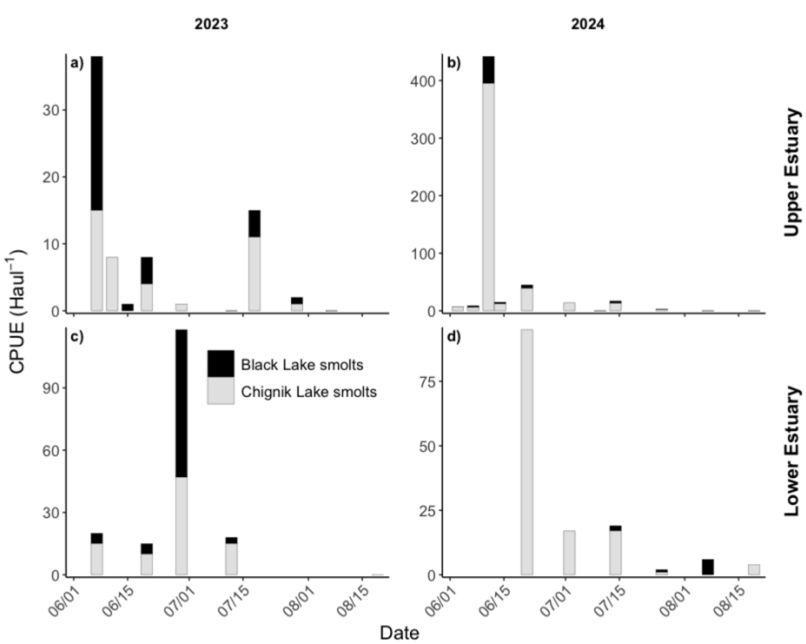


Figure 2.7 Sockeye salmon smolts catch per unit effort (CPUE) in the upper (a, c) and lower (b, d) Chignik Lagoon from June 1- Sept. 6 in 2023 and 2024.

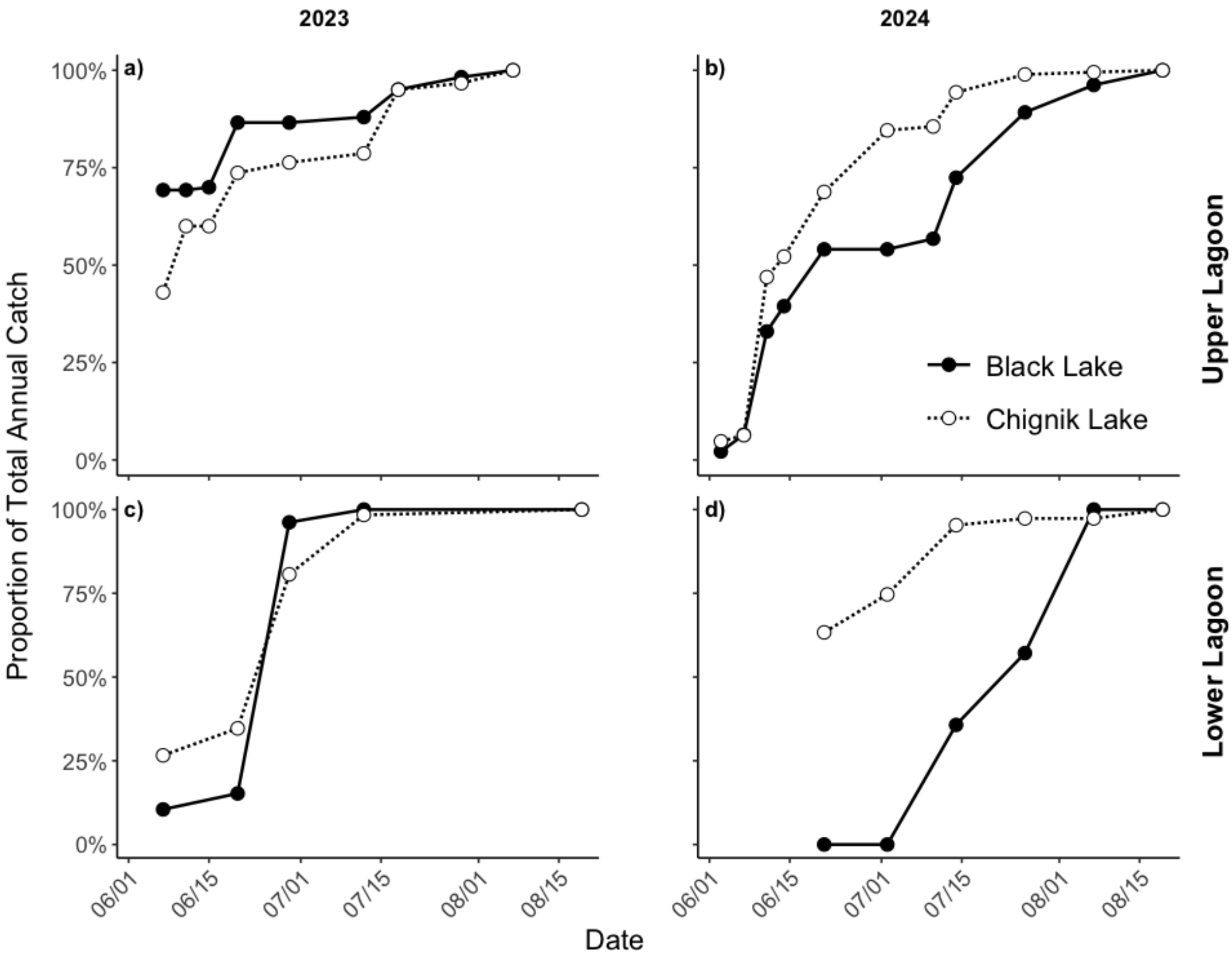


Figure 2.8 Cumulative catch proportion of sockeye salmon smolts in the upper (a, b) and lower (c, d) Chignik Lagoon from June 1- Sept. 6 in 2023 and 2024.

2.7Tables

Table 2.1 Stratified estimates of stock composition (proportion) in each year assigned to each stock group at the 80% threshold, including median, 90% credibility interval, mean and standard deviation (SD), and number of successful assignments. (*) Denotes results from Griffiths et al. 2013. (**) Denotes juvenile sockeye salmon sampled in the Chignik Lagoon in 2023 and 2024.

		Stock Composition					Assignment at 80%	
			90% CI					
Year	Stock	Median	5%	95%	Mean	SD	Assigned	Not Assigned
2010	*Black Lake				0.06			
	*Chignik Lake				0.73			
2011	*Black Lake				0.13			
	*Chignik Lake				0.64			
2019	Black Lake	0.30	0.01	0.76	0.33	0.24	0	
	Chignik Lake	0.70	0.24	0.99	0.67	0.24	2	
2020	Black Lake	0.09	0.02	0.18	0.09	0.05	1	
	Chignik Lake	0.91	0.82	0.98	0.91	0.05	54	
2021	Black Lake	0.25	0.18	0.33	0.25	0.05	21	
	Chignik Lake	0.75	0.67	0.82	0.75	0.05	104	
2022	Black Lake	0.33	0.25	0.40	0.33	0.05	34	
	Chignik Lake	0.67	0.60	0.75	0.67	0.05	101	
2023	Black Lake	0.13	0.07	0.19	0.13	0.03	6	
	Chignik Lake	0.87	0.81	0.93	0.87	0.03	162	
	**Black Lake	0.27	0.22	0.31	0.27	0.02	92	
	**Chignik Lake	0.73	0.69	0.78	0.73	0.02	372	
2024	Black Lake	0.39	0.32	0.47	0.39	0.05	48	
	Chignik Lake	0.61	0.53	0.68	0.61	0.05	93	
	**Black Lake	0.23	0.20	0.28	0.24	0.02	69	
	**Chignik Lake	0.77	0.72	0.80	0.76	0.02	361	
					Total		1520	415

Table 2.2 Length comparison of Black Lake residents and Black Lake emigrants in two lakes.

Year	Test	p-value	df	Test statistic	Stock	n	Length	SD
2010	K-W	0.58	1	$\chi^2 = 0.30$	BL resident	249	65.5	7.9
					BL emigrant	34	64.2	9.5
2011	K-W	0.73	1	$\chi^2 = 0.12$	BL resident	150	64.7	6.7
					BL emigrant	31	65.2	7.7
2021	K-W	<0.001	1	$\chi^2 = 33.21$	BL resident	73	61.6	3.9
					BL emigrant	21	52	5.8
2022	K-W	<0.001	1	$\chi^2 = 56.26$	BL resident	622	67.3	5.2
					BL emigrant	34	54.7	10
2024	K-W	<0.001	1	$\chi^2 = 73.57$	BL resident	238	74	5.3
					BL emigrant	48	62.3	8.6

Table 2.3 Length comparison of Black Lake residents and Chignik Lake residents in two lakes.

Year	Test	p-value	df	Test statistic	Stock	n	Length	SD
2010	K-W	0.76	1	$\chi^2 = 0.092$	BL resident	249	65.5	7.9
					CL resident	416	65.1	7.9
2011	K-W	< 0.001	1	$\chi^2 = 65.40$	BL resident	150	64.7	6.7
					CL resident	150	70.5	8.2
2020	K-W	0.45	1	$\chi^2 = 0.56$	BL resident	39	71.4	5.7
					CL resident	54	69.5	7.5
2021	K-W	< 0.001	1	$\chi^2 = 32.94$	BL resident	73	61.6	3.9
					CL resident	104	57.4	4.9
2022	K-W	< 0.001	1	$\chi^2 = 76.97$	BL resident	622	67.3	5.2
					CL resident	101	57.2	10.8
2023	K-W	< 0.001	1	$\chi^2 = 82.34$	BL resident	100	52.1	5.5
					CL resident	162	59.4	5.3
2024	K-W	< 0.001	1	$\chi^2 = 84.35$	BL resident	238	74	5.3
					CL resident	93	56.8	14.6

Table 2.4 Length comparison of Black Lake emigrants and Chignik Lake residents in Chignik Lake.

Year	Test	*p*-value	df	Test statistic	Stock	n	Length	SD
2010	K-W	0.84	1	$\chi^2 = 0.042$	BL emigrant	34	64.2	9.5
					CL resident	416	65.1	7.9
2011	K-W	<0.001	1	$\chi^2 = 13.09$	BL emigrant	31	65.2	7.7
					CL resident	150	70.5	8.2
2021	K-W	<0.001	1	$\chi^2 = 12.24$	BL emigrant	21	52	5.8
					CL resident	104	57.4	4.9
2022	K-W	0.091	1	$\chi^2 = 2.85$	BL emigrant	34	54.7	10
					CL resident	101	57.2	10.8
2024	K-W	0.004	1	$\chi^2 = 8.50$	BL emigrant	48	62.3	8.6
					CL resident	93	56.8	14.6

Table 2.5 Length comparison of Black Lake parr and Chignik Lake parr in the Chignik Lagoon.

Year	Test	*p*-value	df	Test statistic	Stock	n	Length	SD
2023	K-W	0.013	1	$\chi^2 = 6.23$	BL Parr	49	53.9	9.1
					CL Parr	308	50	10.5
2024	K-W	<0.001	1	$\chi^2 = 28.20$	BL Parr	34	59.3	7.4
					CL Parr	199	46.6	11.9

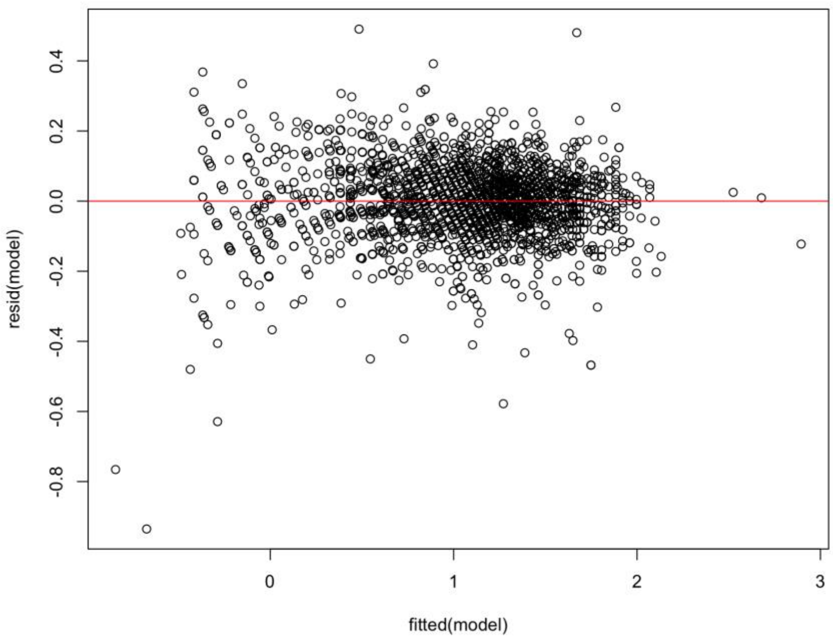
Table 2.6 Length comparison of Black Lake smolts and Chignik Lake smolts in the Chignik Lagoon.

Year	Test	*p*-value	df	Test statistic	Stock	n	Length	SD
2023	K-W	0.18	1	$\chi^2 = 1.82$	BL Smolts	43	80.1	10.4
					CL Smolts	64	82.9	11.8
2024	K-W	0.088	1	$\chi^2 = 2.91$	BL Smolts	35	80.3	10.5
					CL Smolts	162	82.9	10.6

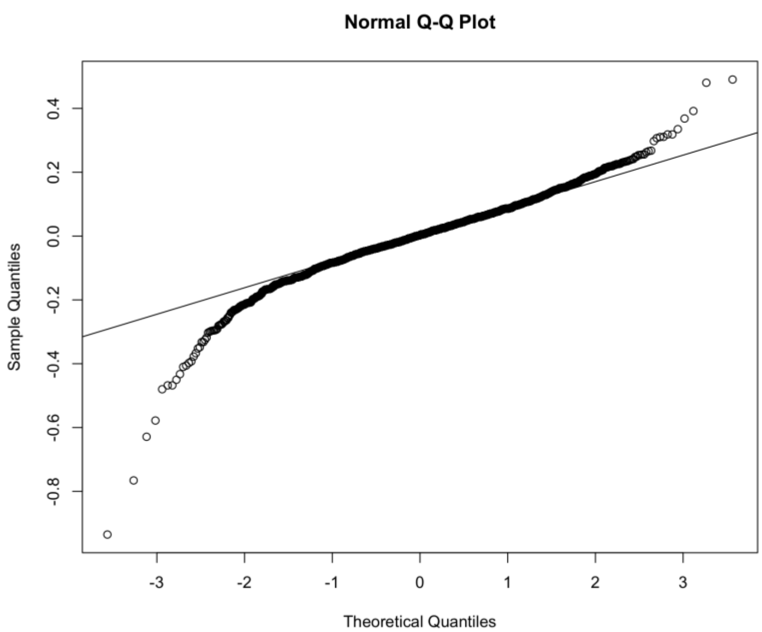
Table 2.7 Sample size, mean length, and standard deviation of lengths of juvenile sockeye salmon stocks. (*) Indicates stocks with <10 samples which were not compared. (**) Indicates stocks sampled in the Chignik lagoon.

Year	Stock	n	Mean Length	SD
2010	Black Lake resident	249	65.5	7.9
	Chignik Lake resident	416	65.1	7.9
	Black Lake emigrant	34	64.2	9.5
2011	Black Lake resident	150	64.7	6.7
	Chignik Lake resident	150	70.5	8.2
	Black Lake emigrant	31	65.2	7.7
2019	Black Lake resident	11	72.5	8.5
*	Chignik Lake resident	2	70.5	7.8
*	Black Lake emigrant	0		
2020	Black Lake resident	39	71.4	5.7
	Chignik Lake resident	54	69.5	7.5
	Black Lake emigrant	1	61.0	
2021	Black Lake resident	73	61.6	3.9
	Chignik Lake resident	104	57.4	4.9
	Black Lake emigrant	21	52	5.8
2022	Black Lake resident	622	67.3	5.2
	Chignik Lake resident	101	57.2	10.8
	Black Lake emigrant	34	54.7	10
2023	Black Lake resident	100	52.1	5.5
	Chignik Lake resident	162	59.4	5.3
*	Black Lake emigrant	6	63.7	4.1
**	Black Lake Parr	49	53.9	9.1
**	Chignik Lake Parr	308	50	10.5
**	Black Lake Smolts	43	80.1	10.4
**	Chignik Lake Smolts	64	82.9	11.8
2024	Black Lake resident	238	74	5.3
	Chignik Lake resident	93	56.8	14.6
	Black Lake emigrant	48	62.3	8.6
**	Black Lake Parr	34	59.3	7.4
**	Chignik Lake Parr	199	46.6	11.9
**	Black Lake Smolts	35	80.3	10.5
**	Chignik Lake Smolts	162	82.9	10.6

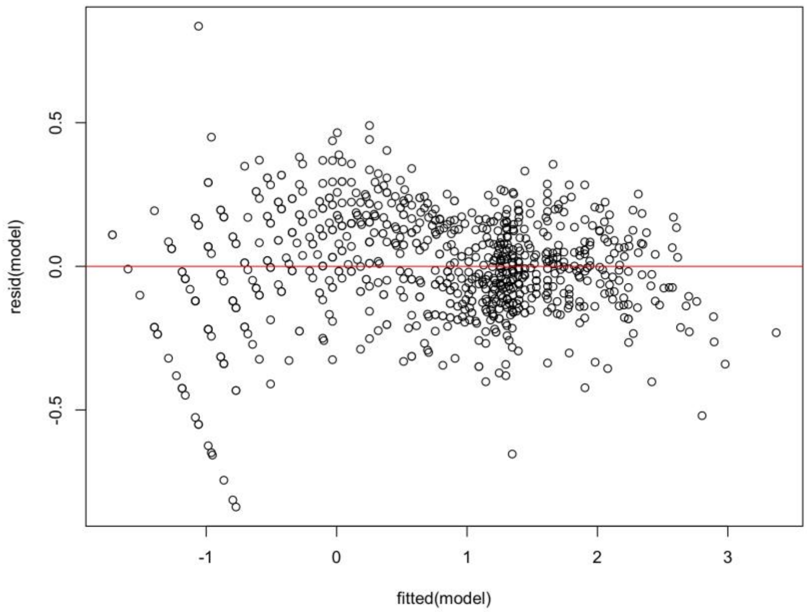
2.8 Supplemental Figures



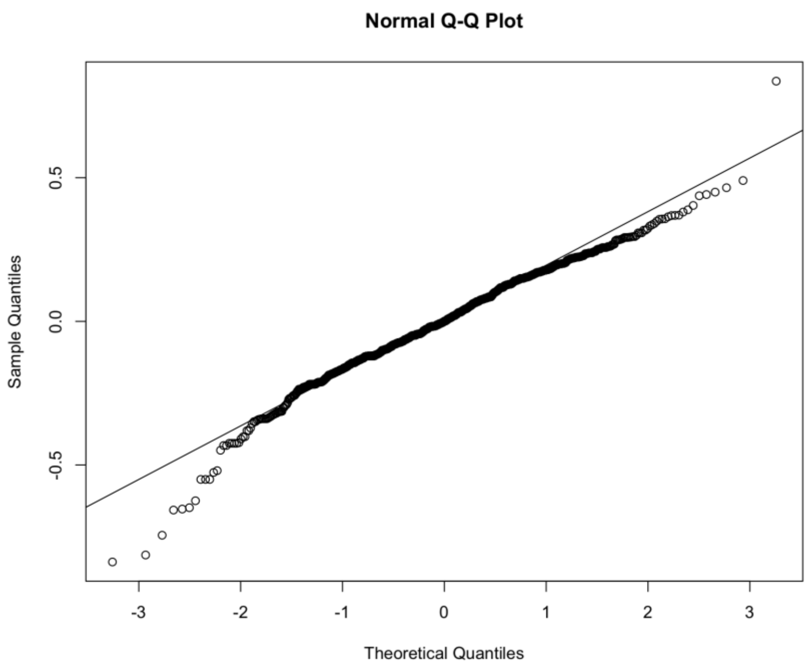
Supplemental Figure 2.1 Residuals vs. fitted plot from linear regression of fish in lake habitats.



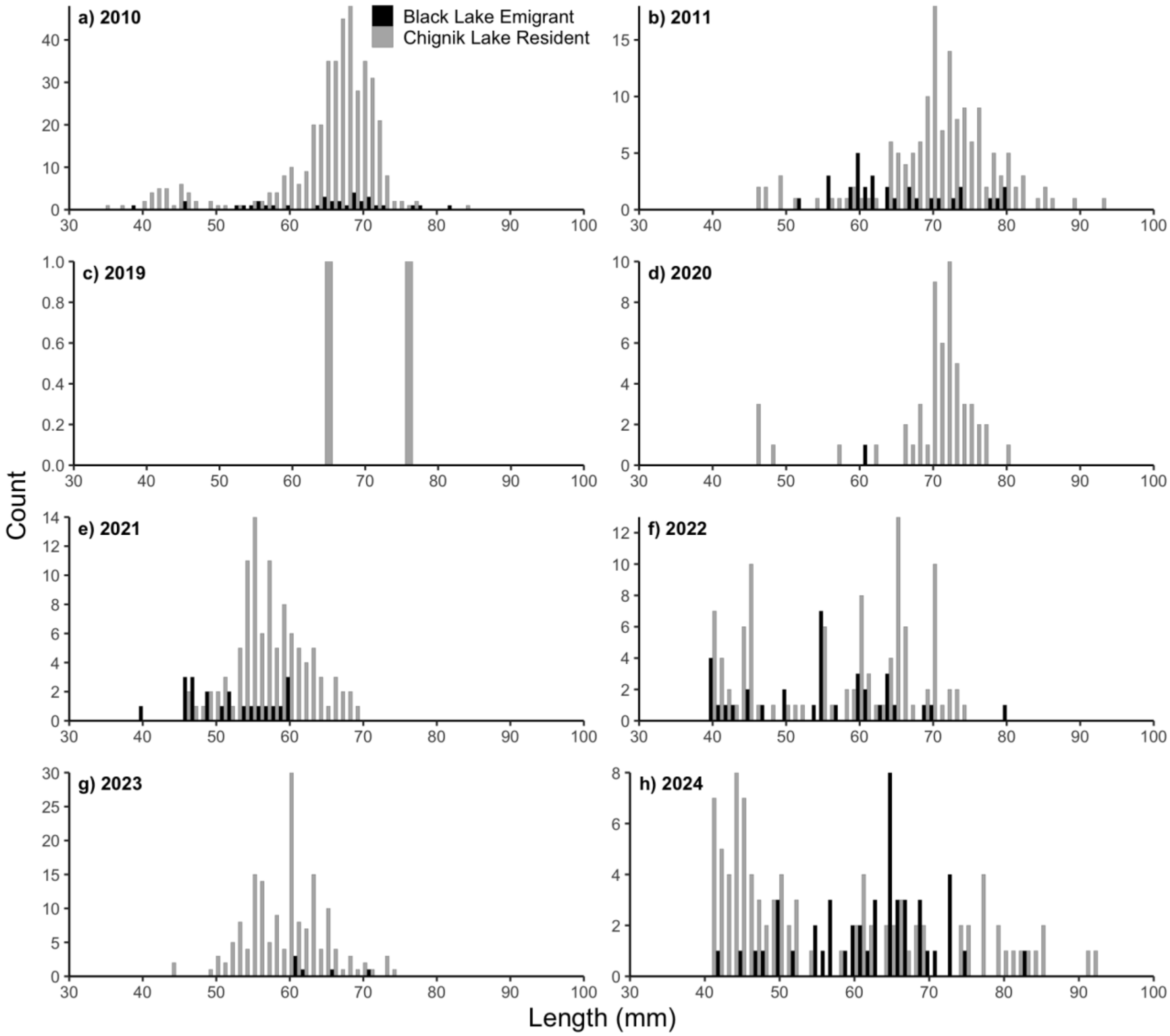
Supplemental Figure 2.2 Q-Q plot of residuals from linear regression of fish in lake habitats.



Supplemental Figure 2.3 Residuals vs. fitted plot from linear regression of fish in estuarine habitat.



Supplemental Figure 2.4 Q-Q plot of residuals from linear regression of fish in estuarine habitat.



Supplemental Figure 2.5 Length distributions of juvenile sockeye salmon of known stock of origin sampled in Chignik Lake in 2010, 2011 and 2019-2024.

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