Climate change and geomorphic evolution in an Alaskan watershed and implications for salmon production

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Abstract

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Freshwater ecosystems are not only the source of a disproportionate number of ecosystem services given their relative area on the planet, but they are also highly sensitive to anthropogenic impacts including climate change. Landscape heterogeneity provides a filter for regional climate forcing in aquatic systems and provides the context in which the biological components of ecosystems will interact with climate change. I used the Chignik watershed, Alaska as a case study in which to explore the response of juvenile sockeye salmon (*Oncorhynchus nerka*) growth and body condition to differences across habitats and variation in climate. Furthermore, I investigated the interaction of climate change and geomorphic evolution and its effects on juvenile sockeye salmon habitat and growth.

I used genetic tools to assess individual performance of sockeye salmon among connected freshwater habitats. I found that individual performance converged on habitat productivity rather than being determined by genetic origin. I investigated the effects of climate variability on juvenile salmon growth among lake habitats using 40 years of freshwater growth data from scales. Growth showed a coherent response to climate variables affecting growing season duration but opposing responses to growing season temperatures. This indicated that different lake habitats not only filter regional climate differently but that this leads to differences in the biological response. Juvenile sockeye salmon length data over a similar timeframe indicated that temperature had a greater effect on growth than sockeye density.

Finally, I assessed the relative importance of air temperature, lake volume and tributary for lake thermal regimes and juvenile sockeye salmon growth. Increases in lake volume had little effect on lake thermal regimes which were highly sensitive to lake temperature. Future increases in air temperature will likely reduce growth of juvenile sockeye although maintaining tributary connectivity is important to reducing the effects of air temperature.

Because uncertainty exists in how freshwater ecosystems will respond to climate change preserving networks of heterogeneous habitat may be critical to supporting ecosystem resilience. Intact ecosystems provide an opportunity to evaluate the relative importance of climate, geomorphology and connectivity for salmon populations and inform the management and restoration of impacted landscapes.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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DEDICATION

To all who have inspired me with their curiosity about the world around them.

Introduction

General Introduction

Human well-being depends on functioning ecosystems to provide a wide range of services from clean water to flood protection to food (Millenium Ecosystem Assessment 2005). Yet, human societies are also altering ecosystems at an unprecedented rate (Vitousek 1994) including changes to the composition and richness of biological communities, biogeochemical cycling, disturbance regimes, and climatic conditions. These changes are imparted through resource extraction (mining, fisheries); land conversion (agriculture, urbanization); introduction of exotic species; natural disaster mitigation; nutrient runoff; and the burning of fossil fuels. Societies are increasingly realizing the value of the services provided by ecosystems (Costanza et al. 1997) and are seeking management strategies that maintain or restore the reliability of these services. Managing ecosystems for ecosystem services depends, in part, upon understanding the processes and characteristics of ecosystems that promote their reliability. Furthermore, we must develop tools to assess the rate and magnitude of ecosystem responses to environmental change so that we can evaluate the sensitivity of ecosystem services to ongoing global change.

Freshwater ecosystems are not only the source of a disproportionate number of ecosystem services given their relative area on the planet, but they are also highly sensitive to anthropogenic impacts (National Research Council 1992). Freshwater ecosystems provide essential provisioning services such as drinking water and food production (fisheries, agriculture). These ecosystems are also important providers of regulating services (flood control) and supporting services (nutrient cycling). At local and regional scales anthropogenic impacts on freshwater ecosystems are profound and can ultimately jeopardize the delivery of these services. These threats include dams, water withdrawal, river channelization, pollution, deforestation and urbanization (Postel and Carpenter 1997).

Freshwater ecosystems are also sensitive to global, more diffuse human impacts. In particular, freshwater ecosystems have been shown to highly sensitive to ongoing climate change (Adrian et al. 2009). Both lotic and lentic systems show strong climate signals in both their thermal and hydrologic characteristics (Carpenter et al. 1992). In lakes, thermal characteristics are particularly important for structuring the physical environment and they have consistently shown climate driven signals including changes ice break-up (Magnuson et al. 2000), depth and duration of stratification (Livingstone 2003, Winder and Schindler 2004), and thermal regimes (Schindler 1997, Arhonditsis et al. 2004). These physical characteristics of the lake environment are key regulators of nutrient cycling, habitat availability, and growth rates in freshwater organisms (Wetzel 1983) and in turn the delivery of ecosystem services. While some of the physcial responses to changing climate appear coherent across diverse lake types (e.g. earlier ice break-up) other responses are dependent upon lake morphology and their watershed structure (Magnuson et al. 2004). Landscape heterogeneity provides a filter for regional climate forcing and provides the context in which the biological components of ecosystems will interact with climate change.

Anadromous Pacific salmon (*Oncorhynchus spp.*) provide both provisioning and cultural ecosystem services. In North America, they support commercial fisheries from California to Alaska worth millions of dollars. In Alaska, for example, the ex-vessel value of the salmon fishery in 2011 was $603 million (ADFG 2011). Additionally, Pacific salmon are an important subsistence resource for Native American communities and play an important role in their cultural traditions. Pacific salmon depend on freshwater habitat for reproduction and juvenile rearing and therefore the effects of climate change may impact salmon at both the beginning and end of their lifecycle. Throughout their range on the west coast of North America, salmon inhabit dynamic freshwater landscapes (Beechie et al. 2006). The glacial, volcanic, and fluvial processes that shape these watersheds have played a pivotal role in the evolution of Pacific salmon (Waples et al. 2008). High rates of natal homing by spawning adults have led to fine scale population differentiation and adaptation to local geomorphic regimes. This is expressed in the extraordinary range of freshwater life history diversity within and among species (Quinn 2005).

While climate change has already had measurable effects on the freshwater environment throughout the geographic range of Pacific salmon, rates of temperature increase in high northern latitudes are twice that of the global average (Christensen et al. 2007). In the coastal regions of Alaska, for example, air temperatures in watersheds supporting salmon are expected to increase by 2°C between 2000 and 2050 under mid-range emission scenarios (Schindler and Rogers 2009). Changes in air temperature have (Schindler et al. 2005, Carter and Schindler 2012) and will continue to have large effects on the thermal characteristics of lakes in these watersheds. Of the Pacific salmon species, sockeye salmon (*O. nerka*), are the most sensitive to changes in lake habitat. Juvenile sockeye salmon rear in lakes for 1 to 2 years prior to migrating to the ocean and their growth during this period plays a critical role in ocean survival (Koenings et al. 1993). The amount of growth sockeye salmon achieve is constrained by both the duration of the growing season and water temperature and these are also the physical characteristics of lakes that highly sensitive to changing climate.

Within and among watersheds, however, diverse habitats are part of an interconnected habitat network and, as mobile organisms, sockeye salmon have the opportunity to exploit different habitats throughout the freshwater rearing period. These habitats may differ in their thermal attributes and the response of those attributes to changing climate as a result of both their structure and the temporal scale of their geomorphic evolution. Fine scale connectivity may therefore be critical for juvenile sockeye salmon throughout their freshwater life history to negotiate growth and survival trade-offs (Scheuerell and Schindler 2003, Armstrong et al. 2010) under changing environmental conditions.

In addition to being subjected to ongoing climate change, lakes may also be affected by geomorphic change occurring on ecological relevant time scales. Lakes are typically considered to evolve on geologic time scales (Hutchinson 1957) unlike rivers systems which are explicitly studied in the context of geomorphic dynamics that govern ecological processes (e.g. Stanford et al. 2005). However, in high northern landscapes influenced by glacial, fluvial, volcanic, and thermokarst processes, there is the potential for the geomorphic dynamics of lakes to operate on time scales relevant to ecological processes. This also means that the geomorphic evolution of lakes has the potential to interact with and respond to climate change and consequently influence ecological responses to climate change.

In this dissertation I use the Chignik watershed, Alaska as a case study in which to explore the interaction of climate change and geomorphic evolution and its effects on juvenile sockeye salmon habitat and growth. Furthermore, I investigated the response of juvenile sockeye salmon growth and body condition to differences across habitats and multiple scales of climate variability. Ultimately, I hope to provide insights into the sensitivity of salmon habitat and growth to climate change and geomorphic evolution and the potential of diverse habitat to buffer freshwater salmon production.

Study System

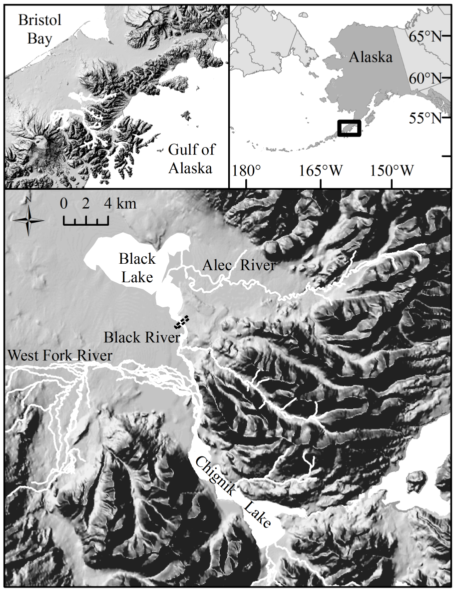

Figure I.1: Chignik watershed, Alaska

The Chignik Watershed (Figure I.1) is a system well suited to study the interaction between climate change and rapid geomorphic evolution. In the upper watershed, Black Lake is a relatively large (35.7 km^2), shallow (max depth < 4 m), and turbid lake surrounded by low lying topography on the northern side of the Alaskan Peninsula. Black Lake is drained by the Black River which flows into deep and cold Chignik Lake (22 km^2, max depth ~ 60 m). Water exits Chignik Lake via Chignik River and flows into Chignik Lagoon before reaching the Gulf of Alaska. Volcanic and glacial activity was important for the formation and evolution the watershed. The recession of the Late Wisconsin glacial ice-cap 12,000-10,000 years ago (Miller and Smith 1987) left a terminal moraine that forms the northern shore of Black Lake (Knappen 1926). Large, caldera forming eruptions of nearby Mt. Veniaminof approximately 3700 years ago created debris flows exceeding 50 km (Miller and Smith 1987) that was likely important for defining the basin of ancient Black Lake.

The Chignik watershed supports several commercially and recreationally harvested, as well as culturally important, salmonid species including sockeye salmon, Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*). Commercial salmon harvest has occurred in the Chignik region since the late 1800s (Ruggerone 2003). Sockeye salmon comprise the majority of the commercial and subsistence harvest. The early run of the sockeye harvest is primarily composed of fish that spawn in Black Lake tributaries while the second run of the harvest spawn in Chignik Lake tributaries (Narver 1966). Due to the productivity of Black Lake as rearing habitat for sockeye salmon, the juvenile life history strategies of the two populations differ. Black Lake juveniles typically migrate to the ocean after rearing for one year in freshwater, while sockeye rearing in the less productive Chignik system often spend two full years in freshwater (Dalhberg 1968). In comparison to other western Alaska sockeye producing lakes, the Chignik watershed has extremely high primary production and sockeye production for its size (Burgner et al. 1969).

As throughout Alaska (Stafford et al. 2000), the Chignik watershed has experienced significant increases in air temperatures since 1960 with spring (April – June) air temperatures increasing by approximately 1.4°C (Westley 2007). These warming air temperatures are also associated with a shift towards earlier ice breakup as observed in several other southwestern Alaskan lakes (Schindler et al. 2005; The University of Washington Alaska Salmon Program (UW-ASP) unpubl. data). Simultaneously, fluvial geomorphic processes of the West Fork River, Black River, and Alec River have driven rapid evolution of the upper Chignik watershed. The West Fork River drains the glaciers of Mt. Veniaminof carrying high loads of volcanic sands and gravels (Knappen 1926) and deposits the sediment at its confluence with the Black River, the outlet tributary of Black Lake. Historically, this confluence was upstream (north) of its current location and West Fork sediment inputs stabilized an underwater sill maintaining Black Lake storage capacity (Ruggerone 2003, Elhakeem and Papanicolaou 2008). Downstream migration of the West Fork and bed erosion in the Black River channel has resulted in a two meter drop in lake level and a 40% loss of Black Lake volume since 1960 (Ruggerone 2003, Elhakeem and Papanicolaou 2008).

Additionally, there have been substantial migrations of Black Lake's primary inlet tributary, the Alec River. The Alec River is a snowmelt and groundwater fed river draining the watershed east of Black Lake. In the 1960s the North channel directed the majority of Alec River volume into the main lake body. Currently, the South channel carries 50 – 70% (Ruggerone 2003; UW-ASP unpubl. data) of the water volume to a bay at the lake outlet and a permanent sand spit has developed between the outlet bay and main lake. With continued migration of the South channel the Alec River may eventually bypass Black Lake and connect directly with the Black River, depriving the lake of its main water source. The continued erosion in Black River coupled with Alec River channel migration is predicted to cause a loss of 80% of the 1960s storage capacity by ~2100 (Elhakeem and Papanicolaou 2008).

Chapter Overview

Chapter 1: How stock of origin affects performance of individuals across a meta-ecosystem: an example from sockeye salmon

In this chapter I looked across the entire watershed to ask how diverse lake habitat affected juvenile sockeye body condition by stock group. Connectivity among diverse habitats is expected to buffer individual populations (or stocks) from environmental variability by providing alternative habitat that may respond differently to regional climate condition or offer different trade-offs between food availability and growth. However, with multiple populations of the same species within a habitat network, it can be difficult to assess habitat use of different populations and the characteristics of individuals within a population that use alternative habitats. The fine scale differentiation of sockeye salmon stock groups in the Chignik watershed, however, allowed me to use genetic markers (single nucleotide polymorphisms) to identify individuals to their stock group of origin.

I found that the individuals of Black Lake origin rearing in Black Lake had substantially higher body condition than the Chignik Lake origin individuals rearing in Chignik Lake. However, the Black Lake origin individuals who emigrated downstream to rear in Chignik Lake were of much lower body condition than Black Lake residents. And, in fact, their condition was indistinguishable from the Chignik Lake origin individuals. These Black Lake emigrants also make up a substantial, although variable proportion, of the juvenile sockeye salmon rearing in Chignik Lake by the end of summer. Clearly connectivity among diverse habitats is used by Black Lake origin juveniles although Black Lake produces individuals that allocate energy to mass accumulation much earlier or at greater rates than Chignik Lake. However, if Black Lake becomes increasing inhospitable, connectivity to Chignik Lake will likely be essential for an increasingly large fraction of the Black Lake population.

Chapter 2: Climate variation is filtered differently among lakes to influence freshwater growth of juvenile sockeye salmon in an Alaskan watershed

Within and across watersheds, we know that the population sockeye salmon exhibit asynchronous population dynamics in response to regional climate forcing (Hilborn et al. 2003, Rogers and Schindler 2008). However, we have yet to quantify how landscape filtering of regional climate leads to differences in survival and therefore differences in sockeye salmon population dynamics. Juvenile growth provides a measure of habitat quality which can be used to assess an integrated response of individuals to climate across heterogeneous habitats and incorporates both direct physical responses to climate (e.g. metabolism) as well as indirect effects (e.g. on prey species). Growth plays an important role in determining the duration of freshwater rearing (Groot and Margolis 1991) as well as overwinter (Quinn and Peterson 1996, Ebersole et al. 2006) and marine survival (Koenings et al. 1993). Also, we know that between watersheds, juvenile sockeye salmon rearing in lakes with different morphologies differ in their growth response to low and high frequency climate variation (Schindler et al. 2005, Rich et al. 2009). However, whether climate variation is differentially filtered by lakes within the same watershed remains unknown. I used two long-term datasets to assess stock-specific freshwater growth sensitivity to high and low frequency climate variation in the Chignik watershed.

Using 40 years of scale records, I found that age-0 growth juvenile sockeye salmon has been increasing over time. Both stocks showed a positive growth response to the Pacific Decadal Oscillation and winter air temperature, as well as overall positive trends in growth over time. While Chignik Lake age-0 responded positively to increases in spring and fall air temperatures, however, Black Lake age-0 growth had a negative response, especially to fall air temperatures. These results were based upon data collected from returning adult salmon and therefore are a small fraction of the individuals which survive the first growing season. Therefore, we might expect that if we look at the growth of juvenile salmon at the end of the first growing season, we may see how environmental conditions affect growth without the confounding effects of marine survival. When we assessed Black Lake age-0 summer growth using a 30-year dataset of juvenile lengths, we found that spring air temperature was positively related to juvenile length while density showed a weak inverse relationship to length. And, overall, the length of juvenile salmon that have reared in Black Lake for an entire summer has increased over time. These fish represent some fraction of the individuals of Black Lake origin because not all individuals rear in Black Lake for an entire summer (Westley et al. 2008, Simmons et al. 2012). While it appears that different lake habitats filter climate differently and consequently alter the outcomes of juvenile sockeye growth, our observations of growth sensitivity to climate depend upon the period of observation and subsequent life history events.

Chapter 3: Effects of simultaneous climate change and geomorphic evolution on thermal characteristics of a shallow Alaskan lake

In this chapter, I focused on how the physical lake environment responds to both climate change, rapid geomorphic evolution and their interaction. Specifically, lake thermal characteristics were the focus of these analyses because they are known to be highly sensitive to climate change and are critical determinants of sockeye salmon growth. Using a one-dimensional hydrodynamics model (DYRESM; Imberger and Patterson 1981), I assessed the sensitivity of Black Lake thermal regimes to air temperature, changes in lake volume, and the connectivity of the Alec River (inlet tributary). Current air temperatures were contrasted with air temperatures from the early 1970s during which we know that juvenile sockeye salmon habitat use and their summer emigration patterns were substantially different from the present (Westley et al. 2008). Lake volume was explored to understand both how past volume affected lake temperature, the potential for restoration actions to alter lake temperature patterns, and the consequences of continued geomorphic evolution. Last, I considered hydrologic connectivity of the inlet tributary at three levels with scenarios if current or decreased lake volume. The analyses from this chapter showed that increasing Black Lake volume through increasing lake level does not alter lake thermal regimes. Thermal regimes in this shallow lake are highly sensitive to air temperature and this response is not mediated by increased lake volume. Lake residence times are relatively rapid and these decrease rapidly with further declines in lake volume. Interacting changes in volume and tributary connectivity do alter lake thermal regimes, especially under shallowing conditions. This also amplifies the effects of air temperature on lake thermal regimes. Overall, we conclude that restoration efforts will not alter lake thermal conditions for juvenile sockeye salmon in Black Lake and that air temperatures remain a clear driver of the physical environment.

Chapter 4: Consequences of changing climate and geomorphology for bioenergetics of juvenile sockeye salmon in a shallow Alaskan lake

In this chapter, I built upon the work in Chapter 3 to translate changes in thermal regimes into bioenergetics consequences for juvenile sockeye salmon. First, I used the hydrodynamics model to forecast the effects of a 2°C increase in summer air temperatures on lake thermal regimes across all volume and tributary connectivity scenarios. Then, using the Wisconsin bioenergetics model (Hanson et al. 1997), I assessed the relative magnitude of air temperature, volume, and tributary connectivity thermal effects on the metabolic costs of Black Lake juvenile sockeye salmon.

An increase in juvenile sockeye salmon metabolic rates is expected when water temperatures warm. Under current air temperature scenarios, metabolic rates increased as tributary connectivity decreased. However, faster water residence times under the volume decline scenario actually decreased metabolic rates. The scenario restoring lake volume to historic levels had little effect on metabolic rates. Increases in air temperature did not have a large effect on metabolic rates via the increase in water temperature and this effect was not mitigated by increased lake volume. However, if volume declined and tributary inputs remained high, some of these costs were offset. Consumption rates are also responsive to increases in water temperature and they have the potential to offset some costs associates with tributary connectivity. However, they could not completely offset increased metabolic costs caused by increased metabolic costs. We conclude that the thermal regime changes during the summer growing season that may occur with future increases in air temperature would be sufficient to reduce the scope for growth of juvenile sockeye salmon. The current proportion of maximum consumption sustained by juvenile sockeye salmon would be insufficient to offset metabolic costs. Also, tributary connectivity has a greater effect on juvenile salmon growth than restoration of lake volume.

Looking forward

Understanding the ecosystem characteristics and processes that affect the resilience of salmon populations, the reliability of the ecosystem processes they support, and services they provide is critical to the management of salmon in the face of ongoing climate change.

I found that in a single watershed, lakes with contrasting physical characteristics and evolving on different geomorphic scales offer very different rearing environments for juvenile sockeye salmon. While currently Black Lake produces juvenile sockeye salmon of substantially higher body condition, it is only able to provide rearing habitat for a subset of individuals produced by its spawning populations. Connectivity to Chignik Lake, however, provides alternative rearing habitat for unsuccessful Black Lake individuals. While fish rearing in Chignik Lake are of lower body condition than Black Lake rearing individuals, historic time-series indicate that growth in Chignik Lake has been increasing over time and responds positively to increases in seasonal temperatures. The increases in Chignik Lake growth associated with increases in air temperature indicate that perhaps the capacity of Chignik Lake to support juvenile salmon is improving over time.

Furthermore, it has been pointed out that restoration actions that do not account for changing climate may be ineffective (Battin et al. 2007). Additionally, however, the interaction between changing climate and rapid geomorphic evolution and how this alters climate filtering for biota is an important consideration in dynamic landscapes. The results of this dissertation suggest that in Black Lake, the loss of lake volume has been less important than increasing air temperature on lake thermal characteristics. However, the interaction between future changes in air temperature, tributary connectivity, and volume present a wide range of very different thermal options, and consequently growth potential, for juvenile sockeye salmon.

Because uncertainty exists in how freshwater ecosystems will respond to climate change preserving networks of heterogeneous habitat may be critical to supporting ecosystem resilience. Certainly for mobile organisms such as salmon, maintaining these networks offers individuals the opportunity to navigate the trade-offs in resource quality, predation risk, and growth potential (e.g. Armstrong et al. In review) and these effects can scale up to the population level (Hamann and Kennedy 2012). Intact ecosystems provide an opportunity to evaluate the relative importance of climate, geomorphology and connectivity for salmon populations and inform the management and restoration of habitat impacted landscapes.

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Chapter 1: How stock of origin affects performance of individuals across a meta-ecosystem: an example from sockeye salmon

Introduction

There is increasing appreciation for how habitat complexity (including variation in geomorphic, chemical, and thermal properties) can buffer ecosystem function and the reliability of ecosystem services by promoting species and population diversity (Luck et al. 2003). Ecosystems filter external climate forces differently such that they may offer higher or lower quality habitat depending on prevailing climate conditions. Over time, habitat conditions may vary inversely with one another producing a temporally variable mosaic of habitat quality on the landscape (Stanford et al. 2005). The mosaic of habitats on the landscape is not necessarily composed of discrete ecosystems but instead represents a network of heterogeneous habitats that can be conceptualized as a meta-ecosystem with movement of organisms, materials, and energy among component systems (sensu Loreau et al. 2003). Biological elements of the ecosystem respond to this heterogeneity, producing spatially variable species or population dynamics (Ringsby et al. 2002; Rogers and Schindler 2008) and life history diversity (Beechie et al. 2006). Asynchronous productivity results in more stable aggregated dynamics than that of any individual species or population over time (Hilborn et al. 2003) and so too are the derived ecosystem properties (e.g. ecosystem productivity, Yachi and Loreau 1999) and services (e.g. fisheries, Schindler et al. 2010).

The availability of variation in habitat conditions not only facilitates the persistence of distinct populations but can also buffer a single population from environmental variability (Stenseth 1980; Chesson 2000). For example, butterflies in Britain show more stable population dynamics in landscapes with a broader suite of habitat types and topographic heterogeneity

(Oliver et al. 2010). In order for populations to benefit from habitat heterogeneity, these habitats must be connected such that individuals are able to move among them (Crooks and Sanjayan 2006). Population dependence on different habitats is often associated with migratory species that make feeding, breeding, or overwintering migrations over large distances (described by Dingle 1996). Alternatively, connectivity among habitats types at small spatial and temporal scales allows individuals to move in order to negotiate short-term tradeoffs between food quantity and quality, density, optimal environmental conditions, and exposure to predation (Werner and Gilliam 1984; Schlosser 1991). Life history diversity within a population can lead to the phenomena of partial migration (reviewed by Chapman et al. 2011) such that not all individuals move among alternative habitats. The relative proportion of migrants within a population over time may be reflective of the variation in relative habitat quality with higher migration rates with greater differences in quality (Naslund et al. 1993) or environmental thresholds (Brodersen et al. 2011).

Anadromous Pacific salmon (*Oncorhynchus spp.*) are well known for their large scale migrations between freshwater spawning and rearing habitats and marine feeding habitat. Connectivity between the ocean and freshwater habitat, sometimes thousands of kilometers inland, is necessary for these species to complete their lifecycle. Anthropogenic activities, including dams, irrigation, urbanization, and logging, have threatened connectivity among these ecosystems in many regions (Nehlsen et al. 1991). However, during the freshwater rearing stage, connectivity at finer scales is also important for juvenile salmon to negotiate growth and survival trade-offs. In this context, salmon capitalize on heterogeneous habitat within a single lake or river system through population or individual movement. Population movements may indicate a seasonal change in productivity among habitats such as offshore movement by juvenile sockeye salmon (*O. nerka*, Quinn 2005) or a balance between feeding opportunity, thermal conditions, and predator avoidance (e.g. diel vertical migration, Clark and Levy 1988; Scheuerell and Schindler 2003).

Alternative movement strategies in salmon populations are common, with some individuals in the population occupying a single habitat during a life-stage while other individuals move among alternative habitats in response to habitat quality (Kahler et al. 2001). Habitats may also offer tradeoffs between high resource quality and profitable abiotic conditions (e.g., temperature). Coho salmon (*O. kisutch*), for example, that exploit both habitats grow faster than individuals that do not move among habitats (Armstrong et al. In review).

In freshwater, juvenile salmon can not only exploit heterogeneous habitat within a single lake or stream but throughout watersheds. Some coho salmon exhibit an alternative strategy in which individuals migrate downstream into estuaries in their first year of life and then return upstream to overwinter in freshwater (Koski 2009). Similarly, juvenile steelhead (*O. mykiss*) have been shown to exploit estuarine connectivity during freshwater rearing without continued migration to the ocean within the same year (Hayes et al. 2011). Sockeye salmon also exhibit inter-lake migrations from high to low density lakes (Burgner 1987) or among lakes with very different abiotic conditions (Westley et al. 2008).

The attributes of movers in salmonid populations and the ultimate consequences for those individuals and their populations are context dependent. A variety of factors may influence an individual's propensity to migrate including competition, food availability, and population density (Chapman et al. 2011) which may be reflected in their physical characteristics such as size or body condition. In some systems it appears that while movers and residents do not exhibit initial differences in physical condition, movers have higher growth rates upon moving to alternative habitats (Kahler et al. 2001). In other systems, individuals that become emigrants may be of lower or higher condition than residents depending on the environmental conditions in a given year (Westley et al. 2008).

Assessing the success of movers versus residents poses a challenge when individuals of one population immigrate into new habitats that are already occupied by a different population of the same species. This is likely to happen when migrants exploit habitat connectivity at the watershed scale. Furthermore, movers could have direct or indirect effects on the resident individuals in their new habitat which again requires the identification of individuals to their population of origin. Population structure is often cryptic and only detectable with genetics or intensive tagging studies (Carvalho and Hauser 1994). Genetic tools can provide a useful and less time-consuming alternative to tagging studies, particularly for large systems with high organism densities where recapture rates are low. Genetic techniques are particularly well-developed for Pacific salmon (Utter and Ryman 1993; Seeb et al. 2011a) due to substantial interest in population-level management at both the state and federal level. Furthermore, because of strong natal homing by spawning adults (Quinn et al. 2006), salmon populations are highly differentiated at relatively fine spatial scales (Hendry and Stearns 2004; Creelman et al. 2011; Mcglauflin et al. 2011). Specifically, single nucleotide polymorphisms (SNPs) have become a common and robust tool to allocate Pacific salmon of unknown origin to known spawning populations (Narum et al. 2008; Seeb et al. 2011b).

The Chignik watershed on the Alaska Peninsula provides the opportunity to investigate the performance among alternative rearing strategies in a sockeye salmon meta-ecosystem. Freshwater life histories of sockeye salmon have historically differed between natal lakes in this watershed. Juveniles from Black Lake in the upper watershed spend one year in freshwater and individuals from Chignik Lake in the lower watershed spend two years in freshwater, reflecting the thermal conditions and relative productivity between the two lakes (Narver 1966). Downstream emigrations by a proportion of Black Lake juvenile sockeye salmon population to Chignik Lake appear to be common in this meta-ecosystem, however (Narver 1966; Ruggerone 1994; Westley et al. 2008). Mid-summer juvenile emigrations are only in the downstream direction, and Black Lake juvenile sockeye salmon emigrants spend the remaining portion of their freshwater residence in non-natal habitat. In recent decades, median emigration dates range from mid-June to mid-July with the majority of the emigration concluded by the end of July (Westley et al. 2008). Furthermore, downstream emigrants (captured downstream of the lake outlet) have a lower body condition than fish that remain in Black Lake throughout the summer (Westley et al. 2008).

Once these emigrants enter Chignik Lake, however, their performance in non-natal habitat is unknown. Furthermore, because fish sampled in Chignik Lake cannot be visually identified to stock, characterizing the body condition and growth of Chignik Lake stocks has been historically limited to scale pattern analysis. Recently, SNPs have been used in the Chignik watershed to assess stock specific characteristics in a common rearing environment during a single summer (2008, Simmons et al. 2012). Simmons et al. (2012) found that a substantial fraction of the juvenile sockeye salmon rearing in Chignik Lake in mid-July were of Black Lake origin ,33%, which increased to 46% at the end of August. This study was able to compare the performance of individuals among habitats for a subset of the individuals sampled, but 45 SNP markers were only able to robustly assign 40% of the individuals captured.

Here we build upon the work of previous studies and use the fine scale differentiation of salmon populations among diverse lake habitats on the Alaska Peninsula to assess how rearing habitat and stock of origin affect the body condition of juvenile sockeye salmon. We were able to robustly assign individuals of unknown origin to stock groups using a greater number of SNPs than previously available and in turn characterize ecologically relevant attributes across habitats and stocks. We addressed the following questions. 1) How variable is the stock composition of juvenile sockeye salmon in a common rearing environment (Chignik Lake) among years? 2) Does habitat quality differ among lakes as expressed by juvenile sockeye salmon body condition? 3) Is emigration from warm (Black Lake) to cold (Chignik Lake) summer habitat linked to body condition?

Methods

Study site

In the Chignik watershed, Alaska Peninsula, USA (Figure 1), sockeye salmon (*O. nerka*) are the numerically dominant anadromous species and support a valuable commercial fishery (average annual harvest 1.7 million since 1977, data from the Alaska Department of Fish and Game (ADFG)) and a local subsistence harvest. Sockeye salmon spawn in tributaries to both Black and Chignik lakes, rear in freshwater for 1-2 years, migrate to the ocean for 3 years on average, and then return to natal streams and lake beaches to spawn. The number of spawners (escapement) is tightly controlled by ADFG and was relatively constant during our study years. The escapement for the Black Lake stock was 391,474 in 2009 and 432,535 in 2010. In Chignik Lake, juvenile sockeye captured may be age-0 or age-1. Escapements producing the juvenile sockeye we sampled were 328,479 (2008), 328,586 (2009), and 310,634 (2010).

The attributes of rearing habitat for juvenile sockeye salmon in the Chignik watershed are diverse. Shallow Black Lake (4 m max. depth) is a warm, turbid, and productive lake in the upper watershed. Black Lake is also experiencing geomorphic evolution on ecological time scales and has lost ~40% of its volume since 1960 (Ruggerone 2003). In contrast, deep and cold Chignik Lake (60 m max. depth) downstream has maintained a stable volume over recent decades. Differences in sensitivity to air temperature reflect the geomorphic differences between the lakes. In our sample years, mean daily July and August surface water temperatures in Chignik Lake were 10.8°C (2010) and 10.7°C (2011) while in Black Lake they were 13.1°C (2010) and 12.6°C (2011). Furthermore, air temperatures have increased 1.4°C on average in the watershed between1960 and 2005 (Westley 2007).

Sample collection 2010-2011

Juvenile sockeye salmon in Chignik and Black lakes were sampled at end of August using townets. In 2010, sample dates were August 25th and August 28th in Chignik Lake and Black Lake, respectively. In 2011, samples were collected on August 24th in Chignik Lake and August 25th in Black Lake. Five sites on Chignik Lake were sampled using a 2m x 2m net, which was pulled at the lake surface between two boats for duration of 10 minutes per set. The same protocol was used to sample five Black Lake sites but a 1.2 m x 1.2 m net was deployed. If samples were large, a known fraction of the catch was retained. Fish were euthanized in a buffered MS222 solution and were returned to the lab for processing. Sockeye salmon were measured to the nearest mm (fork length) and weighed to the 0.1 g. Genetic samples were collected from Chignik Lake by removing the entire caudal fin. Sample tissues were pressed to gridded filter paper and air dried for later DNA extraction. The association between each fish's length, weight, and genetics sample was retained.

Laboratory analysis

A subset of individuals captured in Chignik Lake was genotyped in 2010, and all captured individuals in 2011 were genotyped. In 2010, samples were grouped by lake section, north (2 sites) and south (3 sites), and 285 samples were selected from each. The majority of fish captured were between 61-70 mm in the north and 61-75 mm in the south. Because we believed that length may reflect stock at the tails of the distribution, the samples from all fish ≤ 60 mm and > 70 mm were taken for analysis (n=98) for the northern section. The remaining 187 samples were taken in random draws in proportion to the sample numbers in the remaining two 5-mm length bins. Similarly, in the south area, samples from all fish ≤ 60 mm and > 75mm were retained for analysis (n=48). The remaining 237 samples were taken in random draws in proportion to the sample numbers in the remaining three 5-mm length bins.

Genomic DNA was extracted following standard protocol with Qiagen DNeasy 96 Tissue Kits. Multiplex preamplification PCR was conducted to reduce error and failure rates in case of low concentrations of template DNA (Smith et al. 2011). A 96 SNP panel was assayed using TaqMan reactions as in (Seeb et al. 2009). The 96 SNP panel included 3 mitochondrial SNPs and 93 nuclear SNPs now used in mixed stock analyses by ADFG (T. Dann, personal communication). The Fluidigm Biomark 96.96 was used genotype the samples. For quality control, 8 out of every 95 individuals were reanalyzed to confirm that genotypes were reproducible and identify laboratory errors.

Genetic Analysis

ADFG provided the genotypes for the Chignik watershed baseline populations (T. Dann, personal communication). Monomorphic loci were identified and removed prior to further analyses. We followed the approach of (Creelman et al. 2011) for dealing with loci in linkage disequilibrium (LD). *Tf_ex11-750* was dropped from the LD pair *Tf_ex11-750* and *Tf_in3-182*. In case of the two MHC loci (*MHC2_190* and *MHC2_251*), we treated them as phenotypic characters (Habicht et al. 2010) to retain the information contained by both loci. The three mitochondrial loci were combined into composite haplotypes.

All stock identification analyses were carried out using a Bayesian approach developed by Pella and Masuda (Pella and Masuda 2001) (BAYES). Baseline populations were pooled to 13 populations following Creelman et al. (2011). Five populations belonged to the Black Lake stock group, seven to the Chignik Lake stock group, and one to the Chignik River stock group (geographic extent shown in Figure 1). A uniform prior was used with each pooled baseline population given equal weight and the probabilities summing to one. For each mixture, 3 Monte Carlo Markov chains were run with randomized starting locations. Each chain had a length of 140,000 iterations with every 7th sample retained for a total of 20,000 samples per chain (burn-in 10,000). This level of thinning was determined by the Rafterty-Lewis diagnostic (Raftery and Lewis 1996) across multiple runs. A unique combination of starting stock proportions was used for each chain. Starting proportions of 0.3 were randomly assigned to 3 populations and the remaining 0.1 divided among all other populations.

Mixture allocations

The relative contribution of each stock group to the unknown mixture sample was assessed using mixture allocation. BAYES established posterior densities of mixture proportions at the stock group level (Black Lake, Chignik Lake, Chignik River) for each chain. Convergence of the posterior densities among the chains was verified using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) and visual assessment. A 95% credibility interval, mean, and median stock group proportions were calculated for the combined chains for each mixture. For the 2010 samples we targeted genotypes at the tails of the length distribution to improve our characterization of stock group performance across all lengths. Therefore, using all genotypes in the mixture allocation may bias our stock composition estimates. Instead, we based our mixture allocation on the 61-75mm fish randomly selected for genotyping from the south section of the lake (n=237). 94.4% of fish captured in 2010 were in the south section of the lake and 92% of these fish were from 61-75mm in length. Therefore, we believe the stock composition of this random sample best reflects the lake wide composition.

Individual Assignment

The ability to robustly assign individuals to a stock group depends on the number of markers and the level of differentiation among reporting groups. Our ability to assign individuals in the Chignik watershed has increased since past studies have been conducted due to the increase in the number of SNP markers available (96 rather than 45).

We assessed the individual assignment ability of the baseline by conducting tests using mixtures created from individuals from known baseline populations following the methods of Simmons et al. (2012). We randomly selected individuals from the baseline populations to create a test mixture of 200 individuals and generated a new baseline without the selected individuals. The representation of each stock group in the mixture reflected observed mixture allocations to stock group in 2010 and 2011 (25% Black Lake, 75% Chignik Lake). We repeated the randomization process 10 times each time generating test mixtures and baselines with the same stock group proportions. We then used BAYES to assign posterior densities of mixture proportions to stock groups (as above) as well as assign individuals to the 13 populations. For each individual in a test mixture, we summed the population level assignments by stock group. We then assessed the number of individuals assigned to each stock group at assignment thresholds ranging from 50 to 90% (Simmons et al. 2012). At each threshold level, we calculated the error rate by determining the proportion of individuals incorrectly assigned to that stock group. We calculated the mean error rate and standard deviation across all ten test mixtures by threshold and stock group. To determine the threshold to use for further analyses we sought to maximize the number of individuals assigned while minimizing the rate of incorrect assignment.

Assignment of unknown individuals to stock group in 2010 and 2011 was conducted using BAYES as previously discussed. We used the 80% threshold to assign individuals to a reporting group based upon the analyses above. This allowed the use of individual attributes (length, weight, condition) of each fish to define the attributes of each stock group by rearing environment and movement status.

Stock of origin, rearing lake, and body condition statistical models

For individuals assigned to either the Chignik Lake or Black Lake stock as described above, we tested for differences in length between three combinations of stock of origin and location of capture (subscript): natal rearing environment of different stocks (Black Lake$_{\text{Black}}$ and Chignik Lake$_{\text{Chignik}}$); emigrant/resident status of the same stock (Black Lake$_{\text{Chignik}}$ and Black Lake$_{\text{Black}}$); and common rearing environment but different stocks (Black Lake$_{\text{Chignik}}$ and Chignik Lake$_{\text{Chignik}}$). Within the Black Lake$_{\text{Chignik}}$ and Chignik Lake$_{\text{Chignik}}$ comparison, there was a third group, Unknown$_{\text{Chignik}}$, which were the individuals not assigned at the 80% threshold. Given highly unequal sample sizes for most of the comparisons, we first tested for homogeneity of variances using Bartlett's test (Zar 1999). If variances were homoscedastic, we used Analysis of Variance (ANOVA) while if they were heteroscedastic we used the non-parametric Kruskal-Wallis test (Zar 1999).

To explore the differences in the length-mass relationship and the relative body condition of the above pairs, we assessed four alternative regression models to predict fish mass. This approach is consistent with previous work in the watershed (Simmons et al. 2012) and was suggested by Cone (Cone 1989) as the preferred way to evaluate fish condition. In the first model to compare stocks rearing in their natal lake (Black Lake$_{\text{Black}}$ and Chignik Lake$_{\text{Chignik}}$), all individuals (j) belonging to the stock groups (*i*) shared a slope and an intercept relating mass to length. The second model had different intercepts by stock group but the same slope while the third model had the same intercept but different slopes. The final model had different intercepts and slopes for each stock group.

1. $\ln(mass_{ij}) = \beta_0 + \beta_1 \ln\,(length_{ij})$
2. $\ln(mass_{1j}) = \beta_{01} + \beta_1 \ln\,(length_{1j})$; $\ln(mass_{2j}) = \beta_{02} + \beta_1 ln(length_{2j})$
3. $\ln(mass_{1j}) = \beta_0 + \beta_{11} \ln\,(length_{1j})$; $\ln(mass_{2j}) = \beta_0 + \beta_{12} \ln\,(length_{2j})$
4. $\ln(mass_{1j}) = \beta_{01} + \beta_{11} ln(length_{1j})$; $\ln(mass_{2j}) = \beta_{02} + \beta_{12} \ln\,(length_{2j})$

The Black Lake emigrant versus resident comparison (Black Lake$_{\text{Chignik}}$ and Black Lake$_{\text{Black}}$) used the same model approach where individuals were grouped by location of capture instead of stock group. Finally, the shared rearing environment comparison (Black Lake$_{\text{Chignik}}$ and Chignik Lake$_{\text{Chignik}}$) were compared using the same model framework. In these two comparisons samples sizes were unequal because of the few Black Lake origin individuals identified in Chignik Lake.

Models were compared using Akaike Information Criteria for small sample sizes (AICc) (Burnham and Anderson 2002). Additionally AIC weights (w_i) (Burnham and Anderson 2002) were calculated for each model within a comparison. Given the suite of models considered, each w_i is the estimated probability that the given model is the best model for the data.

These analyses included fish that were individually assigned to a reporting group at the 80% level. To test the robustness of our results to the assignment threshold used, we compared our results to those obtained when using a 70% (less conservative) or 90% (more conservative threshold (Table 1.3, Figures 1.6-8). Analyses were conducted using R statistical software (Team 2010) including the package "AICcmodavg" (Mazerolle 2010)

Results

Sample collection 2010-2011

In Chignik Lake, 1000 juvenile sockeye salmon were sampled for length, mass, and fin clip in 2010 and then later sub-sampled for genotyping. In 2011, catch rates were lower, and all sockeye salmon caught at all sites were retained for later analysis (n = 233). In Black Lake, juvenile sockeye sample sizes were 341 and 770 in 2010 and 2011, respectively.

Laboratory & Genetic Analysis

Five hundred-seventy fish were genotyped from 2010 samples and 233 fish were genotyped from 2011 samples. The assay for the *SUMO1-6* locus failed for all samples and was excluded from the analysis. In 2011 the locus *U1016-115* was also excluded due to assay failure. Two loci were monomorphic (*metA-253, txnip-401*) across the Chignik populations and were not used in further analyses. Additionally, in 2010 two fish were missing genotypes for at least 15% of the loci and were excluded.

Mixture allocations

Here we report the mean of the posterior density distribution for each stock group and the 95% credibility interval. In 2010, Chignik Lake August stock composition (n = 236, estimated only from the randomly selected individuals in the south lake section) was 10.1% (3.1-18.6) from Black Lake$_{\text{Chignik}}$, 89.7% (81.2-96.8) from Chignik Lake$_{\text{Chignik}}$, and 0.1% (0-1.45) from Chignik River$_{\text{Chignik}}$ (Figure 2). In 2011, Chignik Lake August stock composition (n = 233) was 24.9% (16.5-34.1) from Black Lake$_{\text{Chignik}}$, 74.5% (64.9-83.1) from Chignik Lake$_{\text{Chignik}}$, and 0% (0-.05) from Chignik River$_{\text{Chignik}}$ (Figure 2).

Individual Assignment

Individual assignment of mixtures comprised of known individuals demonstrated that the 80% threshold assigned a substantially larger number of individuals than the 90% level and still retained low error. At the 80% threshold, on average 75% of the individuals in the mixture were assigned to either Black Lake or Chignik Lake stock groups. The mean error rate for individuals assigned to Black Lake was 11% (SD ±7%) while the Chignik Lake error rate was 4% (SD ±2%). At the 90% threshold, 59% of individuals were successfully assigned to a stock of origin and there was a greater decrease in the proportion of fish assigned to Black Lake as opposed to Chignik Lake. Mean error rates at the 90% threshold were 3% (± 4%) for Black Lake and 3% (±2%) for Chignik Lake.

Overall, we were able to assign 78% and 80% of individuals to a stock group at the 80% threshold for 2010 and 2011, respectively (Table 1). The majority of individually assigned fish were from the Chignik Lake stock due to their numerical dominance in the mixtures in both years. Of the 568 individuals sampled in 2010, 34 were assigned to Black Lake and 416 were assigned to Chignik Lake. In 2011, 31 of 233 individuals were assigned to Black Lake and 150 to Chignik Lake.

Stock of origin, rearing lake, and body condition statistical models

We used the individual assignments at the 80% threshold to assess the length distributions and relative body condition of juvenile sockeye salmon among stocks and rearing lakes. Our analyses show that lake rearing habitat strongly affects juvenile sockeye salmon body condition. Differences in body condition differentiated emigrant (low condition) versus resident (high condition) individuals within a single stock group (i.e., from Black Lake). Despite emigrants originating from the more productive lake, they did not differ in body condition from the individuals originating the lower productivity, recipient habitat. While populations exploit diverse habitats, these habitats differ in productivity, and emigration may not improve attributes such as body condition.

Black Lake$_{Black}$ and Chignik Lake$_{Chignik}$

In both years, there were significant differences in length between stocks rearing in their natal lakes (2010: df = 1, K-W χ^2=89.4743, p = 2.2 x10^{-16}; 2011: df = 1, K-W χ^2=134.0431, p = 2.2 x10^{-16}). In 2010, stocks rearing in Black Lake$_{\text{Black}}$ were longer ($\bar{x}$=69.7 mm, sd=5.4) than Chignik Lake$_{\text{Chignik}}$ ($\bar{x}$=65.1mm, sd=7.9), however the reverse was true in 2011 (Black Lake$_{\text{Black}}$:$\bar{x}$=64.0mm, sd=5.4; Chignik Lake$_{\text{Chignik}}$:$\bar{x}$=70.5mm, sd=8.2).

There were clear differences in body condition among individuals rearing in their natal lakes. Black Lake$_{\text{Black}}$ individuals were of higher body condition in both 2010 and 2011 than Chignik Lake$_{\text{Chignik}}$ individuals (Figure 3). In 2010, there was strong support for the different slope and intercept model (w_i = 1.00). This is probably because the Black Lake$_{\text{Black}}$ individuals had a much narrower length range than Chignik Lake$_{\text{Chignik}}$ individuals and small Chignik Lake$_{\text{Chignik}}$ individuals were of very low condition. In 2011, the support was strongest for a different intercept and same slope model, but there was also similar support for models with either different slopes or different intercepts (Table 2).

Black Lake$_{Chignik}$ and Black Lake$_{Black}$

In 2010 there was a significant difference in length between Black Lake emigrants and residents, Black Lake$_{\text{Chignik}}$ and Black Lake$_{\text{Black}}$ (df = 1, Kruskal-Wallis (K-W) χ^2=12.0891, p=0.005) in which Black Lake$_{\text{Black}}$ were longer than Black Lake individuals caught in Chignik Lake (Black Lake$_{\text{Chignik}}$; $\bar{x}$=64.2mm, sd=9.5). No difference in length was detected among emigrants and residents in 2011 (Black Lake$_{\text{Chignik}}$; $\bar{x}$=65.2mm, sd=7.7).

In both 2010 and 2011, Black Lake$_{\text{Chignik}}$ individuals were of lower body condition than Black Lake$_{\text{Black}}$ individuals (Figure 4). In 2010, there was strong model selection support for a model with different intercepts and slopes ($w_i = 0.75$) likely driven by the low body condition of smaller Black Lake$_{\text{Chignik}}$ sockeye. In 2011, there was no support for the null model but relatively similar support for the other three models (Table 2).

Black Lake$_{Chignik}$ and Chignik Lake$_{Chignik}$

We found significant differences in 2011 among-group lengths (ANOVA, df= 230, F = 7.1867, p = 0.001) but not in 2010 (ANOVA, df= 565, F = 0.4104, p = 0.66331) (mean lengths provided in above sections). A Tukey test for multiple comparisons indicated that in 2011 Black Lake$_{\text{Chignik}}$ were significantly smaller than Chignik Lake$_{\text{Chignik}}$ (p = 0.004) but there were not significant differences between either group of known origin and Unknown$_{\text{Chignik}}$.

In 2010 there was strong support for a model describing the relationship between length and mass with different slopes and intercepts by natal origin (Table 2). Small Black Lake$_{\text{Chignik}}$ sockeye salmon had a higher body condition than small Chignik Lake$_{\text{Chignik}}$ sockeye salmon (Figure 5). As length increased, however, Chignik Lake$_{\text{Chignik}}$ sockeye increased in mass more rapidly than Black Lake$_{\text{Chignik}}$. In 2011, there was little visual difference between stocks in their body condition and no model showed substantially stronger support than the shared slope and intercept model (Table 2).

Discussion

Our mixture analyses showed that juvenile sockeye salmon spawned in Black Lake tributaries made up a substantial but variable proportion of the fish that were rearing in Chignik Lake by the end of the growing season when compared to a survey from 2008 (Simmons et al. 2012). Using individual genetic assignment to stock of origin, we characterized the body condition of juvenile sockeye salmon residents in their natal lakes as well as those that immigrated to new habitat. Individuals from Black Lake that were rearing in their natal habitat were in substantially better body condition than Chignik Lake fish rearing in their natal, less productive habitat. Juvenile sockeye salmon that emigrated from Black Lake to Chignik Lake tended to have lower body condition near the end of their first growing season than individuals that stayed in their natal Black Lake habitat. Finally, within the common rearing environment of Chignik Lake, fish of Black Lake and Chignik Lake origin had similar body conditions, and the subtle differences detected were size-dependent in the year they were statistically significant.

Residency in productive, warm Black Lake led to highest body condition for juvenile sockeye salmon observed throughout the Chignik watershed. This result likely reflects the differences in ecosystem productivity between Black Lake and Chignik Lake. Further, high body condition of fish rearing in Black Lake may indicate that successful Black Lake residents are able to achieve critical length thresholds earlier in the season and switch to an energy allocation strategy that favors overwinter survival by allocating more energy to storage rather than further growth in length (Biro et al. 2005). Mean length comparisons between Black Lake residents and Chignik Lake residents produced opposite patterns in 2010 and 2011. We think this is likely caused by changes in the Chignik Lake age composition (relative proportions of age-0 and age-1) rather than by differences in lake productivity among years.

Poorer body condition emigrants from Black Lake were always present in Chignik Lake but made up a variable proportion of the juvenile sockeye salmon. While credibility intervals show a slight overlap between 2010 (Black = 3.1-18.6%) and 2011 (Black = 16.5-34.1%) these proportions are quite different from those observed in August 2008 (Black = 37-56%). Westley et al. (2008) showed that Black Lake emigrants were of lower body condition when departing

Black Lake in early to mid-summer than Black Lake residents. We show that these individuals continue to have lower body conditions in alternative rearing habitat. Given the emigration timing reported for recent decades (Westley et al. 2008) as well as the substantial fraction of emigrants observed in Chignik Lake in July by Simmons et al. (2012), we believe that emigrants have likely spent a month rearing in Chignik Lake and that their body condition is reflective of Chignik Lake growth conditions. Their convergence on Chignik Lake growth potential is also reflected in the shared body condition with Chignik Lake residents in the common rearing environment in 2010 and 2011(consistent with Simmons et al. 2012).

Interestingly, while earlier observations of poor condition Black Lake emigrants occurred during the extremely warm summers of 2005 and 2006 (Westley et al. 2008), we show that this also occurs during more average climate conditions. Mean Black Lake temperature from June 12 - August 26 was 12.6°C and 12.1°C in 2010 and 2011, respectively, and the maximum temperature was 15°C. These temperatures were substantially cooler than when poor body condition emigrants were observed in 2005 and 2006. In those years, the mean water temperatures over the same period were 14.1°C and 12.4°C with maximum temperatures reaching over 17°C in both years. If sockeye salmon are feeding at maximum consumption, the optimal temperature for growth is 15°C (Brett 1971); however, if food is limited optimal growth temperatures are lower. Therefore, the coolest temperatures of the last decade may be at optimal growing conditions in Black Lake while the warmest years are likely sub-optimal for much of the population.

However, our results indicate that conditions are limiting for growth in Black Lake for at least a fraction of the population in Black Lake even during cool summers. For these individuals, emigrating downstream may offer benefits even though growth potential in Chignik

Lake is lower. These cooler temperatures in Chignik Lake, although reducing the scope for growth, may also reduce metabolic stress potentially improving survival. A longer growing period in fall due to Chignik Lake's large thermal mass may also provide growth opportunities unavailable in Black Lake in the fall. Finally, it is unclear whether Black Lake emigrants ultimately show differences in freshwater rearing duration. Given little differences in length with Chignik Lake individuals (some of which are age-1), Black Lake emigrants may achieve sufficient length to smolt in the following spring or they may rear an additional year in freshwater. The relationship between condition of downstream emigrants and the duration of freshwater rearing could be important for quantifying the importance of emigration for survival. Based on ADFG brood tables, however, there appears to be no large scale shifts in Black Lake freshwater age composition seen in returning adult sockeye.

The proportion of juvenile sockeye of Black Lake origin in Chignik Lake is a function of both the downstream emigration rate and the production of sockeye salmon in Chignik Lake. With only three years of observation our inferences about what causes variation in the contribution of Black Lake fish to the juvenile population in Chignik Lake are limited. We found no relationship between the proportion of Black Lake juvenile sockeye in Chignik Lake and either Black Lake temperature or the ratio of Black Lake to Chignik Lake adult spawners in the previous year. One hypothesis is that in warm years Black Lake is more stressful (Griffiths and Schindler 2012) which increases the downstream emigration rate. Similarly, greater competition during years of high densities in Black Lake could lead to increased emigration downstream. Temperature variation was very low between our study years and 2008, as was the adult escapement in the preceding years, however. In Chignik Lake, newly emerged fry are particularly susceptible to predation by coho salmon (Ruggerone and Rogers 1992) and variation in predation pressure among years could alter late season stock composition in Chignik Lake. Furthermore, while sockeye dominate the pelagic fish community in Chignik Lake, the community composition has become less sockeye dominant in recent decades (Westley et al. 2010) and this could alter interspecific interactions and the opportunities for growth by Chignik Lake populations. Given the two year duration of freshwater rearing for Chignik Lake stocks, changes in predation or competition may affect the age composition and stock composition in Chignik Lake in subsequent years.

Our ability to make inferences about the attributes of a stock group depends on the success of our individual assignment. While we successfully assigned 78-80% of the individuals in our sample at an 80% probability threshold, there may be some underlying bias in the subsequent analyses based upon the individuals we were able to assign. A review of our known mixture error rate tests, however, showed that there were not differences among populations in the likelihood of not being assigned at the 80% probability threshold.

Additionally, we must be cautious when comparing mixture allocations generated using different numbers of genetic markers. In this case, differences among the proportion of Black Lake individuals observed in 2008 using 45 SNP markers and the proportions observed in 2010 and 2011 using 96 SNP markers may not be directly comparable. Instead, differences may be exacerbated or dampened by different levels of stock group differentiation between marker sets as well as the different genotypes that may be present in sample among years. We would expect that this would affect the mean estimates more than the credibility intervals.

The identification of individuals to populations of origin is essential to our ability to assess the role of migration and habitat connectivity across multiple scales of ecological organization. Emerging genetic tools offer a robust approach for investigating the presence and attributes of multiple populations within a meta-ecosystem. For species or regions where tagging studies face many logistical challenges, genetic markers provide an alternative approach that is relatively economical and efficient at tracking the stock identities of mixed-stock populations.

The consequences of movement and emigration for individuals, populations, and ecosystems can be profound. Moving to new habitat may improve growth rates over similar sized individuals (Kahler et al. 2001) or allow inferior competitors the opportunity to improve growth rates (Naslund et al. 1993). Assessing the effects of alternative movement strategies on individual condition is a first step to evaluating the fitness consequences of these strategies. As habitats vary in their productivity among years, rates of migration among habitats may vary as well as the contribution of migratory individuals to population productivity (Naslund et al. 1993; Brodersen et al. 2011). Migration or movement at one life stage may also alter the probability of later life history outcomes. For example, Hamann and Kennedy (2012) found that juvenile Chinook salmon dispersal was related to the probability that adults would spawn in non-natal habitats. At the population level, this could affect the relative differences among populations and their adaptive fitness as well as the size of the reproductive population. Ultimately, the movement of individuals among connected habitats may drive the function and properties of meta-ecosystems by influencing trophic pathways (Brodersen et al. 2011) or the flux of materials among systems and in turn creating a feedback to the success of individuals and populations.

Our results highlight the importance of connectivity among the habitats that comprise a meta-ecosystem for juvenile salmonids. In the Chignik watershed, it has become apparent that Black Lake, while a more productive habitat than downstream Chignik Lake, can become unfavorable for juvenile sockeye salmon as the growing season progresses (Griffiths et al. 2011; Griffiths and Schindler 2012); this effect is particularly pronounced when lake temperatures are warmer than average (Westley et al. 2008). Biologically compromised individuals tend to be the ones that emigrate from Black Lake (Westley et al. 2008) but their performance downstream has never been established (with the exception of Simmons et al. 2012). Our application of modern genetics tools enabled us to assess the performance of these emigrants in new habitats. The development of landscape genetics (Manel et al. 2003) has mostly focused on how the physical dimensions of landscapes affects microevolutionary processes. However, this study is one example where landscape genetics shed new perspectives on ecological processes such as migration and condition of migrating individuals. Only by understanding how individuals respond to diverse landscapes can we scale up to understanding the relative importance of different configurations of habitat networks to populations and ecosystems. Combining landscape genetics with meta-ecosystem perspectives will likely be a powerful approach for developing effective strategies for protecting and restoring habitats and their connectivity. It is becoming increasingly recognized that the connectivity of diverse habitats is important for maintaining resilient populations and the variety of ecosystem services and products they provide to people.

Table 1.1: Individual Assignment. The proportion of the sample in each year assigned to each stock group at the 80% probability threshold.

Year	Black Lake	Chignik Lake	Chignik River	Not Assigned
2010	0.06	0.73	0.00	0.20
2011	0.13	0.64	0.00	0.22

Table 1.2: Comparison of alternative condition factor models. Models include: the same slope and intercept for each factor (B_0, B_1); different intercepts and the same slope by factor (B_{01}& B_{02}, B_1); same slope but different intercepts by factor (B_0; B_{11} & B_{12}); and a different slope and intercept by factor (B_{01} & B_{02}; B_{11} & B_{12}). The ΔAICc value and AICc model weight (w_i) are given for each model.

Model	**2010**		**2011**	
	ΔAICc	**w_i**	**ΔAICc**	**w_i**
Black Lake$_{Black}$ and Chignik Lake$_{Chignik}$				
B_0;B_1	278.86	0.00	249.35	0.00
B_{01} & B_{02}; B_1	26.49	0.00	0.00	0.49
B_0; B_{11} & B_{12}	30.29	0.00	0.98	0.30
B_{01} & B_{02}; B_{11} & B_{12}	0.00	1.00	1.68	0.21
Black Lake$_{Black}$ and Black Lake$_{Chignik}$				
B_0;B_1	72.30	0.00	85.92	0.00
B_{01} & B_{02}; B_1	3.05	0.16	0.78	0.28
B_0; B_{11} & B_{12}	4.44	0.08	0.00	0.41
B_{01} & B_{02}; B_{11} & B_{12}	0.00	0.75	0.56	0.31
Black Lake$_{Chignik}$ and Chignik Lake$_{Chignik}$				
B_0;B_1	7.96	0.02	0.93	0.30
B_{01} & B_{02}; B_1	4.71	0.08	2.91	0.11
B_0; B_{11} & B_{12}	5.15	0.06	2.95	0.11
B_{01} & B_{02}; B_{11} & B_{12}	0.00	0.84	0.00	0.48

Table 1.3: Comparison of alternative condition factor models based upon individuals assigned at alternative probability thresholds. Models include: the same slope and intercept for each factor (B_0, B_1); different intercepts and the same slope by factor (B_{01}& B_{02}, B_1); same slope but different intercepts by factor (B_0; B_{11} & B_{12}); and a different slope and intercept by factor (B_{01} & B_{02}; B_{11} & B_{12}). AICc model weights (*w_i*) for each threshold and year are shown for each factor comparison.

Model	**2010 w_i**		**2011 w_i**	
	70% threshold	**90% threshold**	**70% threshold**	**90% threshold**
Black Lake$_{Black}$ & Chignik Lake$_{Chignik}$				
B_0;B_1	0.00	0.00	0.00	0.00
B_{01} & B_{02}; B_1	0.00	0.00	0.48	0.43
B_0; B_{11} & B_{12}	0.00	0.00	0.33	0.41
B_{01} & B_{02}; B_{11} & B_{12}	1.00	1.00	0.19	0.15
Black Lake$_{Black}$ & Black Lake$_{Chignik}$				
B_0;B_1	0.00	0.00	0.00	0.00
B_{01} & B_{02}; B_1	0.13	0.02	0.26	0.33
B_0; B_{11} & B_{12}	0.06	0.01	0.40	0.44
B_{01} & B_{02}; B_{11} & B_{12}	0.82	0.97	0.34	0.23
Black Lake$_{Chignik}$ & Chignik Lake$_{Chignik}$				
B_0;B_1	0.02	0.01	0.29	0.24
B_{01} & B_{02}; B_1	0.06	0.40	0.10	0.26
B_0; B_{11} & B_{12}	0.05	0.34	0.10	0.27
B_{01} & B_{02}; B_{11} & B_{12}	0.87	0.25	0.50	0.22

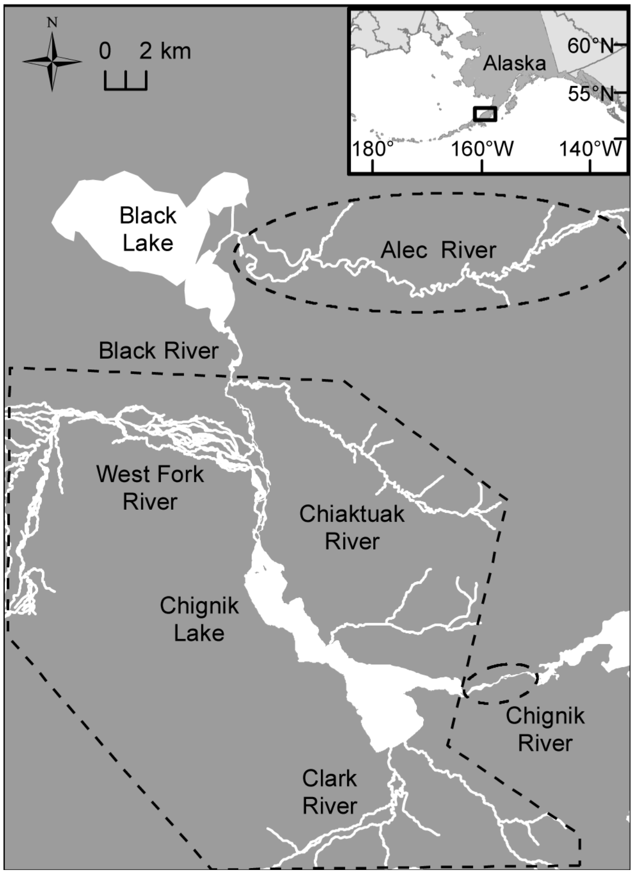

Figure 1.1: Map of the Chignik watershed. The spawning habitat encompassed within each stock group is outline by a dashed polygon. Black River spawning populations occur primarily in the Alec River and adjacent Fan Creek (not shown). Chignik Lake spawning populations include the West Fork and Chiaktuak Rivers, Chignik Lake beaches, Clark River and other minor tributaries. The Chignik River spawning population occurs downstream of the Chignik Lake outlet.

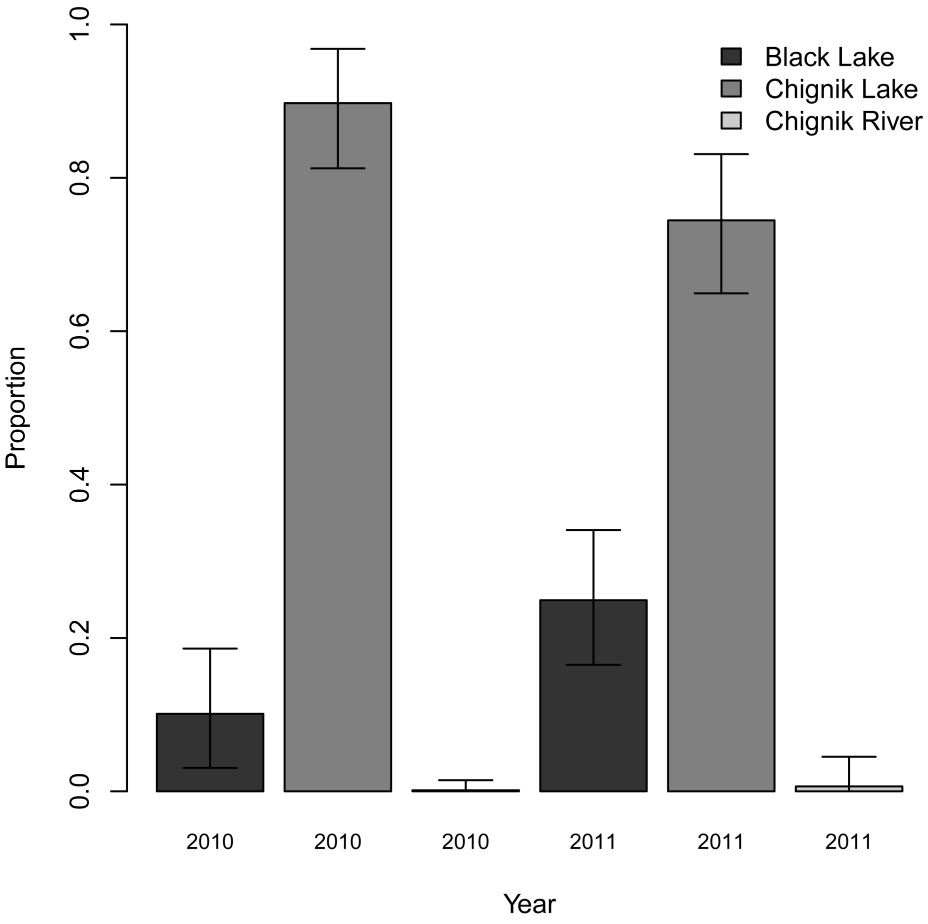

Figure 1.2: Stock group mixture proportions in Chignik Lake in August. The 2010 and 2011 mixture allocation was based on the 96-SNP baseline provided by ADFG. The 2010 mixture composition is based upon the randomly sampled individuals from the south section of the lake that reflected the majority of the catch in 2010 (see Methods for additional details).

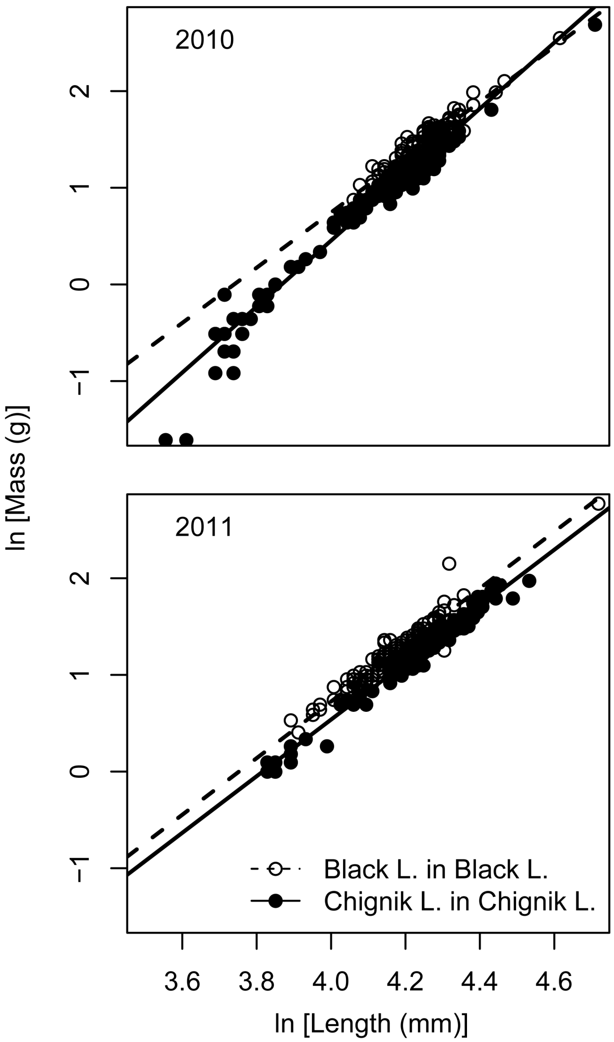

Figure 1.3: Length-mass relationship for sockeye salmon rearing in their natal lake of origin. These populations are referred to in the text as *Black Lake*$_{\mathit{Black}}$ and *Chignik Lake*$_{\mathit{Chignik}}$. Circles are individual fish and the lines represent the AICc selected model. For 2010 the best model included different intercepts and slopes by natal lake of origin and capture. For 2011 while the best model included different intercepts and the same slope by natal lake of origin and capture, two other models were within 2 AICc units (Table 2).

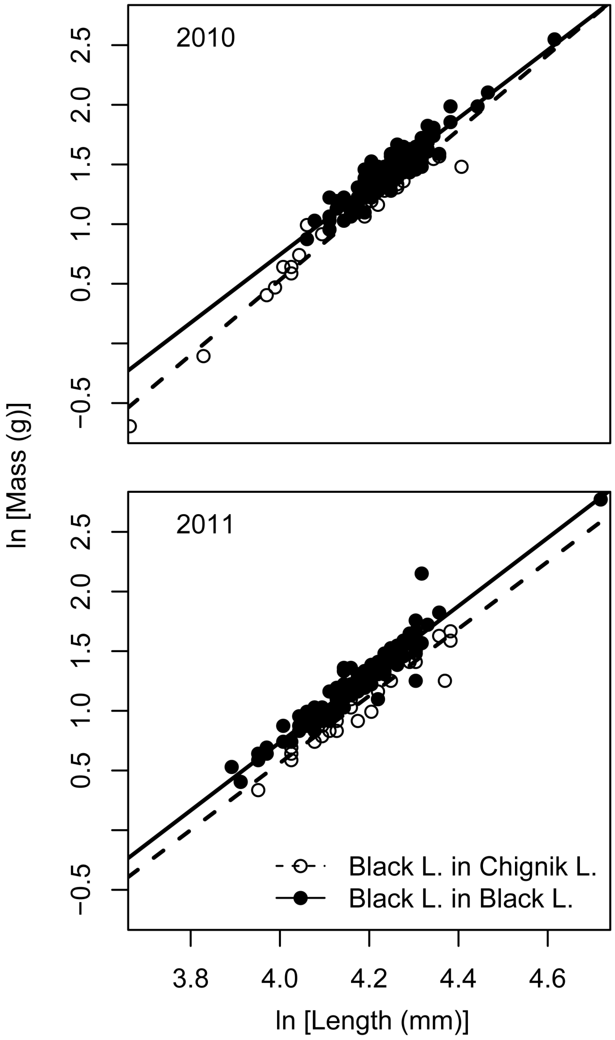

Figure 1.4: Length-mass relationship for sockeye salmon of Black Lake origin by lake of capture. These population sub-groupings are referred to in the text as *Black Lake*$_{Chignik}$ and *Black Lake*$_{Black}$. Circles are individual fish and the lines represent the AICc selected model. For 2010, the best fit model contained different intercepts and slopes by lake of capture. For 2011, the model shown has the same intercept but different slopes by lake of capture. This model had only slightly greater support than two other models (see Table 2).

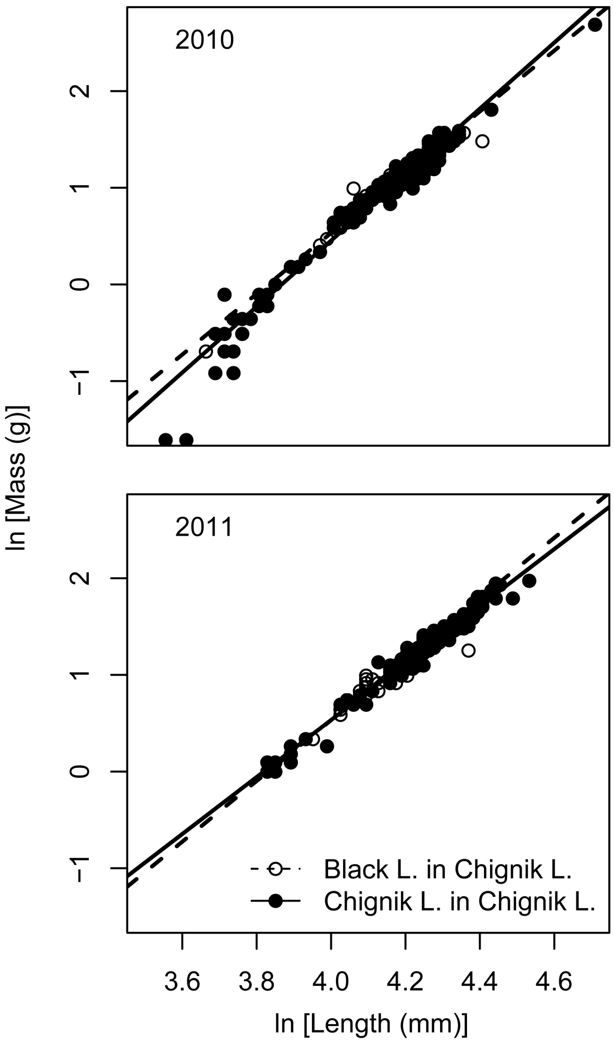

Figure 1.5: Length-mass relationship for sockeye salmon captured in Chignik Lake by natal origin. These populations are referred to in the text as *Black Lake$_{Chignik}$ and Chignik Lake$_{Chignik}$*. Circles are individual fish and the lines represent the AICc selected model. For 2010 and 2011, the best fit model contained different intercepts and slopes by natal origin. However, for 2011 this model differed less than 2 AICc units from a model with the same slope and intercept for both stocks (Table 2).

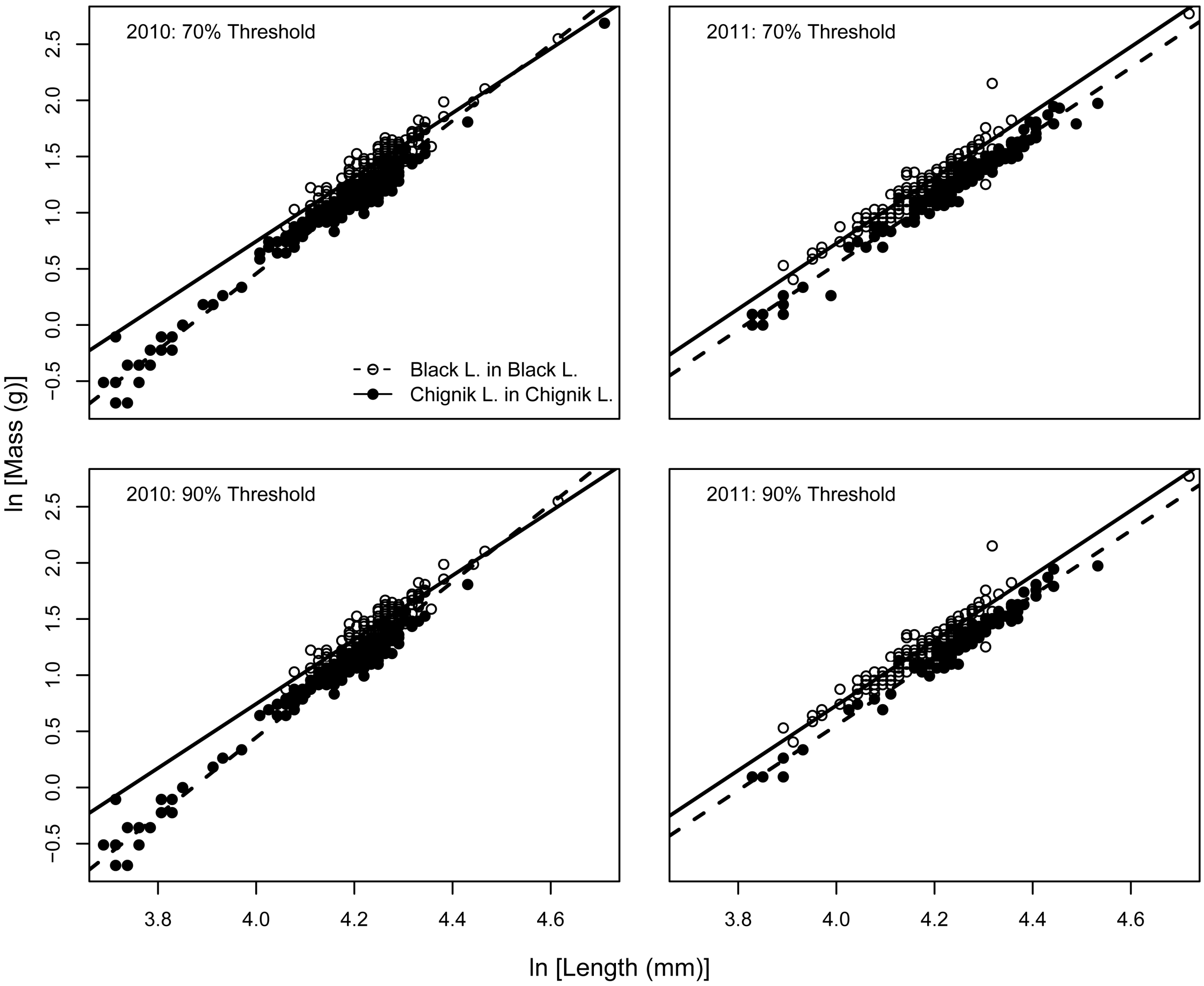

Figure 1.6: Length-mass relationship for sockeye salmon rearing in their natal lake of origin using alternative individual assignment probability thresholds. Individuals are shown at both the 70% and 90% assignment probability thresholds. Data presented as in Figure 3.

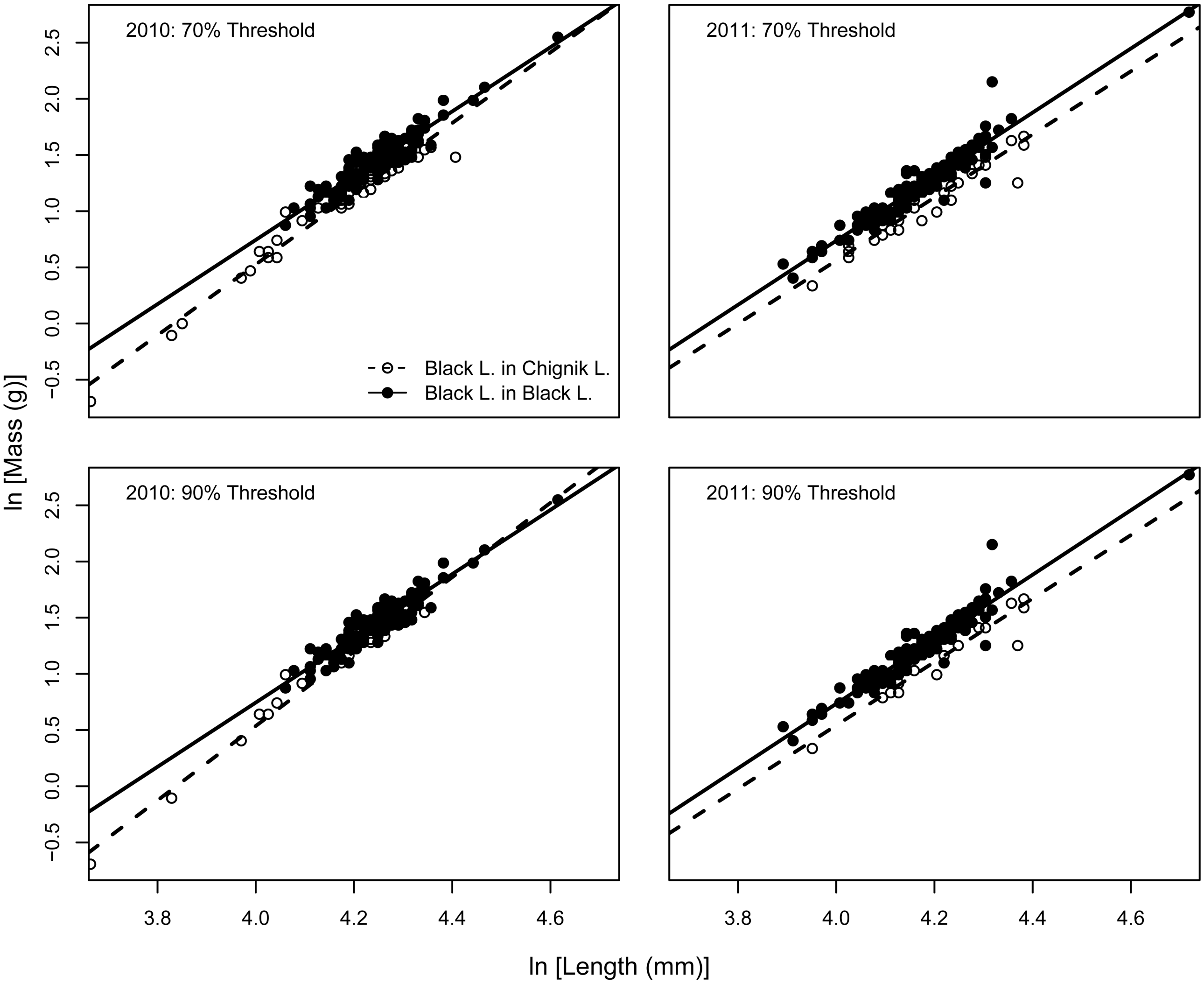

Figure 1.7: Length-mass relationship for sockeye salmon of Black Lake origin by lake of capture using alternative individual assignment probability thresholds. Individuals are shown at both the 70% and 90% assignment probability thresholds. Data presented as in Figure 4.

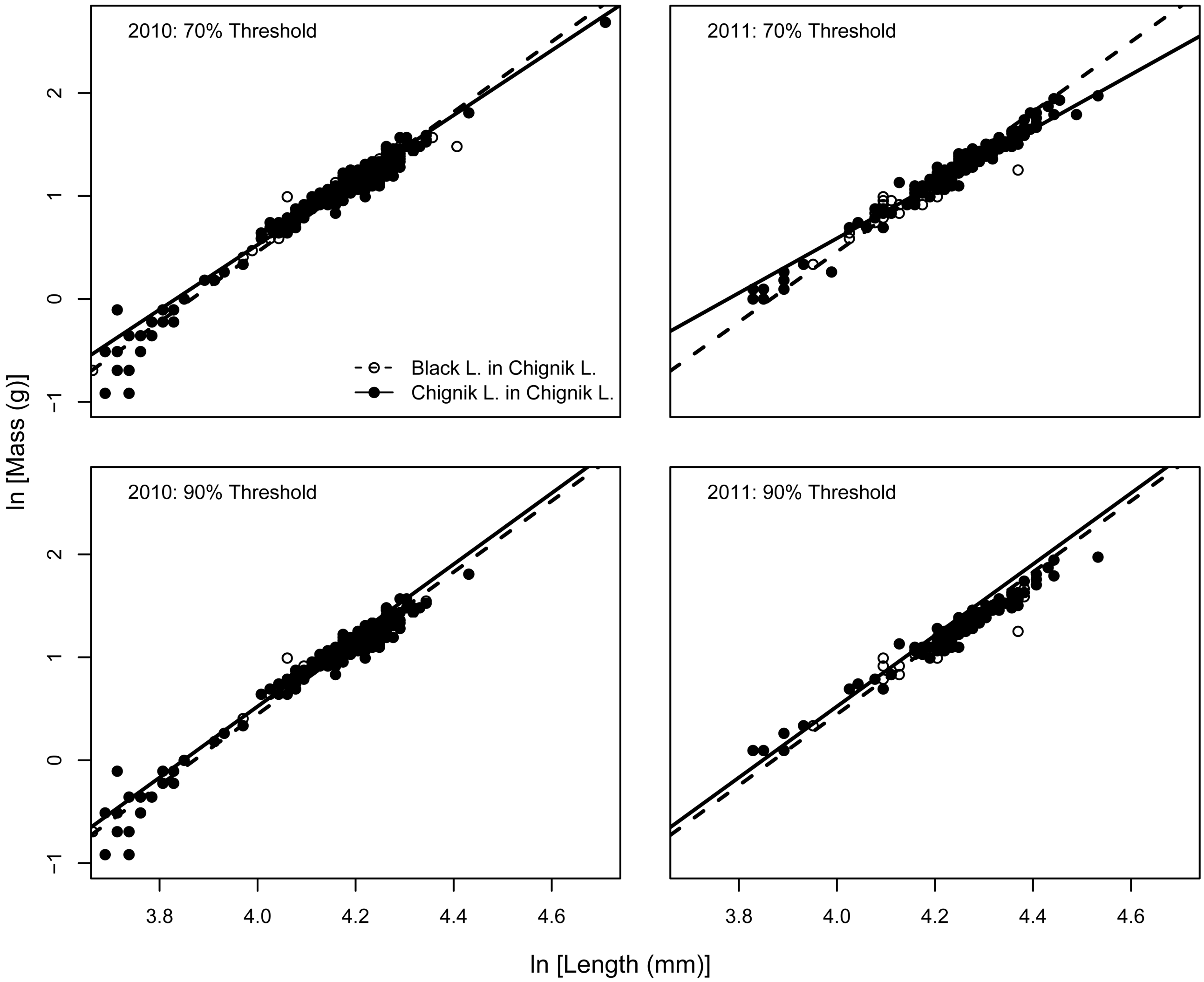

Figure 1.8: Length-mass relationship for sockeye salmon captured in Chignik Lake by natal origin using alternative individual assignment probability thresholds. Individuals are shown at both the 70% and 90% assignment probability thresholds. Data presented as in Figure 5.

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Chapter 2: Climate variation is filtered differently among lakes to influence freshwater growth of juvenile sockeye salmon in an Alaskan watershed

Introduction

Organisms do not experience climate directly but instead respond to how climate variability is filtered by the physical landscape that characterizes their habitat. The interactions between climate processes and habitats are complex because climate is expressed through many different variables including precipitation, temperature, and wind. For locally-adapted populations within heterogeneous landscapes, shared regional climate forcing can produce asynchrony in the dynamics among neighboring populations (Ringsby et al. 2002; Rogers and Schindler 2008) such that average abundance among all the populations is more stable than for anyone population alone. Further, networks of heterogeneous habitat also buffer individual populations from climate variability by allowing mobile individuals to move to more optimal habitat (Naslund et al. 1993; Oliver et al. 2010). In both cases, organisms are responding to habitat filtering across the suite of climate variables and therefore our detection of climate sensitivity may depend on the variables (single or integrated) used to measure climate (Hallett et al. 2004).

Freshwater ecosystems are highly sensitive to climate variation (Adrian et al. 2009) and are naturally structured as heterogeneous habitat networks at the watershed scale (Benda et al. 2004). They also provide a wide range of ecosystem services to humans (e.g. drinking water, fisheries, and nutrient cycling) and the delivery of these services is influenced by climate (Schroter et al. 2005). Understanding the temporal sensitivity of biological processes to climate variation across heterogeneous landscapes may therefore be important for evaluating the reliability of freshwater ecosystem services subjected to changing climate regimes.

Fisheries represent a significant ecosystem service to humans (Millenium EcosystemAssessment 2005) and anadromous Pacific salmon (*Oncorhynchus spp.*) are an iconic example of both a provisioning and cultural service through their commercial and subsistence fisheries. They also exhibit wide-ranging life history diversity among populations generated from genetically distinct, locally adapted populations that are maintained by strong natal homing (Quinn 2005). Underpinning the population diversity in Pacific salmon is dynamic and heterogeneous freshwater habitat (Waples et al. 2008). Their population dynamics are responsive to climate processes that operate at a range of spatial (Mueter et al. 2002) and temporal scales (Mantua et al. 1997; Schindler et al. 2008) in the marine environment leading to significant coherence at coarse regional scales (e.g. Alaska, Pacific Northwest, Peterman et al. 1998). However, at watershed scales, Pacific salmon population dynamics are surprisingly asynchronous in regions with pristine freshwater habitat and the full suite of historic life history diversity (Rogers and Schindler 2008). This asynchrony among populations within stock complexes produces portfolio effects that buffer fisheries from environmental variability (Schindler et al. 2010).

Throughout the range of Pacific salmon, climate change is affecting freshwater habitats through changes in temperature, precipitation, and associated properties in lakes and rivers (Stafford et al. 2000; Mantua et al. 2010). A large amount of research has focused on the potential responses of salmon populations including changes in their survival (Crozier and Zabel 2006), phenology of life history events (Reed et al. 2011), and growth (Schindler et al. 2005; Rich et al. 2009). In particular, growth provides an integrated measure of habitat quality which includes the direct response of individuals to climate as filtered by their habitat and their indirect response to the biological interactions in the ecosystem. Growth also plays an important role in determining the duration of freshwater rearing (e.g. one or more summer growing periods, Groot and Margolis 1991) as well as overwinter (Quinn and Peterson 1996; Ebersole et al. 2006) and marine survival (Koenings et al. 1993). Climate conditions can affect juvenile salmon growth by altering the duration of the growing season (Schindler et al. 2005), affecting metabolic and consumption rates (Griffiths and Schindler 2012), and altering the dynamics and production of prey resources (Winder and Schindler 2004; Hampton et al. 2006).

In southwest Alaska, juvenile sockeye salmon (*O. nerka*) growth has responded to low frequency climate variation (Schindler et al. 2005) as expressed through the Pacific Decadal Oscillation (PDO) affecting lake ice spring break-up dates and therefore growing season duration on Lake Aleknagik. In the same system, ongoing warming has further lengthened the growing season and has amplified PDO effects growth of juvenile sockeye salmon over the period 1962-2002. In Iliamna Lake, a nearby lake system, spring air temperatures explain variation in growth. Increases in spring temperatures over the 1962-2006 period has increased growth rates as well as decreased freshwater rearing time in the population (Rich et al. 2009). These two lakes differ in size and temperature as well as the density of juvenile sockeye salmon (Rich et al. 2009) and illustrate how growth responses will vary with changing climate and are mediated by geomorphology and biological interactions.

Whether climate variation is differentially filtered by lakes within the same watershed remains unknown, though salmon population dynamics suggest that it is (Rogers and Schindler 2008; Rogers and Schindler 2011). We used two different long-term datasets, scales from returning adults and juvenile length measurements, to assess the response of sockeye salmon freshwater growth to direct and integrated measures of climate. Within a watershed with substantial contrasts in habitat conditions, the first dataset is used to evaluate if habitat filtering results in differential growth responses of juvenile sockeye salmon to climate variation. The second dataset focuses on a single lake environment and is used to assess climate variation in conjunction with biological interactions (e.g. density dependence) removing the confounding effects of mortality experienced at later life stages. We address the following questions in this study:

1. Does the first year of freshwater sockeye salmon growth differ over time between two lakes with distinct habitat features within a single watershed?
2. Does juvenile salmon growth in these lakes show differential responses to both single climate variables and composite climate indices?
3. Within a single lake type, does accounting for biological interactions alter the response of growth to climate variability?

Methods

Study area

On the Alaska Peninsula, the Chignik watershed (Figure 2.1), which includes Chignik and Black Lakes, drains southward into the Gulf of Alaska. Tributaries to warm and shallow Black Lake (max depth 4m) support a stock group (multiple spawning populations) of sockeye salmon that are genetically distinct (Creelman et al. 2011) from the stock group spawning in the tributaries and beaches of cold and deep Chignik Lake (max depth 60m) downstream. The two lakes are connected by Black River and the outflow of Chignik Lake connects the system to a large tidal lagoon before entering the Gulf of Alaska.

The Black and Chignik Lake stock groups differ in life history characteristics that reflect the productivity of their principal natal habitats. Black Lake populations typically grow rapidly in their first year and assume a freshwater residency for one year, then migrate to the ocean in their second spring where they then spend three years, and return to spawn during a contracted period from early June to early July (Narver 1966). Chignik Lake populations typically grow more slowly and rear in freshwater for two years, and adult spawners return between July and September after three years of marine growth (Narver 1966). These sockeye salmon support a commercial and subsistence fishery and the allocation to fishery harvest and spawning populations (escapement) are regulated by the Alaska Department of Fish and Game (ADFG) for each stock group. The average escapement between 1950 and 2009 for both stocks combined is 678,000 with an average 1.9 million fish returning each year.

Data collection

Sockeye salmon freshwater growth was measured both from lengths of juveniles caught at the end of their first growing season in Black Lake, and inferred indirectly from scales collected from returning adults to each of the early (Black Lake) and late (Chignik Lake) stock groups. These two datasets offered different temporal coverage as well as differences in the habitats and life histories they characterize.

Adult sockeye scales

Sockeye scales were collected by either the University of Washington Fisheries Research Institute (now the UW-Alaska Salmon Program, UW-ASP) or the Alaska Department of Fish and Game (ADFG) from 1955-1997. The primary sampling location was the commercial fishery in Chignik Lagoon but in some years scale collection occurred at the Chignik Weir, ~5 km upstream from the lagoon (Figure 2.1). Scales were collected from the "preferred area" (i.e., between the dorsal and adipose fins in the two to three rows above or below the lateral line), mounted on gummed cards, covered with a clear acetate card and pressed in a heated hydraulic press (Dalhberg 1968).

Scales from the dominant age group of each stock were used in this study, although several age groups are present in both Black and Chignik Lake stocks. The stocks differ in their return timing to freshwater (Dahlberg 1968) and this was used to ensure that samples reflected the stock desired. Scales for early run (Black Lake) fish from the 1.3 age group (one winter in freshwater, three winters in the ocean) were selected from sampling dates no later than June 30th (Bumgarner 1993). The collected samples characterize freshwater growth years 1951 -1993 (1959 missing). Similarly, late run (Chignik Lake) samples for the 2.3 age group were selected from fish arriving no earlier than July 24th (Bumgarner 1993). The collected samples characterize the first year of freshwater growth from 1950 – 1992. In most years approximately 50 individuals (equal proportions of males and females) were collected for each age group. Sample size for all return years after 1988 was approximately 100 individuals. Bumgarner (1993) and Ruggerone et al. (2007) provide more detailed description of scale selection.

Age 1.3 returns until 1992 and age 2.3 returns until 1991 were read by J. Bumgarner and thereafter by M. Ferguson. The scale growth measurement procedure followed Davis et al. (1990). Freshwater growth on scales was measured with the Optical Pattern Recognition System (Model OPRS-512, BioSonics Inc., Seattle) at a magnification of 169x, allowing for minimum distances between adjacent measurements of 3.1 microns (μ) (< 1 mm juvenile fish length). The scale measurement axis bisected the scale focus and was perpendicular to a line drawn from each end of the first salt water annulus. Distance (μm) from the focus of the scale to the first annulus was defined as the first year of freshwater growth (FW1). If the individual spent two years in freshwater, the distance between the first and second annulus was defined as FW2. Spring plus-growth (FWPL), growth accumulated after the winter but prior to the migration to the ocean, was measured for individuals following their last full year of growth in freshwater (Ruggerone et al. 2007). We focused on FW1 growth in our analyses here.

Juvenile sockeye lengths and catch rates in townets

Juvenile sockeye salmon and resident species were collected between August 25th and September 8th via townet in Black Lake to characterize summer growth and fish density from 1961-1977 and 1992-2010. A net was towed between two boats at constant speed and sampling was conducted at night to reduce net avoidance (Narver 1966). Tow duration during the 1961 to 1977 period was either 5 or 10 minutes and differed among years. Since 1992, tow duration has been standardized to 10 minutes. Declining lake volume (Griffiths et al. 2011) has affected the gear dimensions and lake areas accessible to the gear. Prior to 2003 a net with a 1.8 m x 1.8 m opening was used while a net with a 1.2 m x 1.2 m opening has been used since 2003. Current lake volume also has prevented the sampling of the outlet bay since 2003 (Ruggerone 2003). A complementary time series for Chignik Lake could not be used for these analyses because of our inability to distinguish between the Chignik Lake stock from multiple freshwater age classes and Black Lake emigrants in this common rearing environment.

Prior to 2005, fish were immediately preserved in 10% formalin and measured at least 24 hours after preservation (Narver 1966). From 2005 to 2010, fish were euthanized in a buffered MS-222 solution, stored in cold water and measured within 12 hours of capture. All species were measured (fork length) to the neared millimeter. If catches were large, a subsample of 100 individuals was retained for measurement and the fraction retained was recorded. Juvenile sockeye lengths were adjusted by 4% for shrinkage if preserved (Rogers 1964) and standardized to length on September 1st using a growth rate of approximately 0.3mm per day (UW-Alaska Salmon Program unpublished data). All tows were included in the analysis if multiple nights of towing were conducted in a year within between August 25th and September 8th. Following the inspection of annual length frequency distributions, all individuals greater than 90 mm were removed prior to conducting analyses to focus specifically on individuals in their first year of growth.

The catch rates of sockeye and the common resident fishes (pond smelt (*Hypomesus olidus*), 3-spine stickleback (*Gasterosteus aculeatus*), and 9-spine stickleback (*Pungitius pungitius*) were used as measures of the density of planktivores for comparison with juvenile sockeye lengths. Catch rates were standardized to account for variation in net size and tow duration. We evaluated the correlation between catch rates of juvenile sockeye and adult spawning escapements in the previous year to evaluate alternative measures of density.

Climate

We used mean seasonal air temperatures to reflect high frequency climate variation in the region. Monthly air temperatures were obtained from the Scenarios Network for Alaska Planning (SNAP, http://www.snap.uaf.edu/). These data are downscaled to 2 km grid cells and derived from Climate Research Unit (CRU) datasets. Temperature data are available for 1901-2009. A single grid cell (N56.4588 W158.9977) centered on Black Lake was chosen to represent climate conditions for this analysis. Because the townet dataset extends through 2010, the relationship between the SNAP dataset and Cold Bay (Monthly Surface Data, COOP-WBAN ID: 502102-25624, National Climatic Data Center) temperatures was used to predict the spring temperatures in 2010. The Cold Bay station was the nearest station with complete monthly datasets for the entire period. The r^2 values from the regression fits between SNAP monthly temperature predictions and Cold Bay monthly mean temperature observations ranged from 0.64 to 0.88 (1951-2009). We used the monthly average temperatures to calculate average winter (January-March), average spring (April –June), average summer (July-August), and average fall (September-October) air temperatures. .

The Pacific Decadal Oscillation (PDO, Mantua et al. 1997) is a low frequency climate process measured by sea surface temperature variability in the North Pacific. Salmon production in the northeast Pacific is correlated with the intensity of the PDO as well as air temperature and precipitation conditions along the west coast of North America. The PDO is associated with warmer and wetter winters over Alaska during its positive phase. Monthly PDO index values were obtained from a website maintained by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO, http://jisao.washington.edu/pdo/PDO.latest, accessed 16 January 2012). Index values averaged across November to March were used in our analyses reflecting the average PDO index value during the winter prior to sockeye emergence.

Statistical Modeling

We used linear mixed-effects models to explain variation in freshwater growth as a function of climate and biological covariates. Linear-mixed effects models accounted for data structure in which we had multiple individuals measured for each year of data collection. For each of the scale-derived and townet growth datasets we used two approaches. First, models were fit containing only one biological or climate covariate to assess their relationship to juvenile sockeye salmon growth. Second, from all potential fixed effects we evaluated which combination of fixed effects best explained the observed variation in growth.

In the case of each dataset and modeling approach we followed the approach of Zuur et al. (2009) for determining the inclusion of random and fixed effects in our models. First, we fit models including all potential fixed effects using restricted maximum likelihood (REML) and evaluated whether random effects should be included in the model structure using the Akaike Information Criteria (AIC, Burnham and Anderson 2002). If multiple fixed effects were included in the model, we then iterated through all fixed effects combinations, fitting each combination with maximum likelihood (ML), and used AIC to determine the most parsimonious model fit to the data. Finally, models within a delta AIC (ΔAIC) of <=2 were refit using REML to determine coefficient estimates.

For the scale growth data, models in the first approach took the form:

$$\ln(s_{yli}) = \beta_0 + \beta_1 covar_y + \beta_2 Stock_l + \beta_3 covar_y \times Stock_l + b_y + \varepsilon_i$$

The response $\ln(s_{yli})$ is the natural log transformed scale growth measurement for individual i in stock l in year y. The random intercept for year b_y was normally distributed as were the residual errors ε_i. The βs are fixed effects coefficients and all models contained stock (Chignik or Black) as fixed effect to account for data structure. In separate models, we then evaluated the addition of each of the following fixed effects ($covar_y$) and their interaction with stock: winter air temperature, spring air temperature, fall air temperature, winter PDO, and year. Year assessed as a fixed effect to allow for a potential linear trend over time. We used the number of adult sockeye salmon spawners (escapement) by lake in the previous year as a proxy for juvenile density. The Alaska Department of Fish and Game (ADFG) tightly regulates escapement and escapement trends through time reflect changes in the target escapement objective (particularly in the 1950s-1960s) as well as environmental fluctuations.

For our second approach, we only included covariates as fixed effects that improved the fit to the data over model with only stock as a fixed effect in the previous analysis. In this case, all covariates previously discussed were included as well as their interaction with stock with the exception of escapement which performed poorly. The full model considered was:

$$\ln(s_{yli}) = \beta_0 + \beta_1 Winter_y + \beta_2 Spring_y + \beta_3 Fall_y + \beta_4 PDO_y + \beta_5 Stock_l + \beta_6 Year_y + \beta_7 Spring_y \times Stock_l + \beta_8 PDO_y \times Stock_l + \beta_9 Year_y \times Stock_l + b_y + \varepsilon_i$$

For the juvenile length data, models in the first approach took the form:

$$L_{iy} = \beta_0 + \beta_1 covar_y + b_y + \varepsilon_i$$

Where *L* is the length of individual *i* in year *y* and *covar* is the fixed effect of interest in each year. Potential covariates included winter air temperature, spring air temperature, winter PDO, year, juvenile sockeye density (townet catch rate), and resident fish species density (townet catch rate). Random effects were treated the same as in the scale growth models.

In the second approach for the length data the full model only included the fixed effects that improved the model fit over an intercept-only model. The full model was as following:

$$L_{iy} = \beta_0 + \beta_1 Winter_y + \beta_2 Spring_y + \beta_3 PDO_y + \beta_4 Sockeye_y + \beta_5 Year_y + \beta_6 Spring_y \times Sockeye_y + \beta_7 PDO_y \times Sockeye_y + b_y + \varepsilon_i$$

All analyses were conducting on the R platform using the nmle library (Pinheiro et al. 2010). All environmental and biological covariates were centered to the mean prior to performing the analyses. For each dataset, the earliest year observed was designated year 0.

Results

Observed growth data and climate covariates

First year scale growth for Black Lake stocks (1.3 life histories) had median values ranging from 213µm -343µm between 1951 and 1993 (Figure 2.2a). In contrast, first year growth in the Chignik Lake stock (2.3) had median values ranging from 140µm to 273µm between 1951 and 1992 (Figure 2.2a). The number of juvenile sockeye salmon lengths measured among years varied substantially (30 – 3362) due to differences in the number of tows conducted among years as well as catch rates with median lengths ranging from 5mm to 82mm (Figure 2.2b). Catch rates of sockeye salmon ranged from 0.66 – 49.12 fish per m^2 per min and resident fish catch rates ranged from 2.34 – 105.32 fish per m^2 per min (Figure 2.3). Juvenile coho salmon (*O. kisutch*) and pygmy whitefish (*Prosopium coulterii*) were infrequently observed in catches and not included in resident fish catch rates. There was no relationship between juvenile sockeye catch rate and adult spawning escapements (Figure 2.3) in the previous year (an alternative measure of density, r^2 =0.002) as has been noted in other systems (Schindler et al. 2005).

Mean air temperatures ranged from -7 to 0.5 in winter, 3.2 to 7.7 in spring, and 5.5 to 9.0 in fall between 1950 and 2010 (Figure 2.3). We did not use average summer air temperature because it was highly correlated with spring air temperature (r^2 = 0.57). Mean PDO index values (November to March) ranged from -2.7 to 1.9 9 (Figure 2.3).

Sockeye salmon scale growth patterns

Single climate covariate models

Stock group strongly affected freshwater sockeye salmon growth with Chignik Lake stocks exhibiting substantially lower growth than Black Lake stocks (Figure 2.2a). Stock group also mediated the response of growth to climate variables (Figure 2.4). The growth of both Chignik Lake and Black Lake had positive relationships with year, PDO, and winter air temperature, but Chignik Lake showed a larger magnitude response to variation in these variables. The stocks diverged in their responses to spring and fall air temperatures, however, with a positive response by Chignik Lake and negative response by Black Lake (negligible in the case of spring air temperature). For all models linking growth of sockeye salmon in their first year to environmental and density factors, including year as a random intercept substantially improved the model fit. In all cases, the inclusion an environmental covariate and its interaction with stock improved the model fit to the data over a stock-only model. The model structure containing year and its interaction with stock group had the lowest AIC value. The performance of this model was followed by one with fall air temperature and its stock group interaction (ΔAIC = 35.3), spring air temperature and its stock group interaction (ΔAIC = 48.8), PDO and its stock group interaction (ΔAIC = 88.7), and winter air temperature and its stock group interaction (ΔAIC = 95.4). The model including lake specific escapement and stock group performed worse (ΔAIC = 107.1) than the stock group only model (ΔAIC = 105.5), therefore escapement data were not used in further analyses. A lack of relationship between escapement and growth was also shown by Ruggerone and Rogers (2003) for Chignik Lake only using a subset of these data.

Growth models with multiple climate covariates

In models with multiple climate covariates, the stock specific effect of each climate variable on age-0 growth was the same direction as in the single covariate models. The best model predicting the growth of age-0 sockeye included spring air temperature, fall air temperature, PDO, year, and stock (Table 2.1). It also included interaction terms between stock and three other covariates; spring air temperature, fall air temperature, and year. We considered 211 different alternative fixed effects models including an intercept only model after determining the necessity of the random intercept for year and four other models were within 2 AIC units of the top model (Table 2.3a). These models all included spring air temperature, fall air temperature, and year of growth and their interactions with stock. They differed in either the absence of any other covariates or included PDO or winter air temperature or their interactions. The sign and magnitude of the shared covariates among all models did not change.

We assessed the effects on growth of each covariate in the model given that all other covariates were held at their mean value. The model estimated a 1.1% decrease in growth of Black Lake sockeye salmon with a 1°C increase in spring air temperature while the same change in temperature led to a 0.7% increase in growth of Chignik Lake fish. Fall air temperatures had a larger negative effect on Black Lake growth, with an increase of 1°C leading to a 2.1% decrease in mean growth. On the other hand, a 1°C increase in fall temperatures led to a 1.4% increase in Chignik Lake stock growth. The PDO had a positive effect on both stock groups, with a 3% increase in mean growth associated with a 1 unit increase in the PDO. There was a positive linear trend in growth over time for both stock groups after accounting for climate covariates, but the Chignik Lake stock group exhibited a faster rate of increase.

Direct assessment of juvenile sockeye growth from townet data

Single covariate models

The length of juvenile sockeye salmon from Black Lake on September 1st was positively related to winter and spring air temperatures as well as the PDO whereas the density of conspecifics had a negative effect on length (Figure 2.5). Between 1961 and 2010, juvenile length on September 1st has increased by 15.4% when year is the only covariate included in the model.

In all models, the inclusion of year as a random intercept substantially improved the model fit of juvenile sockeye salmon growth in Black Lake. Spring air temperature as a fixed effect performed the best in explaining variation in juvenile sockeye salmon length as determined by AIC. The year model was essentially as good (ΔAIC = 0.7) followed by PDO (ΔAIC = 6.9), juvenile sockeye salmon density (ΔAIC = 7.2), winter air temperature (ΔAIC = 7.9), and resident fish density (ΔAIC = 8.7). While there was a slight positive relationship between resident fish density and sockeye length, the model performed more poorly (ΔAIC = 8.7) than an intercept only model (ΔAIC = 8.0). Thus, we did not include resident fish density as a covariate in subsequent models.

Multiple covariate growth model

The summer freshwater growth of sockeye salmon in Black Lake showed positive responses to spring air temperature and negative effects of juvenile sockeye salmon density. Additionally, juvenile sockeye salmon length on September 1 has increased over time and was not accounted for by changes in spring air temperature or density.

The optimal structure modeled the mean length of juvenile sockeye as a function of spring air temperature, sockeye salmon density, and year as fixed effects and year also as a random intercept (Table 2.2). This model was chosen from the 51 fixed effects model structures we considered after determining the necessity of a random intercept (year). However, there were 4 other models within 2 AIC units of this model (Table 2.3b) and therefore should be considered equally plausible (Burnham and Anderson 2002). These models all included spring air temperature and year and the majority also included sockeye salmon density. The sign of the covariates coefficients were the same among all models.

We assessed the predicted effects on growth of each covariate in the top model given that all other covariates were held at their mean value for the best fit model. The model estimated a 4.4% increase in juvenile sockeye salmon length with a 1°C increase in spring air temperature. Additionally, the model estimated a 9.5% increase in length over 50 years. Sockeye salmon density had a negative effect on growth. An increase of 10 sockeye/m^2/min resulted in a 2.6% decline in mean length under mean spring temperature conditions. Models within 2 AIC units that included additional covariates indicated a negative effect of winter air temperature, PDO and the density – spring air temperature interaction on juvenile sockeye salmon length.

Discussion

Taken as a whole, our results suggest that within a single watershed, habitat plays an important role in filtering climate. Moreover, this filtering is expressed through differential growth responses to climate variation among distinct sockeye stocks occupying different habitats within the same watershed. Using the adult scale data, we were able to simultaneously assess the first year freshwater growth of both Chignik Lake and Black Lake stocks over time. Juvenile sockeye salmon first year freshwater growth increased, on average, between 1950 and 1993 in the Chignik watershed. While the growth of Chignik Lake individuals was consistently lower than for Black Lake individuals, Chignik Lake showed a more rapid increase in growth over time than Black Lake. This pattern was evident in models that considered only single fixed effects in addition to stock, as well as in the model results from iteratively assessing all combinations of fixed effects.

The two stocks differed, however, in their growth responses to the two seasonal climate variables that ranked highest among the single covariate models. While Chignik Lake stock growth increased with both increasing spring and fall air temperatures, Black Lake stock growth had a negative response to increases in spring and fall air temperatures. The Black Lake stock's negative growth response to both spring and fall increases in air temperature is likely due to the high sensitivity of Black Lake water temperature to changes in air temperature. In Black Lake, warmer than average months may have maximum daily water temperatures that increase metabolic stress for juvenile sockeye salmon (Griffiths et al. 2011; Griffiths and Schindler 2012). On the other hand, Chignik Lake is cold and warms slowly and daily air temperature is less likely to affect the thermal experience of juvenile sockeye salmon. However, the cumulative effect of warmer than average air temperatures on a monthly scale should increase water temperatures and increase the scope for growth.

First year freshwater growth for the two stocks did show a coherent response to both winter air temperature and the PDO, however, these two covariates had less explanatory power for changes in growth. Positive phases on the PDO are associated with warmer and wetter winters in coastal Alaska (Mantua et al. 1997) and are correlated with earlier ice break-up dates (Schindler et al. 2005). This increases the duration of the growing season in a region in which climate conditions substantially limit the growing season (Brylinski and Mann 1973). If food is not limited in the early season, it is expected that increases in the growing season length will enhance growth rates of fishes. Our results suggest that growth responses are not explained as well by integrated climate indices (PDO) than by direct measures of temperature based upon model fits for single climate covariates. This may be because temperature is the climate feature that shapes these habitats and therefore mean seasonal temperatures provide the greatest explanation of variation in growth.

The dataset from townet samples of juveniles in Black Lake was consistent with the scale growth dataset on the overall trend of increasing freshwater growth over time (1961-2010) but there were differences in the response of growth to some important climate covariates. In contrast to the scale growth analyses, the juvenile length data indicated that there was a strong positive response of age-0 sockeye summer growth to increases in spring air temperature and a weak negative effect of juvenile sockeye density. The positive response to spring air temperature seen in the juvenile length data differs from the relatively weak negative effect of spring air temperature on growth seen in the scale growth data. The PDO effect on growth, however, was also observed to be positive in the juvenile length time series.

The difference in growth-climate relationships between the two datasets may reflect the fact that they capture overlapping but different years, a different temporal extent of the growing season, and potentially capture different components of the Black Lake stock group. During the years for which we have overlapping data (1961-1977, 1992) the correlation between mean townet length and mean scale growth was positive but low ($r^2 = 0.2$). The scale growth time series begins a decade earlier and does not have coverage over the most recent 15 years. In contrast, while the townet dataset captures recent years, including some years with very early and warm springs, it does not have coverage during and following the transition of the PDO in the 1977 and therefore lacks the strong contrast in conditions associated with the PDO. Additionally, the scale growth dataset measured all growth occurring from emergence through the first winter while the juvenile length dataset measures growth only until September 1. The effect of fall air temperatures was pronounced in the scale growth dataset and growth achieved from September 1st until at least mid-October is likely to be an important contribution to overall size prior to winter.

Differences in the Black Lake stock response may also reflect a combination of the life histories captured in the datasets. The juvenile length dataset describes the growth of all Black Lake origin individuals who reared in Black Lake for the entire summer during their first year in freshwater. We assume the majority of these individuals only spend one year in freshwater, however, some fraction of the population also overwinters in freshwater and spends a second year rearing in the watershed. Additionally, we know that there are mid-summer emigrations of Black Lake individuals downstream (Parr 1972; Westley et al. 2008) and that in recent years that

Black Lake individuals make up a significant fraction of juvenile sockeye salmon rearing in Chignik Lake (Griffiths et al. In review; Simmons et al. 2012). Juvenile length data are capturing only a single rearing strategy of the age-0 Black Lake stock and these individuals may pursue a range of life history options in subsequent years. In addition, emigration may also reduce the negative effect of juvenile sockeye density on growth. This may explain the weak effects of density which is often an important determinant of juvenile sockeye growth (Hyatt and Stockner 1985; Mazumder and Edmundson 2002; Schindler et al. 2005).

In contrast, the scale growth data are focused on the dominant age cohort for each stock group. We are confident that given the timing of the sampling that the individuals reflect the stock group assigned. We are unable, however, to know with complete certainty the habitat use by individuals in their first year of freshwater growth. Chignik Lake individuals have the potential to access downstream river (Chignik River) and estuary habitat as age-0 fry (Simmons 2009) while Black Lake individuals can use downstream Chignik Lake as well as Chignik River and estuary habitat. Currently we do not know the relative contribution of different rearing habitats to the return of adult spawners or its variability among years.

Significant mortality occurs following the emigration from freshwater (Quinn 2005) and marine survival has been shown to be strongly size-dependent (Koenings et al. 1993). Consequently, the individuals that we measured for freshwater scale growth are those that had grown sufficiently in their first freshwater year to survive the winter, second freshwater year (2.3 fish only), and three years in the ocean. Depending on the consistency in the direction of size selectivity among years and the strength of selection, the true differences in freshwater growth among years may not be observable in the returning adults. This may account for the variation in the data and why, while we can assess the direction of climate effects on growth, there remains large amount of residual variation.

Changes in growth could alter the duration of freshwater rearing (Groot and Margolis 1991) which would be reflected in the age-composition of the returning adults. However, without genetic assignment, there is not a clear way to separate out the age-composition between Black Lake and Chignik Lake stocks. ADFG bases escapement allocations to stock groups on changes in age composition over the period of the adult return. Therefore it is circular to use stock specific escapement values to evaluate age composition changes. However, exploratory analyses indicated that there has not been a change in overall watershed age composition between the brood years of 1950 to 1994.

Given the expected increases in air temperature through the end of the century due to climate change (Christensen et al. 2007), the historic response of juvenile sockeye salmon growth in Chignik Lake indicates that rearing conditions may continue to improve for juvenile sockeye salmon. Improved growing conditions in Chignik Lake may buffer sockeye salmon productivity in freshwater if Black Lake growing conditions for juvenile sockeye salmon plateau or deteriorate (Griffiths et al. 2011; Griffiths and Schindler 2012). While both datasets suggest that there have also been increases in Black Lake growth over time, it is clear that this is only for a subset of the population and there are already temperature increases that lead to reduced growth. What we do not know is what fraction of the population Black Lake moves to alternative, downstream rearing environments. However, Chignik Lake juvenile sockeye salmon are showing increased growth despite potentially high emigration rates from Black Lake in some years.

It is clear that restoration or conservation actions that do not consider climate variation may be unsuccessful (Battin et al. 2007). Moreover, the response of salmon populations to future climate change will in part depend on the spatial scale of the landscape that individuals and populations use. Growth is an important indicator that incorporates behavioral and physiological responses to climate and can help characterize the spatial scales of ecological importance. Understanding the magnitude of different responses within watersheds may be important to assess the buffering capacity of the watershed in the face of future change both by producing asynchronous population responses and providing alternative habitats for single populations. Developing policies focused on maintaining the reliability of ecosystem services requires considering the heterogeneity of landscape climate filtering and how this filtering process contributes to enhanced response diversity in populations.

Table 2.1: Coefficient estimates from the AIC selected model for scale growth. Standard errors (SE) and the degrees of freedom (DF) are shown. The response variable is *ln[FW1 (μm)]*.

Model Component	Estimate	SE	DF
Fixed Effects			
Intercept	5.5314	0.0349	4883
Spring Air Temp	-0.0107	0.0177	39
Fall Air Temp	-0.0252	0.0226	39
PDO (Nov-Mar)	0.0292	0.0182	39
Stock (0,1)*	-0.4053	0.0115	4883
Year of Growth	0.0038	0.0014	39
Spring Air Temp:Stock	0.0173	0.0057	4883
Fall Air Temp:Stock	0.0387	0.0070	4883
Year of Growth:Stock	0.0029	0.0004	4883
Random Effects (SD units)			
b_y	0.0998		

*0 = Black L.; 1 = Chignik L.

Table 2.2: Coefficient estimates for the AIC selected model for juvenile length data. The response variable is *length (mm)*.

Model Cor	Estimate	SE	DF
Fixed Effects			
Intercept	60.7151	1.6931	25190
Spring Air	2.6738	1.1481	26
Sockeye (n	-0.1600	0.0922	26
Year of Gr	0.1153	0.0588	26
Random Effects (SD units)			
b_y	5.062738		

Table 2.3: Top 10 models selected via AIC. ΔAIC values and AIC model weights (AIC w_i) shown for each model. AIC weights are the probability that a model is the best model for the data given all the models considered. While only 10 models are shown, all models explored were used in the w_i calculation. a) Models explaining variation in sockeye salmon FW1 scale growth, b) models explaining variation in juvenile sockeye salmon length.

a) Scale Growth

Fixed Effects	ΔAIC	AIC w_i
Spring + Fall + PDO+ Year + Stock + Spring:Stock + Fall: Stock + Year:Stock	0.00	0.23
Winter + Spring + Fall + PDO + Year + Stock + Winter:Stock + Spring:Stock + Fall:Stock + Year:Stock	0.72	0.16
Spring + Fall + Year + Stock + Spring:Stock + Fall:Stock + Year:Stock	0.79	0.15
Spring + Fall + PDO + Year + Stock + Spring:Stock + Fall:Stock + PDO:Stock + Year:Stock	1.66	0.10
Winter + Spring + Fall + Year + Stock + Spring:Stock + Fall:Stock + Year:Stock	1.73	0.10
Winter + Spring + Fall + PDO + Year + Stock + Spring:Stock + Fall:Stock + Year:Stock	2.00	0.08
Winter + Spring + Fall + PDO + Year + Stock + Winter:Stock + Spring:Stock + Fall:Stock + PDO:Stock + Year:Stock	2.04	0.08
Winter + Spring + Fall + PDO + Year + Stock + Spring:Stock + Fall:Stock + PDO:Stock + Year:Stock	3.66	0.04
Fall + PDO + Year + Stock + Fall:Stock + Year:Stock	5.31	0.02
Fall + Year+ Stock + Fall: Stock + Year:Stock	6.09	0.01

b) Juvenile Length

Fixed Effects	ΔAIC	AIC w_i
Spring + Density + Year	0.00	0.13
Winter + Spring + Density + Year	1.25	0.07
Spring + Year	1.29	0.07
Spring + Density + Year + Spring:Density	1.76	0.05
Spring + PDO + Density + Year	1.77	0.05
Spring + Density	2.14	0.05
Spring + PDO + Density + Year + PDO:Density	2.29	0.04
Winter + Spring + Year	2.62	0.04
Winter + Spring + Density + Year + Spring:Density	2.68	0.03
Winter + Spring + Density	3.16	0.03

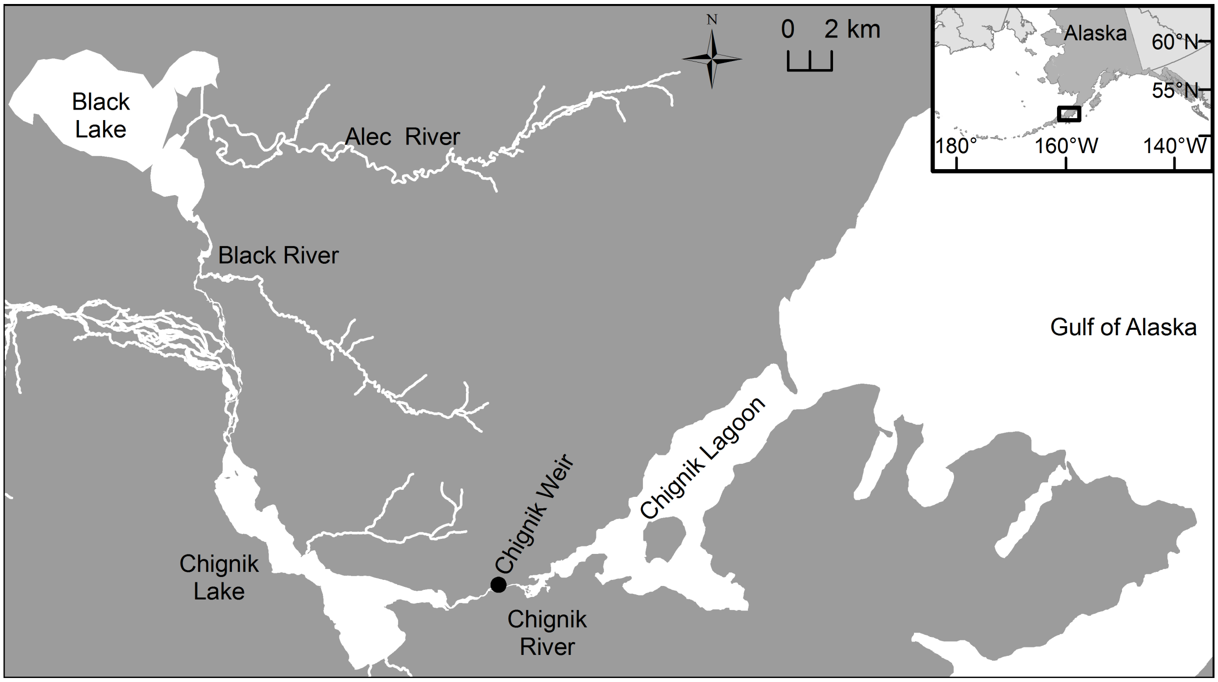

Figure 2.1: Map of the Chignik watershed with major watershed features labeled. The Alec River is the main tributary to Black Lake and spawning habitat for sockeye salmon. Chignik River has numerous tributaries and spawning habitat includes river and lake beaches. The majority of scale samples were collected from the commercial fishery operating in Chignik Lagoon but some were collected at the Chignik Weir.

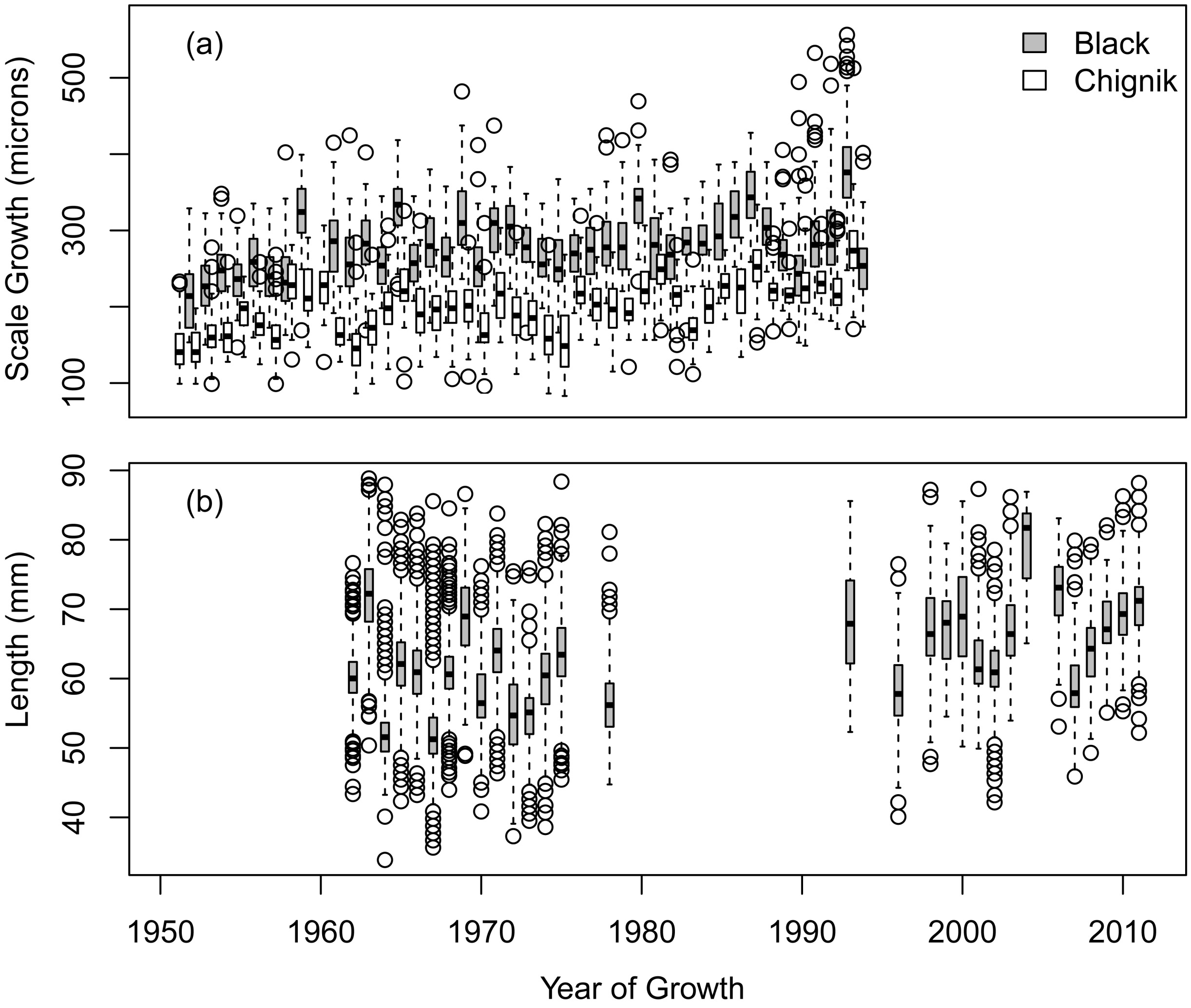

Figure 2.2: Observed freshwater growth data. The first year of freshwater scale growth data is in (a) and Black Lake juvenile length data shown in (b). The thick black line is the median, the box encapsulates the first and third quartiles, and the whiskers indicate ±1.5*IQR.

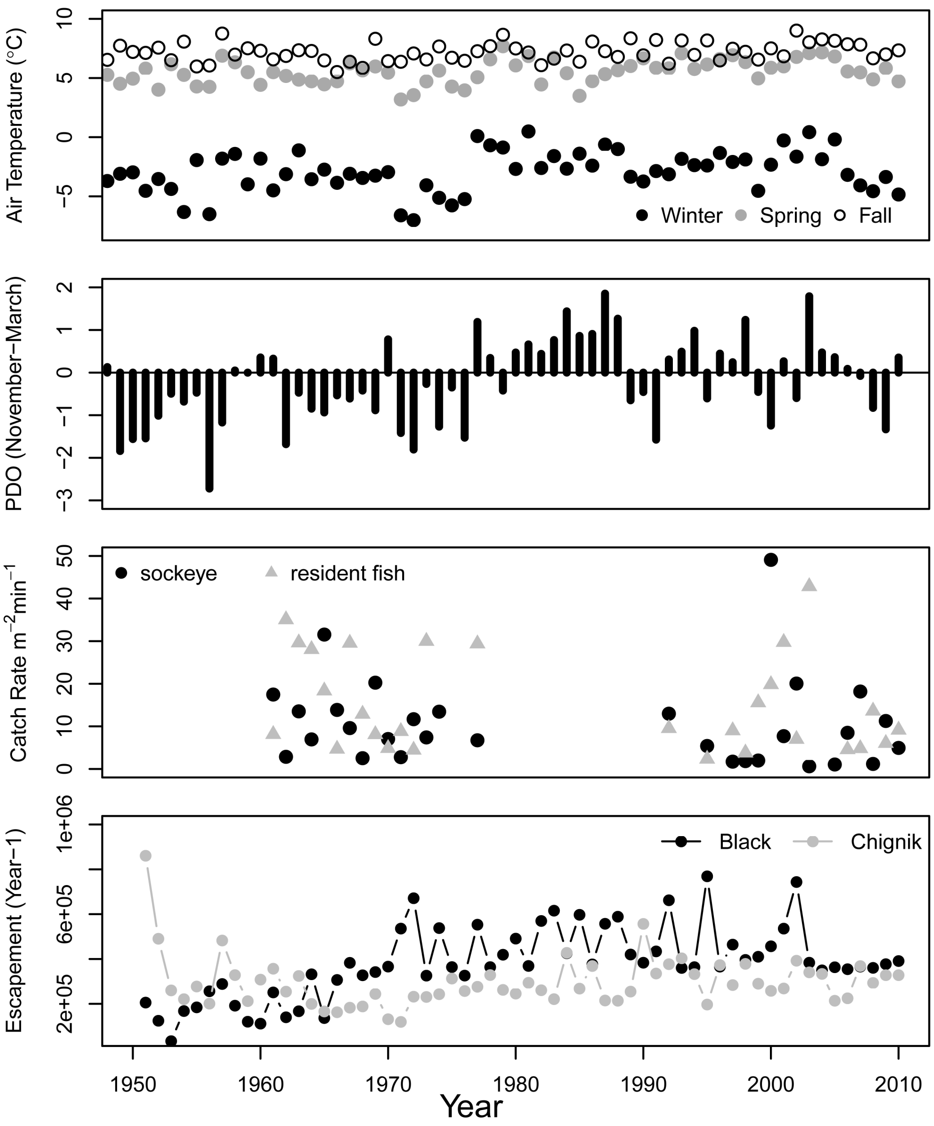

Figure 2.3: Model covariates from 1950 – 2010. These include seasonal air temperatures (Winter, Spring, Fall); PDO winter index values averaged from November to March (shown at year for November); catch rates of juvenile sockeye salmon and resident fish in Black Lake; and escapement (number of spawners) by lake in the year prior. Escapement data are collected by the Alaska Department of Fish and Game.

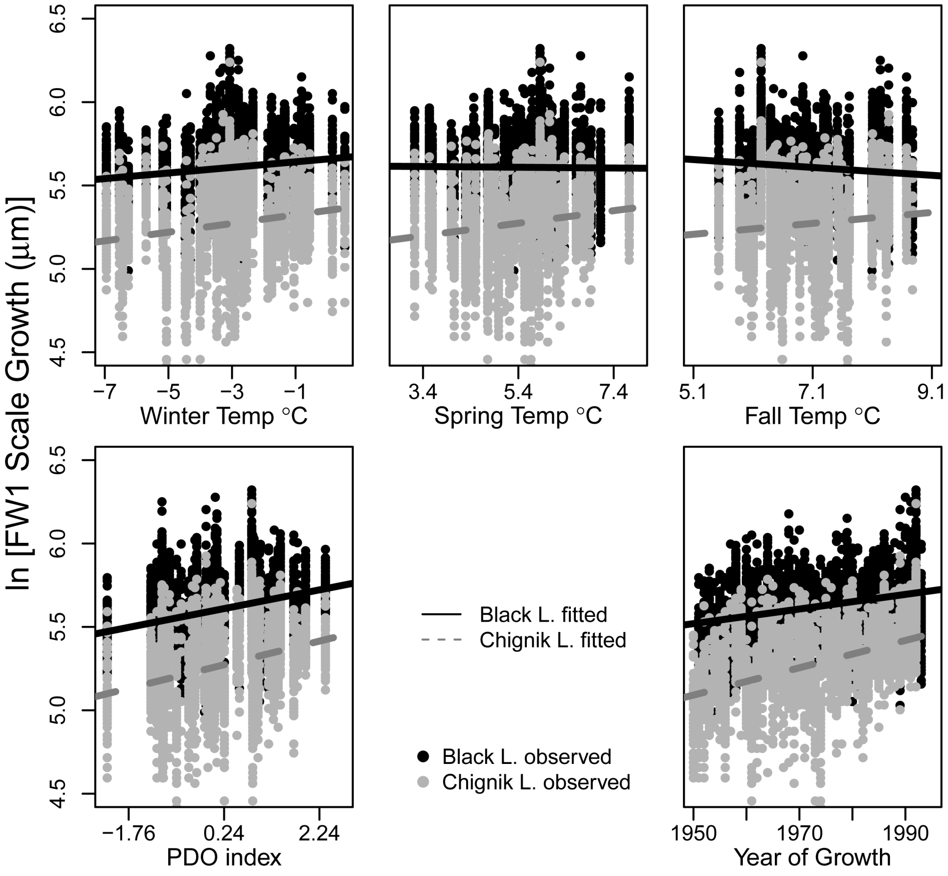

Figure 2.4: Predicted mean juvenile scale growth based upon single climate covariate models. This includes seasonal air temperature, PDO index, and year. All models are of the form: $\ln(s_{yli}) = \beta_0 + \beta_1 covar_y + \beta_2 Stock_l + \beta_3 covar_y \times Stock_l + b_y + \varepsilon_i$. Models were fit using covariates centered to the mean, however, for interpretation, the x-axis are labeled with the true covariate values.

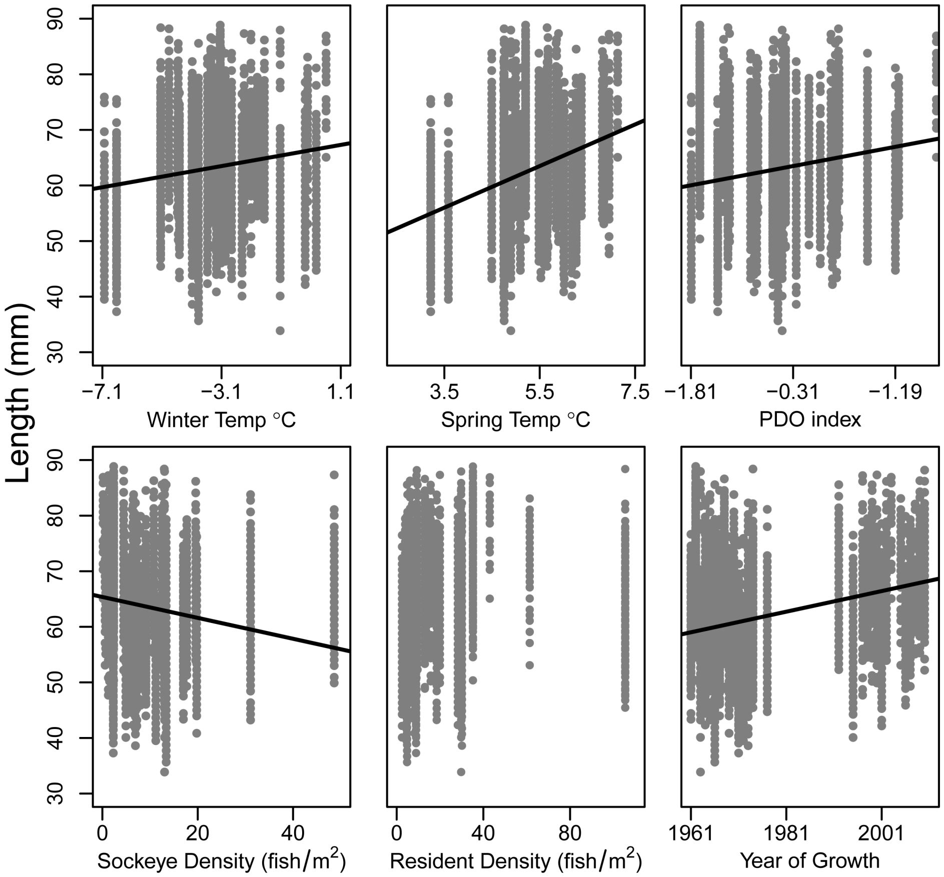

Figure 2.5: Predicted mean townet growth based upon single covariate models This includes seasonal air temperature, PDO index, juvenile sockeye salmon density, and year. All models are of the form: $L_{iy} = \beta_0 + \beta_1 covar_y + b_y + \varepsilon_i$. Models were fit using covariates centered to the mean, however, for interpretation, the x-axis are labeled with the true covariate values.

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Chapter 3: Effects of simultaneous climate change and geomorphic evolution on thermal characteristics of a shallow Alaskan lake[1]

Introduction

Lakes in high northern landscapes are experiencing air temperature increases up to twice the global mean (Christensen et al. 2007) and it is now well established that physical, chemical, and biological characteristics of lakes are sensitive to climate change. In particular, lake thermal characteristics including the length of the ice-free season (Magnuson et al. 2000), mean summer water temperatures (Schindler 1997), and the duration and stability of stratification (Schindler 1997; Livingstone 2003; Winder and Schindler 2004) are directly affected by increased air temperatures. While substantial research has focused on quantifying and predicting changes in lake thermal regimes and the implications for aquatic fauna (De Stasio et al. 1996; Fang and Stefan 1999), little research has focused on how changes in the landscape mediate lake thermal responses. Natural geomorphic processes are the dominant agent of landscape change in high northern landscapes and have the potential to amplify or dampen the effects of climate change in lake ecosystems. Research to understand lake responses to the interaction of geomorphic evolution and climate change is lacking, however, outside of permafrost systems.

Lakes are transient features of the landscape over geologic time (Hutchinson 1957) and lake extinction occurs through several mechanisms including outlet erosion, overfill from sediments deposited by tributaries (Garcia-Castellanos 2006), and migration of inlet streams (Milner et al. 2007). In limnology, lakes are typically treated as geomorphically static features

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of the landscape and much of the research focused on lake thermal responses to climate change does not account for underlying geomorphic evolution. While this assumption is reasonable in geomorphically stable regions, northern high latitude landscapes are highly dynamic systems driven by glacial, fluvial, volcanic, and thermokarst processes. These processes can act on ecologically relevant scales (Swanson et al. 1988) and their interaction with projected climate change has the potential to affect a wide range of aquatic ecosystem properties.

There are two ways in which geomorphic processes can influence lake thermal regimes. Geomorphic processes occurring independently of climate change can control the responses of lakes to increasing air temperatures. In recently deglaciated basins, lakes can become detached from inlet streams due to unstable channels that frequently migrate across the landscape (Milner et al. 2007). Thus, loss of hydrologic connectivity could amplify the effects of increasing air temperatures and evaporation rates. Or, climate change may affect the rates of geomorphic processes that then drive changes in lake characteristics. Regions with high erosion rates are particularly sensitive to climate driven changes in flow regimes (Dunne and Leopold 1978) and increased erosion may change the shape, volume, and hydrology of lakes in ways that affect their sensitivity to climate change.

Research on arctic lakes and ponds, which have undergone large declines in number since the 1970s (Smith et al. 2005; Smol and Douglas 2007), has addressed both aspects of climate-geomorphology interactions. Arctic ponds underlain with granitic bedrock are more susceptible to increases in the evaporation to precipitation ratio leading to pond desiccation under warm climate regimes (Smol and Douglas 2007) rather than changes to lake morphology or drainage. Thus, direct climate forcing will be the primary driver of ecosystem change in these systems. Alternatively, thermokarst lake morphology is substantially altered as permafrost thawing occurs and changes the rates of important erosional processes. Thermokarst lakes develop and expand under initial warming followed by rapid lake drainage with increased rates of permafrost loss (Smith et al. 2005; Marsh et al. 2009) leading to further geomorphic evolution due to terrain slumping and sediment transport and deposition (Prowse et al. 2006*a*). Responses across the permafrost landscape will not be uniform with some regions experiencing complete loss of lakes due to drainage and evaporation while other areas may see increases in wetlands and aquatic ecosystem connectivity. Climate driven changes in geomorphic processes will alter sediment transport, nutrient-loading, and lake chemistry, which all interact with air temperature to affect lake thermal characteristics and productivity (Prowse et al. 2006*a*). However, the implications of simultaneous climate change and geomorphic evolution for lakes in high northern latitudes has not been examined beyond permafrost systems.

We investigated the relative importance of non-permafrost driven geomorphic evolution and climate change on the thermal characteristics of a large and shallow Alaskan lake that supports regionally critical fisheries for sockeye salmon (*Oncorhynchus nerka*). Specifically, we use a hydrodynamics model to evaluate how lake thermal characteristics have responded to contemporary climate warming and lake shallowing, and to assess the potential efficacy of restoration strategies targeted to limit or reverse the trajectory of geomorphic evolution (outlet erosion and inlet tributary migration) in this lake.

Study site

The Chignik system (N56°16' W158°50', Figure 3.1) on the Alaska Peninsula is a topographically diverse watershed, draining southward to the Gulf of Alaska through two lakes and a semi-enclosed lagoon. Our focal lake, Black Lake, is a large (35 km^2), shallow (max depth ~ 4 m, volume ~ 0.041 km^3), and turbid lake surrounded by low lying topography on the north side of the Alaska Peninsula (Figure 3.1). Volcanic and glacial activity was important for the formation and evolution of Black Lake. The recession of the Late Wisconsin glacial ice-cap 12,000-10,000 years ago (Miller and Smith 1987) left a terminal moraine that forms the northern shore of Black Lake (Knappen 1926). Large, caldera forming eruptions of Mt. Veniaminof approximately 3700 years ago created debris flows exceeding 50 km (Miller and Smith 1987) that was likely important for defining the basin of ancient Black Lake.

As throughout Alaska (Stafford et al. 2000), the Chignik watershed has experienced significant increases in air temperatures between 1960 and 2005 with spring (April – June) air temperatures increasing by approximately 1.4°C (Westley 2007). These warming air temperatures are also associated with a shift towards earlier ice breakup as observed in several other southwestern Alaskan lakes (Schindler et al. 2005; The University of Washington Alaska Salmon Program (UW-ASP) unpubl. data). Simultaneously, fluvial geomorphic processes of the West Fork River, Black River, and Alec River have driven rapid evolution of the upper Chignik watershed (Figure 1). The West Fork River drains the glaciers of Mt. Veniaminof carrying high loads of volcanic sands and gravels (Knappen 1926) and deposits the sediment at its confluence with the Black River, the outlet tributary of Black Lake (Figure 3.1). Historically, this confluence was upstream (north) of its current location and West Fork sediment inputs stabilized an underwater sill maintaining Black Lake storage capacity (Ruggerone 2003; Elhakeem and Papanicolaou 2008). Downstream migration of the West Fork and bed erosion in the Black River channel has resulted in a two meter drop in lake level and a 40% loss of Black Lake volume since 1960 (Ruggerone 2003; Elhakeem and Papanicolaou 2008).

Additionally, there have been substantial migrations of Black Lake's primary inlet tributary, the Alec River. The Alec River is a snowmelt and groundwater fed river draining the watershed east of Black Lake. In the 1960s the North channel carried the majority of Alec River volume into the main lake body. Currently, the South channel carries 50 – 70% (Ruggerone 2003; UW-ASP unpubl. data) of the water volume to a bay at the lake outlet causing a permanent sand spit to develop between the outlet bay and main lake (Ruggerone 2003). With continued migration of the South channel the Alec River may eventually bypass Black Lake and connect directly with the Black River, depriving the lake of its main water source. The continued erosion in Black River coupled with Alec River channel migration is predicted to cause a loss of 80% of the 1960s storage capacity by ~2100 (Elhakeem and Papanicolaou 2008).

Warming air temperatures and landscape evolution have coincided with changes in Black Lake juvenile sockeye salmon life histories. Sockeye salmon are the dominant salmonid in the Chignik watershed and are the primary target of commercial and subsistence fisheries. Annual commercial harvests averaged 1.7 million fish between 1977 and 2009. Sockeye salmon spawn in the inlet tributaries to Black Lake, notably in the Alec River, and fry migrate to Black Lake in early spring. Fry spend most of their first summer growing rapidly in the warm and productive habitat of Black Lake then migrate downstream to Chignik Lake in mid- to late-summer to overwinter. The following spring, smolts migrate to the Gulf of Alaska. Median date of Black Lake summer fry emigration was significantly earlier in 1991-1992 and 2005-2006 than in the early 1970s (Westley et al. 2008). Migrants in 2005 had lower body condition (weight at a given length) than fry remaining in Black Lake, an indication that emigrating fry were experiencing metabolic stress. Juvenile sockeye also no longer overwinter in Black Lake (common in the 1960s), either because summer thermal stress causes pre-winter downstream migration or overwintering fish do not survive due to low dissolved oxygen during ice cover (Ruggerone 2000).

Concerns about diminishing harvests and lack of rearing capacity for sockeye salmon in Black Lake are the motivation for developing restoration strategies to reestablish historical lake water storage capacity, decrease winter oxygen stress, and reduce summer thermal stress. An outlet control structure has been proposed to stabilize the Black River sill and restore Black Lake storage capacity (Elhakeem and Papanicolaou 2008), but its effects on Black Lake habitat quality have not been evaluated. We validated the use of a hydrodynamics model to predict Black Lake thermal regimes and then reconstructed two lake thermal regimes pre-1977 and two current lake thermal regimes to assess the relative importance of changes in air temperature and geomorphically driven lake volume decline on lake thermal characteristics. We also evaluated the relative consequences of restoration or continued landscape evolution and tributary connectivity for future lake temperature regimes.

Methods

Model

We used the Dynamic Reservoir Simulation Model (DYRESM; Imberger and Patterson 1981), a process-based, one dimensional hydrodynamics model designed for lakes and reservoirs to simulate thermal conditions in Black Lake during summer. The hydrodynamics of aquatic systems depend on density differences that can be affected by both temperature and salinity (Antenucci and Imerito 2002) although we only considered thermal conditions here. The majority of energy for heating, mixing, and stratifying the lake is drawn from surface energy fluxes (e.g., evaporation, sensible heat, long wave radiation) and wind stress (Antenucci and Imerito 2002). Daily meteorological and hydrological data in conjunction with lake bathymetry and a lake specific light extinction coefficient are used to predict daily vertical temperature profiles during the ice-free season. Our model simulations are limited to days 163 to 237 (11 June – 24 August) of the year based on input data availability from 2008.

There are two overarching questions addressed by our modeling scenarios. We compared the effects of changes in air temperature and lake volume between historical and contemporary conditions in years which juvenile sockeye salmon out migration timing was observed. These simulations compared the effects of changing lake volume vs. warming air temperatures on Black Lake thermal regimes. We assessed future lake thermal conditions under outlet stabilization (restoration) and further volume decline scenarios. In these latter simulations, we compared situations of relative connectivity of Alec River to Black Lake (100%, ~50% with observed inseason variation, and 0%). We compared the lake thermal responses to restoration and further volume decline under both warm (e.g., 2005) and cool (e.g., 2008) air temperature conditions. The simulations are described in greater detail in the Modeling Scenarios section.

Model inputs

Bathymetry

A geo-referenced bathymetric survey of Black Lake was conducted in July 2007. Depth was measured using a stadiarod and a bathymetric map was created in ArcGIS 9.2 (Environmental Systems Research Institute) using the kriging algorithm. The horizontal lake area upstream of the lake outlet was estimated for two meters above the existing water elevation from United States Geological Survey (USGS) 15-minute digital elevation models for the region. A second order polynomial model was fit to describe the lake horizontal area - depth relationship. This model explained >99% of the variation in the data and both coefficients were significant (area (m^2) = 5299983 x elevation + 919604 x elevation^2; where elevation is the height in m from the deepest point of the lake bottom).

Extinction coefficient

The Alaska Department of Fish and Game measured light (photosynthetically active radiation (PAR)) intensity at 0.5 m intervals at a single Black Lake site once per month during summer (Finkle 2006). These data were used to calculate the light extinction coefficient. DYRESM uses a single light extinction value, therefore the seasonal average extinction coefficients were used for 2005 (mean = 0.95 m^{-1}, May, June, August sampled) and 2008 (mean = 1.5 m^{-1}, May, June, July sampled).

Hydrology

The Alec and Black Rivers were gauged by the United States Geological Survey (USGS 15297580, USGS 15297585) from 19 May 2004 until 30 September 2005. The Alec River gauge was located upstream of the channel divergence. Additionally, we have conducted regular cross-sectional discharge measurements at high and low flows in both Alec River channels since 1990. In 2008, Intech Water Height Temperature Loggers (Christchurch, New Zealand) were installed in the two Alec River channels, Black River, and two minor tributaries to provide a more comprehensive view of Black Lake hydrology. Water height – discharge relationships were established for each river and used to calculate daily discharge in 2008. A fraction (~15-20%) of the hydrologic budget for Black Lake is composed of unmeasured groundwater inputs and small surface flows. For both 2005 and 2008, we used a mass balance approach (external to the DYRESM model) to solve for this unknown component on a daily time step. Change in lake volume is equal to the precipitation and inflows minus the outflow and evaporation. Lake level change was estimated for 2005 using outlet height measurements taken approximately every two weeks. In 2008, it was directly measured with stage gauge installed in Black Lake. Evaporation was estimated as in Antenucci and Imerito (2002). During model simulations we input all inflows, including the unknown contribution calculated above, and allowed DYRESM to calculate outflow for each simulation. DYRESM calculated the outflow based on the specified outlet height which was set to 4.0 m for the baseline simulations. This maintained a specified lake level for each simulation and allowed the energy fluxes to determine outlet discharge.

Discharge from the Alec River peaked in late June in 2008 due to a cold spring (Figure 3.2B). This volume was two times greater than the peak flows observed during the 2005 simulation period. Peak spring runoff in 2005 occurred prior to the simulation period (month of May) due to the very warm spring. However, 2008 discharge declined steadily over the simulation period, resulting in low late summer flows during August. In contrast, 2005 experienced several summer precipitation events leading to higher and variable discharge in late summer (Figure 3.2B).

Average daily inflow temperature inputs to the model were taken from observations by USGS (2005) and University of Washington (2008) stage gauges. Inflow temperatures during the summer of 2005 ranged from 6.5 – 13.5°C and in 2008 ranged from 3-11°C. Unknown water source temperatures (surface and groundwater) were input as the minimum daily Alec River temperature.

Meteorology

DYRESM meteorological inputs include air temperature, vapor pressure, short wave solar radiation, cloud cover, wind speed, and precipitation. For 2005 simulations we used meteorological data collected by the National Oceanic and Atmospheric Administration (NOAA) near Chignik Bay (~30 km from Black Lake). These data include air temperature (Figure 3.2A), cloud cover, precipitation, dew point and wind speed. Vapor pressure was calculated from dew point measurements (Glassy and Running 1994). Daily mean insolation was not measured and was calculated using Reed's formula (1977; Eq. 1) based upon latitude and seasonal sun position and corrected for cloud cover (Reed 1977); Eq. 3). Air temperatures in the summer of 2005 were among the warmest of the decade. Following a warm and early spring (NOAA Climate Data Online, http://www7.ncdc.noaa.gov/CDO/cdo), air temperatures ranged from 10-18°C over the course of the summer.

In 2008, we mounted a Microstation Data Logger (Onset) on a cabin on the shore of Black Lake. The data collected were air temperature (Figure 3.2A), relative humidity, solar radiation, wind speed and precipitation. Vapor pressure was calculated from air temperature and relative humidity (Antenucci and Imerito 2002). Cloud cover data were obtained from the Chignik Bay station. Air temperatures during the summer of 2008 were among the coolest of the decade ranging from 7-13.5°C (Figure 3.2A).

Black Lake water temperature measurements

Temperature loggers were deployed in Black Lake in 2005 and 2008 during the June – August time period. In 2005, a single iBCod-Z thermister (Alpha Mach, accuracy ±1°C), was deployed at approximately 1.0 m from the bottom off Hydro Point (N56.47153 W158.99966), the deepest location in Black Lake. In 2008, Onset HOBO Pro v2 Water Temperature Data Logger (accuracy ±0.2°C) loggers were deployed at approximately 0.5 m below the surface at three stations: Hydro Point, Alec Bay (N56.46622 W158.96517), and Outlet Bay (N56.43559 W158.95186). Additionally, an Onset HOBO Pro v2 Water Temperature Data Logger was deployed 0.5 m from the lake bottom at Hydro Point in order to detect any lake stratification. These observations were used to verify model predicted water temperatures.

Modeling scenarios

After demonstrating agreement between observations and model predictions for Black Lake during 2005 and 2008, we explored several alternative scenarios as described below.

Relative effects of climate change and geomorphic evolution

We assessed whether contemporary Black Lake thermal characteristics differ from conditions in 1971 and 1972, as indicated by juvenile sockeye behavior and body condition, due to either geomorphic or climate conditions. We asked whether climate variables in 1971, 1972, and 2005 generated differences in Black Lake thermal regimes. We assessed if geomorphic evolution (lake volume or depth change) would increase or decreases the similarity of lake thermal regimes between 1971-1972, and 2005. These years were compared because data also were collected on juvenile sockeye emigration from Black Lake that indicated substantial change in emigration timing. We limited our climate analyses to variations in air temperature and vapor pressure conditions due to minimal historical meteorological data and a lack of hydrological data for the time period. Input data other than air temperature and vapor pressure were taken from 2005 and 2008 observations, and included all other meteorological inputs (solar radiation, wind speed, precipitation) and inflow discharge and temperature. The simulation for each year (1971, 1972, 2005) was run for each set of background conditions (2005 and 2008). Average daily air temperatures for each simulation year were obtained from the NOAA Chignik Bay station. For 1971 and 1972, vapor pressure was calculated using minimum daily temperature observations as a proxy for dewpoint temperature (Glassy and Running 1994). The years 1971 and 1972 had cold springs and cooler than average summers (mean air temperature 11-12°C, Figure 3.2A). The differences among 1971 and 1972 air temperature regimes and 2005 during our simulation period are most pronounced in early summer. However, 1971 and 1972 air temperatures were similar to those observed in 2008, another cooler than average summer (Figure 3.2A).

The simulations for 1971 and 1972 were initialized with a lake temperature estimated from the strong relationship between Chignik Bay (CB) average daily air temperature and observed Black Lake water temperatures (BLWT) (May – September) across several years between 1990-2008 ($BLWT = 0.853 \times CB - 2.841$, $r^2 = 0.787$, $p<0.0001$). The first five days of the simulation were not included in the analyses to minimize effects of initial conditions.

We addressed geomorphic evolution by conducting the simulations described above for lake basins with maximum depths of four and six meters. These simulations for 1971 and 1972 were compared to 2005 climate simulations with maximum depth of four meters.

Restoration assessment

We assessed the effect of potential management actions on lake thermal regimes under cold year (2008) and warm year (2005) conditions (Figure 3.3). The mean summer air temperature (calculated from the Chignik Bay station) was 2.2°C greater in 2005 than 2008. Mean temperatures in June, July, and August of 2005 (10.9°C, 12.9°C, 13.6°C) were among the warmest in the decade (1998-2008) while 2008 air temperatures (8.3°C, 10.5°C, 11.9°C) were among the coldest (Figure 3.2A).

Outlet stabilization

We assessed the effects of an outlet stabilization and storage capacity restoration strategy (Elhakeem and Papanicolaou 2008) on lake thermal characteristics. In addition, we assumed that lake connectivity to the Alec River tributary was maintained using a gated weir as stated by the restoration objectives described by Elhakeem and Papanicolaou (2008). We evaluated the effect on lake thermal characteristics for increases in storage capacity ranging from 70 -160 percent (maximum depth 5.0 – 6.0 m).

Volume decline and inlet connectivity

We also addressed the effect of continued lake volume declines on Black Lake thermal regimes, ranging from losses of 48 to 80 percent of the contemporary lake volume (maximum depth 3.0 – 2.0 m). Lake volume declines were assessed under three potential hydrologic scenarios: 1) High Alec River connectivity; 2) Reduced Alec River connectivity; and 3) complete loss of (No) Alec River connectivity. These simulations consider only a single basin because DYRESM is a one-dimensional model. The first scenario assumed the total Alec River volume directly enters the lake basin. The second scenario addresses a partial loss of connectivity due to the continued downstream migration of the south channel. The proportion of Alec River discharge carried by the south channel varies between 50% and 70% with higher proportions in the south channel during low flows (Ruggerone 2003). The changing proportion across the season is reflected in the partial connectivity scenario. Proportion of flow delivered via each channel was measured every two weeks in 2005 when instantaneous discharge was measured, while in 2008 gauges in each channel captured the daily relative proportion. This scenario removed South Alec discharge from the lake basin. Finally, the third scenario considered a large scale Alec River channel migration substantially downstream of Black Lake resulting in no Alec River inputs to the lake.

Results

Water temperature observations

Black Lake mean daily water temperature between 06 June and 31 August in 2005 ranged from 9.8°C to 17.5°C in the main lake basin. In 2008, mean daily water temperatures ranged from 8.8°C to 16.5°C. On average, the water temperatures in the lake were 3.4°C warmer than Alec River inflow temperatures in 2005 and 4.5°C warmer in 2008. Water temperatures between the surface and lake bottom differed on average by 0.12°C in 2008, indicating that the lake is well mixed throughout the summer season. Water temperatures measured by temperature loggers in the main basin (Hydro Point and Alec Bay) differed on average by 0.3°C and by less than 1°C over 97% of the time. Water temperatures between these sites and the Outlet Bay site differed by less than 1°C 40% of the time and the mean absolute difference was 1.3°C. The outlet bay is approximately 18% of the lake area and only 10% of the volume. The outlet temperatures are typically cooler than the main lake basin which may be due to the proximity to the mouth of the South Alec channel. Therefore, we believe a one dimensional model, such as DYRESM, is suitable for describing the hydrodynamic characteristics of the Black Lake main basin because it is horizontally homogeneous.

Model validation and calibration

DYRESM simulations for daily temperature were robust for two summers with very different environmental conditions. Simulations captured within-season Black Lake warming and cooling patterns extremely well (Figure 3.4, Table 3.1). DYRESM simulations did not produce thermal stratification, consistent with observations in 2008 (stratification is also not mentioned in historical reports, (Narver 1966; Burgner et al. 1969)).

In 2008, the use of local meteorological and hydrological input data resulted in a robust prediction of Black Lake temperatures through time without adjusting any model parameters. It is expected that DYRESM does not require parameter calibration if the input data are of sufficient quality. DYRESM captured 88% of the observed variation in mean daily water temperature with a mean absolute error of 0.54°C (SD = 0.44, min. = 0.0007, max. = 1.82).

For 2005, the uncalibrated DYRESM simulation captured 67.8% of the variation but over-predicted mean daily water temperatures by 2°C, on average. Insolation formulae can over-predict radiation intensity at the surface (M. Hipsey, Center for Water Research University of

Western Australia, pers. comm.), therefore DYRESM short wave radiation inputs were reduced until we obtained the best model fit. A reduction of 31% led to the best prediction of water temperatures. The 2005 adjusted solar radiation DYRESM simulation captured 73% of the variation in the data and predicted mean daily temperatures with a mean absolute error of 0.69°C (SD = 0.50, min. = 0.01, max. = 2.02). The calibrated inputs were not considered a validation of the model for Black Lake and were used to have an improved baseline from which to conduct simulations. In both years, DYRESM predicted total degree days within less than two percent of the observed over the time period from 11 June – 24 August (Table 3.1).

Thermal characteristic metrics

We used two metrics to compare simulated thermal regimes among scenarios. The seasonal degree days are the sum of the daily mean temperature across the entire simulation. This is a measure of the thermal capacity of the system that has implications for biological production. We also characterized the lake by the number of days where the mean temperature exceeded 15°C. At maximum consumption rates, 15°C is the optimal temperature for growth for juvenile sockeye salmon (Brett 1971). The optimal temperature for growth decreases substantially with decreasing feeding rate. Therefore, we characterize days greater than 15°C as a conservative measure of the days under which sockeye experience sub-optimal and thermally stressful metabolic conditions. These metrics are calculated for a standard period, days 168 to 237, which is shorter than the period used for validation and calibration

Modeling scenarios

Relative effects of climate change and geomorphic evolution

Black Lake thermal regimes simulated using 1971 and 1972 air temperatures were substantially cooler than those using 2005 air temperatures. Cooler thermal regimes in 1971 and

1972 are apparent in both degree days and the proportion of days exceeding 15°C metrics (Figure 3.5). Historic-contemporary year comparisons were made between simulations using the same input conditions (2005 or 2008).

Degree day predictions for a given air temperature simulation (1971, 1972, or 2005) were very similar for 2005 and 2008 inputs and differed on average by 21 degree days (~2% total summer degree days). Therefore, the summer heat content of the lake appears to be strongly tied to air temperature conditions. Comparing scenarios for a lake with a maximum depth of four meters, 2005 had 10% more degrees than 1971 under both input conditions. The same volume comparison with 1972 shows 11% and 13% more degree days in 2005 (2005 and 2008 conditions, respectively) (Figure 3.5A). Simulations with historic air temperatures and greater lake volume (6 m max. depth) had a slight cooling effect, increasing the warming effect observed between 2005 and the historic period to 11-12% (1971) and 13-14% (1972) (Figure 3.5A).

The percent of days exceeding 15°C increased from 17% in 1971 (2005 inputs) to 30% in 2005 (2005 inputs) (Figure 3.5B). While 2008 inputs led to a greater percentage of days exceeding 15°C overall, air temperature conditions still produced a similar increase from 1971 (29%) to 2005 (46%) (Figure 3.5B). The difference in the percent of days exceeding optimal conditions was even greater between 1972 and 2005 with only 0% and 20% of days (2005 and 2008 input conditions, respectively) exceeding 15°C in 1972. Increased volume had weaker influence on lake thermal regimes than change in air temperature alone, but also did contribute to fewer days greater than 15°C in 1971 under both input conditions (Figure 3.5B).

Restoration assessment

<u>Outlet stabilization</u>

A structure placed at the outlet of Black Lake would increase Black Lake maximum depth and substantially increase storage capacity. However, DYRESM scenarios increasing maximum lake depth by up to two meters had little effect on lake thermal characteristics. Thermal stratification did not develop, a result consistent with surveys conducted in the 1960s (Narver 1966; Burgner et al. 1969) when the maximum depth of Black Lake was six meters. Among cold and warm years, increasing maximum depths by one to two meters led to minimal effects in accumulated degree days (-0.6% to 0.3%, Figure 3.6).

DYRESM also predicted that increases in maximum depth have little effect on the number of days surpassing the optimal temperature for juvenile sockeye growth, 15°C (Brett 1971). Warm and cold years exhibit substantial differences in the number of days greater than 15°C (30% and 10%, respectively) (Figure 3.6). However, within-year comparisons among maximum depth simulations showed slight declines in the number of days exceeding 15°C for both warm and cold years.

Volume decline and inlet connectivity

The thermal effects of continued decline in Black Lake volume vary with the hydrologic connectivity to the Alec River. Black Lake experienced a cooling effect if connectivity between the south Alec River channel and the lake was maintained. A loss of 80% of the volume led to a 6-7% decrease in degree days as well as a reduction in days at suboptimal temperatures for juvenile sockeye salmon (Figure 3.7). This appears to be both an effect of decreased heat storage capacity and decreased residence time (from 15 days to 3 days) coupled with relatively cool hydrologic inputs. In the warm year, an 80% volume loss decreased the number of days exceeding 15°C by two thirds. In the cool year, while the number of days exceeding 15°C was unchanged from reference conditions, there were fewer cumulative days exceeding all other temperatures leading to a substantially cooler thermal regime (Figure 3.7).

Lake cooling with decreased lake volume was not as prominent when connectivity of Black Lake to the south Alec channel was reduced. With declines in depth, the number of degree days decreased minimally (~2%) in both warm and cold years with an 80% volume loss (Figure 3.7). There was also a decrease in the coherence of the response between warm and cool year environmental conditions in the two meter basin. Partial connectivity in the warm year provided sufficient hydrologic flow to support lake cooling while in the cool year (with lake temperatures already quite cool) lake thermal regimes were similar to the reference condition, there were greater number of days with temperatures exceeding 15°C.

Complete loss of Alec River connectivity led to increases in degree days with all volume declines as well as increases in the number of stressful days for juvenile sockeye (Figure 3.7). This pattern was strongest under cold environmental conditions, which may be driven primarily by two short intense warming periods in mid-summer (Figure 3.4) where temperatures were close to the 15°C threshold. Thus, the most important effect of geomorphic evolution on lake thermal regimes was the loss of connectivity to cool inlet streams rather than loss of volume due to outlet erosion.

Discussion

Our model results were able to parse out the relative importance of air temperature conditions and morphometric change for simulated lake thermal regimes to provide insights into the mechanisms driving observed biological change in a lake that has become substantially shallower in the last 50 years. It has long been recognized that Black Lake water temperatures are closely coupled to air temperatures and respond quickly to air temperature changes (Narver

1966). However, the interaction between lake volume and air temperature in Black Lake has been less well understood. Substantial differences in air temperature existed between the summers of 1971-72 (cooler) and 2005 (warmer). Simulations incorporating these historic air temperatures showed differences in cumulative degree days and the proportion of summer days exceeding the temperature of optimal growth between the cooler summers of 1971-1972 and warm 2005. These simulations used the same meteorological and hydrological data and therefore do not incorporate differences in discharge, precipitation etc. that may have occurred between the two periods. Differences in temperature did occur between simulations using different base years, indicating that discharge and additional meteorological data influenced lake temperature. The air temperature signal was much stronger than variations in inputs for discharge and other meteorological parameters, thereby lending confidence to our conclusion that the lake thermal regimes did differ due to air temperature among these years.

Accounting for the historic lake volume in the 1971-72 simulations led to minimal decreases in the proportion of days exceeding the temperature thresholds for juvenile sockeye. Overall, changes in air temperature, not lake volume, drove the differences in lake temperature between 1971-72 and 2005 thermal regimes. Lake morphometry can play a more important role for lake thermal regimes when stratification develops. Our modeling results are consistent with a previously developed relationship between stratification and lake geometry. Specifically, the minimum lake depth required for a lake of a given area to develop thermal stratification (Gorham and Boyce 1989). The lake geometry ratio is defined as $A_s^{1/4}:H_{max}$ where A_s is the lake surface area (m^2) and H_{max} is the maximum depth (m). Lakes with a lake geometry ratio greater than 2.9 do not stratify whereas lakes with smaller values may stratify. Black Lake at its current surface area and depth has a ratio of 19.2 whereas during historic conditions the ratio was still large at

14.9. The ratios for both current and historic conditions are substantially larger than the threshold value of 2.9. Therefore, the likelihood of changes in morphology influencing lake thermal regimes through stratification was unlikely and supports the mechanistic predictions based on DYRESM.

The lake geometry ratio was used by Stefan et al. (1996) to explore the relative importance of climate variables for a set of generic lake types. Lake morphometry did not play a strong role in determining surface water temperature, instead the latitudinal differences in climate were very influential. Their findings provide an interesting framework for our simulations. If their generic lake types are viewed as a gradient of lake evolution, rather than static lake shapes, that we may be able to predict when geomorphic evolution that alters lake morphometry may play a larger role for lake thermal regimes. In the case of Black Lake, our approach allowed a greater characterization of lake conditions beyond determining the stratification potential under historic conditions or a restoration scenario. We explored whether a change in lake volume could alter the lake thermal regimes without stratification via increased heat capacity or residence time. Furthermore, a hydrodynamics model approach allowed us to translate these conditions into metrics that were relevant to juvenile sockeye salmon physiology.

Air temperature driven changes in lake thermal conditions provide support for Westley et al.'s (2008) inference that early emigration by juvenile sockeye in 2005 was driven by thermal stress or by the inability to feed at rates necessary to grow under the warm conditions. Median date of juvenile sockeye emigration was almost a month earlier in 2005-2006 than 1971-1972 (Westley et al. 2008). 2005 had a very mild winter and a warm spring (NOAA Climate Data Online) and our simulations indicate very warm early summer water temperatures. It appears that this early summer temperature difference may play an important role in the mechanism underlying juvenile sockeye migration timing out of Black Lake, whereas simulations of lake volume offer little explanation for changes in migration timing due to thermal conditions.

If lake volume continues to decline, hydrologic connectivity of the Alec River to Black Lake will become increasing important in determining summer thermal regimes. Cooler lake thermal regimes are associated with a highly connected, shallow lake whereas reduced or no connectivity leads to unchanged or warmer lake thermal conditions. Therefore, geomorphic processes associated with inlet channel migration drive lake temperature responses to outlet erosion. Lake thermal regimes continue to respond strongly to air temperatures (*see* comparison of 2005 and 2008) but high connectivity has the potential to mitigate air temperature effects. Alternatively, outlet stabilization measures to increase the current storage capacity of Black Lake are likely to have little effect on thermal regimes experienced by juvenile sockeye. This is supported by both modeling the effect of additional volume under current climate conditions and the minimal cooling associated with historic volumes in 1971-72 thermal regimes. If inlet stream temperatures increase substantially in a warmer future climate, then the importance of connectivity to Black Lake will be diminished. However, 2005 was one of the warmest years of the decade and Alec River daily temperatures were on average 3.4 degrees cooler than Black Lake temperatures.

Black Lake morphometry has changed rapidly since the mid-1950s as a result of outlet erosion (Ruggerone 2003; Elhakeem and Papanicolaou 2008). However, our simulations demonstrate that air temperature is a much stronger driver of lake thermal regimes than lake volume. While there is substantial year to year variability in air temperatures, average air temperatures have been increasing on the Alaska Peninsula over the past 50 years (Stafford et al. 2000; Westley 2007). Our simulations demonstrate that increasing air temperature has a much greater effect on Black Lake thermal regimes than current extent of geomorphic evolution. However, hydrologic connectivity became increasing important in outlet erosion simulations and mediated the effects of air temperatures on a shallowing lake. Geomorphic process controlling hydrologic connectivity in these systems may not only have important consequences for lake temperatures but they may also respond to and change with future climate conditions. Considering these dynamics may be important for assessing the full range of lake responses to geomorphic evolution and climate change.

Characterizing how lake thermal properties are governed by changes in climate and ongoing geomorphic evolution is essential to assessing the vulnerability and resilience of aquatic ecosystems to future climate change. The underlying processes that form lakes of the arctic and sub-arctic are varied, including those formed by permafrost, glacial scour or moraine, melting ice blocks (kettle), and isostatic uplift (Mackay and Loken 1974; Prowse et al. 2006*b*). Therefore, lakes across the high northern latitudes are substantially varied in morphometry and associated characteristics such as seasonal stratification patterns. However, similar to Black Lake, many arctic lakes either mix vertically and have reduced stratification or are shallow and do not stratify (Prowse et al. 2006*b*). Additionally, in the sub-arctic, it has been noted that there are large windswept lakes that also do not stratify, limiting thermal refugia for resident fish (Schindler and Smol 2006). The consequences of changing air temperature for this range of lake types is well discussed in the literature, yet with little consideration for altered morphometry due to geomorphic evolution. Further investigations would be essential to explore the consequences of geomorphic evolution for the full range of lake types present in high northern latitudes, especially because the effect changing hydrology could vary substantially among lake types.

Additionally, the global distribution of lakes is heavily dominated by small lakes (area < 10 km^2) (Wetzel 1989; Downing et al. 2006) and lakes with mean depths less than 10m (Wetzel 1989). Shallow lake temperatures are very responsive to air temperature (Gerten and Adrian 2001) which in turn affects the regulation of nutrient cycling, habitat availability, and growth rates (Wetzel 1983). Our simulations of Black Lake confirm that the high sensitivity of shallow lakes to changes in air temperature have important consequences for lake thermal regimes. Air temperatures will likely be a dominant driver of future change in lake ecosystems, especially in northern landscapes experiencing increases in air temperature at rates up to twice the global mean. However, in these highly dynamic landscapes, further consideration of hydrologic connectivity may be important for some lake systems at landscape thresholds.

Table 3.1: Observed and model predicted Black Lake thermal characteristics. Below are mean Black lake temperatures and degree days for days 163 – 237 from 01 January 2005 and 2008.

	Year			
	2005		2008	
	Observed	DYRESM	Observed	DYRESM
Mean summer temperature (°C)	14.1	14.1	12.1	12.4
Degree days	1054.9	1058.4	909.6	928.3

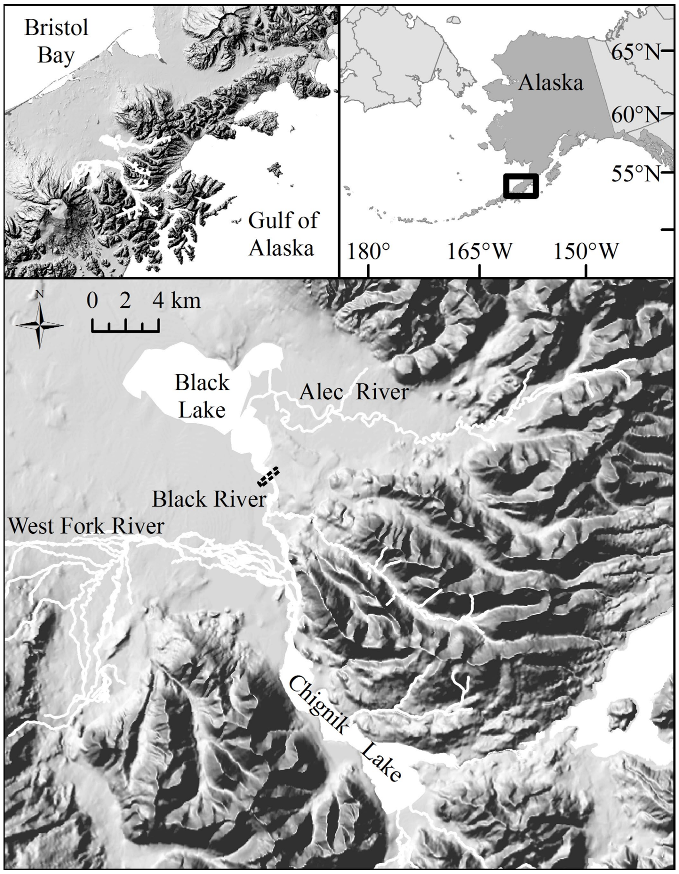

Figure 3.1: Chignik watershed, southwest Alaska, United States. Key features of the upper watershed landscape are indicated. The Alec River carries approximately 80% of the inlet water to Black Lake which flows out to Chignik Lake via the Black River at the southern bay of the lake. The location of the proposed outlet stabilization structure at the lake outlet is shown by the dashed rectangle.

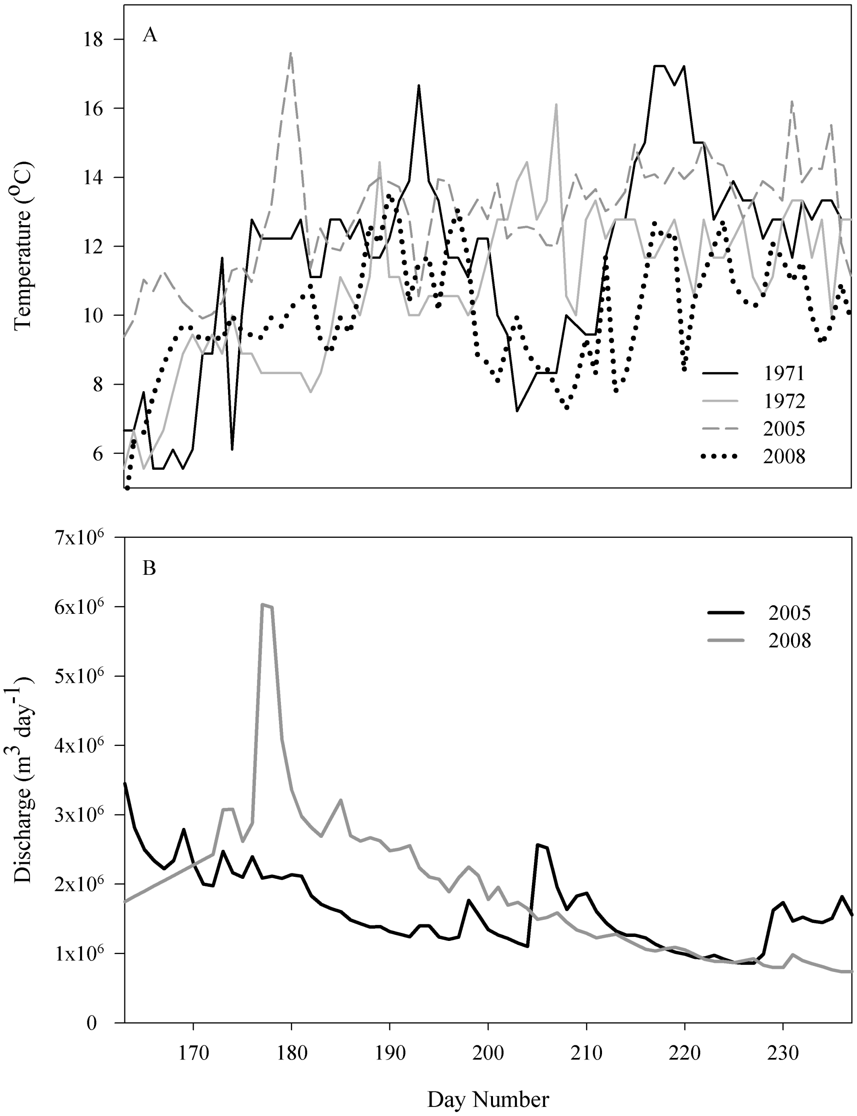

Figure 3.2: Regional air temperatures and Alec River hydrologic regimes during model scenario summers. (A) Mean daily air temperature for the baseline years (2005, 2008) and historic simulation years (19711, 1972) (11 June - 24 August). (B) Daily Alec River discharge during 2005 and 2008 (11 June - 24 August).

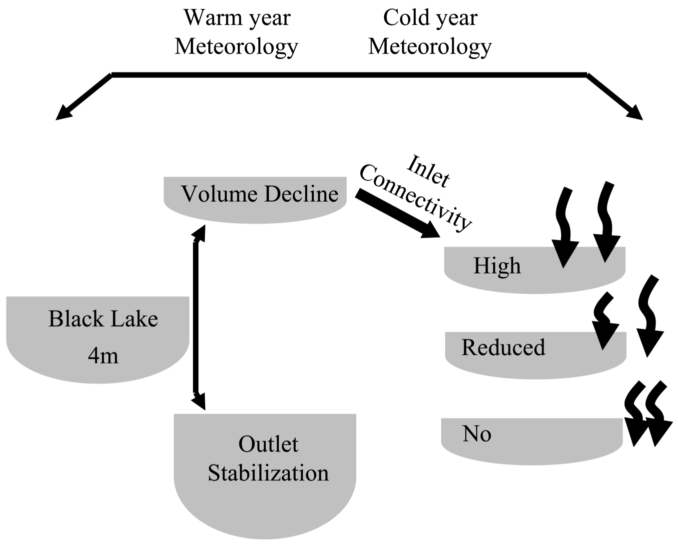

Figure 3.3: Schematic showing hydrologic restoration options under consideration. Under warm (2005) and cold (2008) environmental conditions outlet stabilization strategies and further volume decline scenarios are explored. Three levels of Alec River connectivity with the main lake body (High, Reduced, No) are compared under further volume decline scenarios.

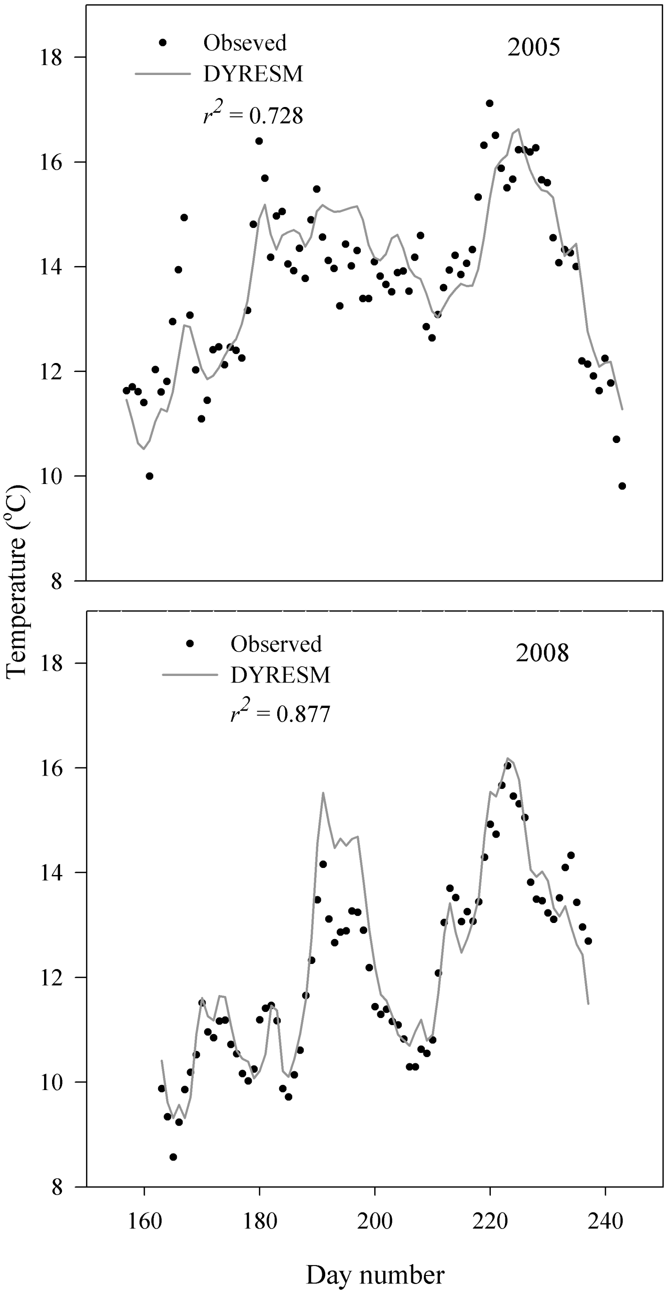

Figure 3.4: DYRESM outputs and observed daily water temperature. Comparison of DYRESM outputs and observations of Black Lake temperatures for 2005 (06 June – 31 August) and 2008 (11 June - 24 August)

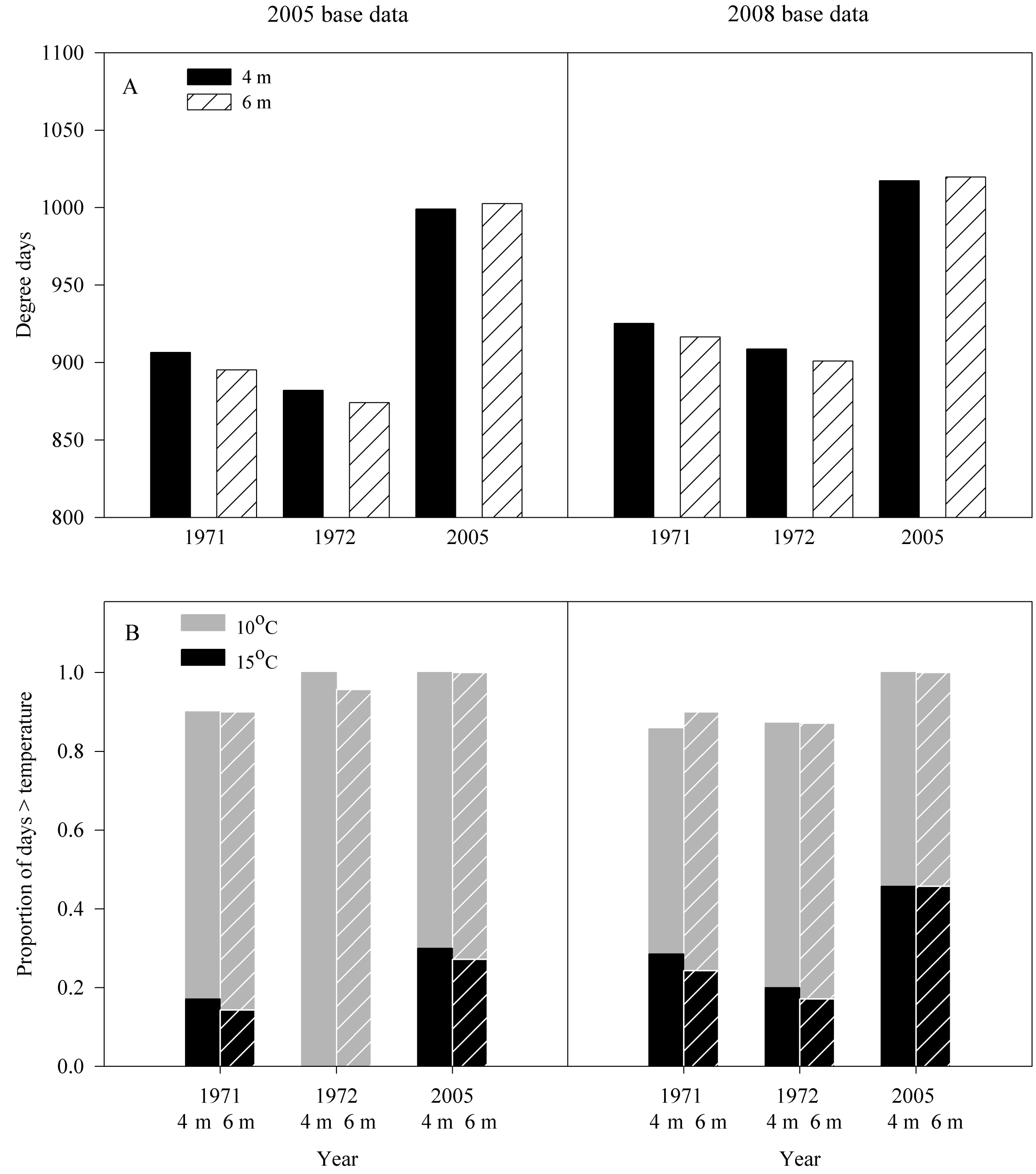

Figure 3.5: Relative affects of climate and landscape evolution on lake thermal regimes between 1971-1972 and 2005. Simulations are compared among like input baselines (2005 or 2008). (A) Number of summer degrees days (16 June – 24 August) and (B) proportion of days where the mean daily temperature exceeded 10°C (gray) and 15°C (black). In both figures the solid bars represent lake bathymetry with a maximum depth of 4.0 m (contemporary) and striped bars represent lake bathymetry with a maximum depth of 6.0 m (historic).

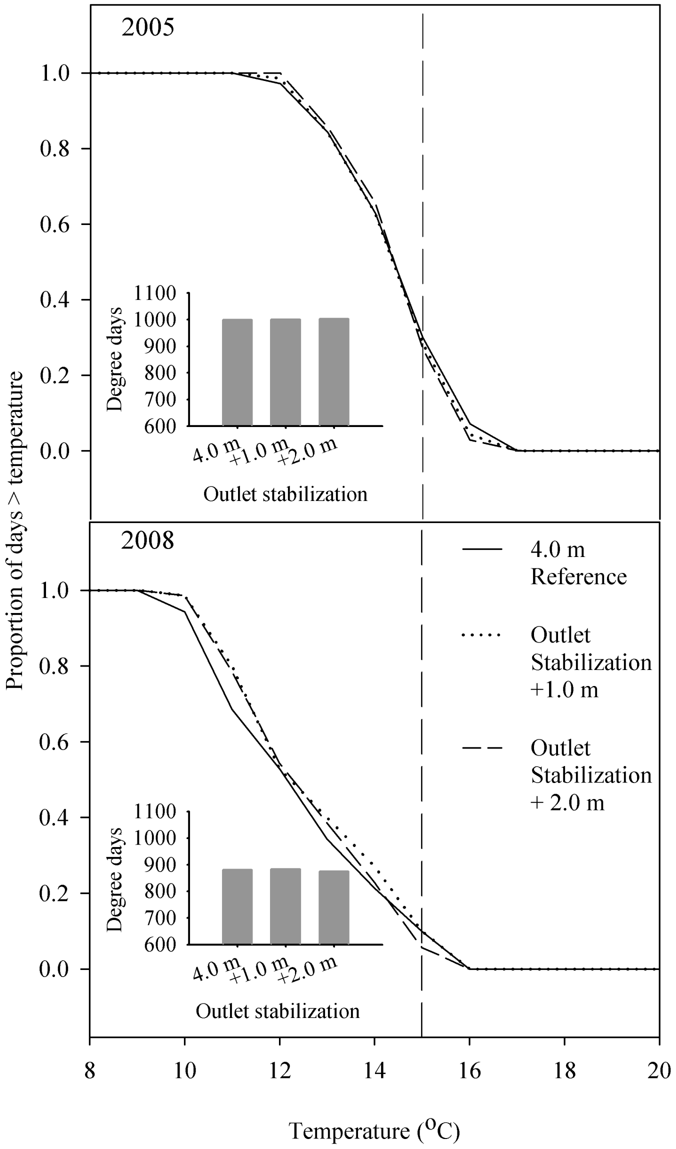

Figure 3.6: Outlet stabilization simulations. For 2005 and 2008, the proportion of days with the mean daily temperatures exceeding temperatures (ranging from 6 – 20°C) for two outlet stabilization scenarios and the reference lake. The vertical dashed line indicates the 15°C threshold. Inset figures show summer degree days (16 June – 24 August) for these three scenarios.

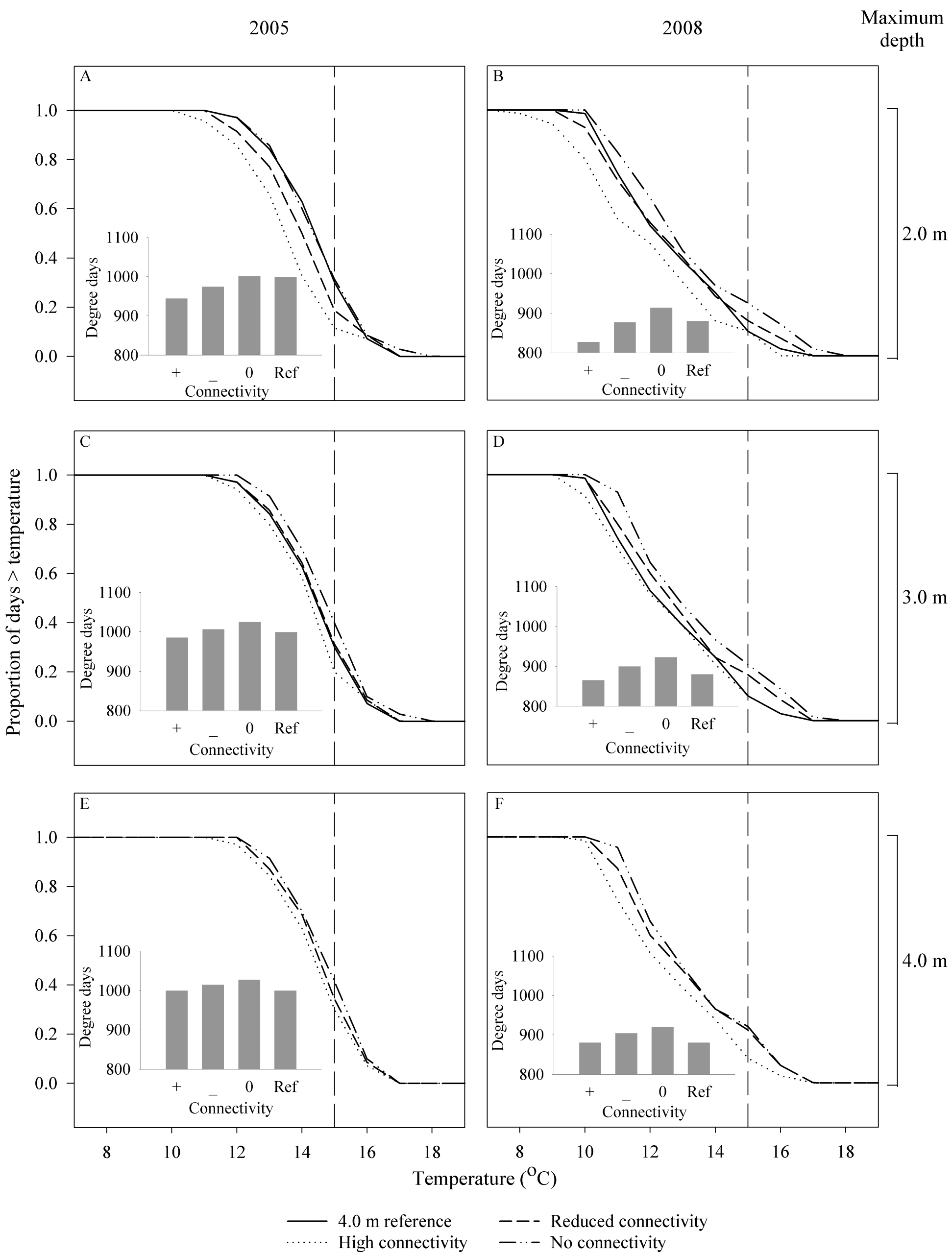

Figure 3.7: Volume decline and connectivity simulations. Under cold (2008) and warm (2005) year environmental conditions main figures show the cumulative proportion of days exceeding temperatures ranging from 6-20°C. (A, B) consider a large magnitude decline in volume (max depth 2.0 m), (C, D) depict a lesser volume decline (max depth 3.0 m), (E, F) depict the current lake volume (max depth 4.0 m). Each line represents a different level of Alec River connectivity to Black Lake. The vertical dashed line indicates the 15°C threshold. Inset figures show summer degree days (16 June – 24 August) for each connectivity scenario (+ = High connectivity, - = Reduced connectivity, 0 = No connectivity, Ref = Reference 4.0 m) for a given basin depth and environmental year.

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Chapter 4: Consequences of changing climate and geomorphology for bioenergetics of juvenile sockeye salmon in a shallow Alaskan lake[2]

Introduction

Temperature is a primary driver of lake ecosystem dynamics, regulating the rates of biological and chemical processes as well as producing physical structure in the water column (Wetzel 2001). The complexity of biological responses is a result of both of direct (physiological) and indirect (ecological) effects of temperature. Because they are ectotherms, environmental temperatures have profound effects on temperature-dependent physiological rates (consumption, metabolism, activity) of fish and ultimately their scope for growth (Elliot 1982, Jobling 1997). Warming due to ongoing climate change has and will continue to alter lake thermal conditions (Livingstone 2003; Magnuson et al. 2000; Schindler 1997; Stefan et al. 1996) and subsequently the growth and ecology of fishes (Magnuson et al. 1997; McDonald et al. 1996; Schindler et al. 2005).

Climatic forcing is overlaid onto a mosaic of regional and local landscape dynamics. Volcanic, glacial, fluvial, and thermokarst processes actively shape landscapes, including lake basins, and may occur over ecologically relevant time scales (Swanson et al. 1988). Ecologically relevant geomorphic evolution of lakes and the surrounding landscape can, therefore, occur simultaneously with contemporary climate change. Such lakes may respond to changing climate differently than lakes evolving on longer geologic times scales and, consequently, the physical and biological responses of these lakes will also differ. A challenge for ecologists is to understand the interactions between climate and geomorphology and the implications for

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[2] Full citation: Griffiths, J.R. and D.E. Schindler. 2012. Consequences of changing climate and geomorphology for bioenergetics of juvenile sockeye salmon in a shallow Alaskan lake. Ecology of Freshwater Fish 21 (3): 349-362

ecological processes and the services they provide (e.g., fisheries). These interactions are also important to the assessment of restoration measures used to address natural or anthropogenic geomorphic evolution. Without explicit consideration of climate change the consequences of restoration for future fish populations will be poorly characterized (e.g., Battin et al. 2007).

In high northern latitude lakes, cold temperatures and short growing seasons limit productivity (Brylinski & Mann 1973). Lakes in these regions are also particularly vulnerable to climate change because warming is occurring at rates up to twice the global average, with expectations that this trend will continue for at least a century (Christensen et al. 2007). Furthermore, these ecosystems are often highly dynamic due to their geologic histories and natural disturbance regimes due to lack of human development. Many such lakes in coastal Alaskan watersheds provide rearing habitat for anadromous Pacific salmon (*Oncorhynchus spp*.). Sockeye salmon (*O. nerka*) are especially dependent on lakes for rearing habitat, typically spending 1-2 years in freshwater prior to migrating as smolts to the marine environment (Quinn 2005). The summer growing period is contracted, occurring from roughly ice break-up in May or June through late September or October. This period of freshwater growth is crucial, as marine survival is positively correlated with smolt body size in Alaskan populations (Koenings et al. 1993). Temperature and growing season length are positively related to summer growth in Alaska (Edmundson & Mazumder 2001; Rich et al. 2009; Schindler et al. 2005) although growth responses will also depend on prey production and density.

Sockeye salmon are valuable as an economic, recreational, and cultural resource to communities throughout Alaska. Therefore, assessing the potential of climatic and geomorphic change to influence fish growth through changes to lake thermal regimes is needed for resource management and developing adaptation strategies for future climate change. Here we build upon previous research that assessed how past climate change and geomorphic evolution may interact to alter lake thermal regimes in a shallow Alaskan lake using a hydrodynamics model (Griffiths et al. 2011). We extend our original analyses to include future climate change and compare juvenile sockeye salmon growth under these thermal regimes to characterize sockeye salmon vulnerability to future climate and geomorphic change. Further, we assess the potential effects of future restoration efforts intended to ameliorate ongoing geomorphic evolution.

Study site

Physical characteristics

The Chignik watershed (N56°16' W158°50', Figure 4.1) on the Alaska Peninsula drains southward to the Gulf of Alaska through two lakes and a semi-enclosed lagoon (Figure 4.1). Black Lake is a large (35 km^2), shallow (max depth ~ 4 m), and turbid lake surrounded by low lying topography on the north side of the Alaska Peninsula. The lake is highly sensitive to variation in air temperature (Narver 1966) with ~50% of the variation in mean daily summer water temperature explained by air temperature and is highly productive for southwestern Alaskan sockeye salmon lakes (Burgner et al. 1969). Volcanic and glacial activity has strongly influenced the formation and evolution of Black Lake. A terminal moraine from the recession of the Late Wisconsin glacial ice-cap 12,000-10,000 years ago (Miller & Smith 1987) forms the northern shore of Black Lake (Knappen 1926). Also the large, caldera forming eruptions of Mt. Veniaminof approximately 3,700 years ago likely had a large impact on ancient Black Lake with debris flows exceeding 50 km (Miller & Smith 1987).

Geomorphic change

Fluvial geomorphic processes in the West Fork River, Black River, and Alec River have characterized the rapid evolution of the upper Chignik watershed. Sediment transport, downstream migration of the West Fork, bed erosion in the Black River channel, and sediment infilling have resulted in a two meter drop in lake level and a 40% loss of Black Lake volume since 1960 (Elhakeem & Papanicolaou 2008; Ruggerone 2003). Substantial migrations of Black Lake's primary inlet tributary, the Alec River, have also occurred during this period. While in the 1960s the North channel carried the majority of Alec River volume into the main lake body, the South channel currently carries 50 – 70% of the water volume to a bay at the lake outlet (Ruggerone 2003, University of Washington-Alaska Salmon Program (UW-ASP) unpublished data). A permanent spit has also developed between the outlet bay and main lake (Ruggerone 2003). With discharge continuing to migrate to the South channel and the growth of the spit, there is concern that the main lake basin may eventually be deprived of its main water source. If lake volume continues to decline at similar rates, a loss of 80% of the 1960s storage capacity is predicted by ~2100 (Elhakeem & Papanicolaou 2008). A proposed restoration strategy would stabilize the lake outlet and raise the lake level to restore the majority of the Black Lake's historic storage capacity (Elhakeem & Papanicolaou 2008). In the process of doing so, migration of the Alec River away from Black Lake would also be eliminated, thereby maintaining connectivity of the main source of water to the ecosystem.

Climate change

Climate warming has been observed throughout Alaska in the last half century (Stafford et al. 2000). Spring air temperature (April – June) has increased in the Chignik watershed by approximately 1.4°C (Westley 2007) between 1960 and 2005. A shift to towards earlier ice breakup has been observed in several southwestern Alaskan lakes (Schindler et al. 2005, UW-ASP unpublished data). For example, ice break-up on Lake Aleknagik in Bristol Bay now typically occurs about 7 days earlier than in the mid 20th century in which a positive phase of the Pacific Decadal Oscillation (PDO) has amplified an underlying warming trend.

Projections of future climate conditions from global circulations models show warming in all seasons in Alaska (Christensen et al. 2007). While the greatest warming in Alaska is projected to be in fall and winter, warming in summer months is also projected to be substantial. Mean summer temperatures of coastal regions around 60°N are projected to increase on average by 2°C by 2050 under mid-range greenhouse gas emission scenarios (Schindler & Rogers 2009).

Sockeye salmon

Sockeye salmon are the dominant fish species in the Chignik watershed and are the primary target of commercial and subsistence fisheries. Sockeye salmon spawn in the inlet tributaries to Black Lake, notably in the Alec River, during August and September. Spawning escapements (i.e., the component of the stock that is not harvested) to Black Lake averaged 460,000 fish annually from 1977-2009. Fry emerge in April and migrate downstream to Black Lake where they rear for a variable amount of time before migrating to the ocean the following spring.

Historically, the majority of sockeye salmon reared in Black Lake for a complete year before migrating to the ocean (Burgner et al. 1969). However, climate change and geomorphic evolution have likely placed a number of constraints on summer rearing and overwintering (Ruggerone 2000) in Black Lake such that fry now emigrate downstream by winter after their first growing season and spend a substantial component of their freshwater rearing in Chignik Lake where they may compete with Chignik Lake origin sockeye salmon (Simmons 2009). Median date of Black Lake summer fry emigration was significantly earlier in the warm years 1991-92 and 2005-06 than in the cold, early 1970s (Westley et al. 2008). Migrants in 2005 had lower body condition (weight at a given length) than fry remaining in the lake. This indicated that emigrating fry were experiencing elevated metabolic rates due to warmer temperatures and were unable to physiologically or behaviorally compensate for those elevated rates while in Black Lake.

Black Lake's sensitivity to air temperature could strongly affect juvenile sockeye salmon rearing conditions under future climate change with lake thermal regimes warming in response to increased air temperature. However, hydrologic connectivity and geomorphic evolution may interact with future climate change to dampen or accentuate thermal stress. Griffiths et al. (2011) used a hydrodynamics model to simulate water temperatures for a range of geomorphic evolution and climate (past and current) scenarios. We expanded upon these simulations, using the hydrodynamics model to assess the effects of future air temperature increases on lake thermal regimes. We coupled water temperature predictions from the hydrodynamics model to a bioenergetics model for sockeye salmon (Beauchamp et al. 1989; Hanson et al. 1997) to assess the metabolic costs and consumption compensation by juvenile sockeye salmon to alternate future climate, geomorphology and restoration scenarios.

Methods

Water temperature model and simulations

Hydrodynamics model

Griffiths et al. (2011) validated the use of the Dynamic Reservoir Simulation Model (DYRESM, Imberger & Patterson 1981) for predicting Black Lake summer mixing patterns and temperatures, with 88% percent of the variation observed in mean daily temperature captured by the model for the summer of 2008 and with a mean absolute error of 0.54°C (±0.44). Meteorology inputs included air temperature, vapor pressure, precipitation, solar radiation, and wind speed. Hydrologic variables included daily inflows and inflow temperature. Griffiths et al. (2011) discussed the sources of input data in detail.

Volume and connectivity

DYRESM was used to predict Black Lake temperatures under alternative scenarios of volume (lake level) and hydrologic connectivity based on 2008 conditions (Griffiths et al. 2011). Volume conditions were a considered 2 m maximum lake level (80% loss of current volume), a 4 m lake level (current volume), and a 6 m lake volume (160% increase in lake volume) via a proposed restoration strategy. Under scenarios of volume decline, three levels of hydrologic connectivity to the Alec River were used to simulate lake water temperatures. The high connectivity scenario (high) simulated the entire discharge of the Alec River entering the main lake basin. The reduced connectivity scenario (reduced) represented the migration of the South Alec channel away from the lake and therefore only water carried by the North Alec channel contributed to the lake water budget. The no connectivity scenario (no) represented no flow from the Alec River entering the lake.

Future climate conditions

We expanded upon the analyses in Griffiths et al. (2011) to generate water temperature scenarios based on future air temperature conditions. Air temperature is a strong driver of Black Lake thermal regimes (Narver 1966) and summer air temperatures are expected to increase on average by about 2°C in coastal southwest Alaska by 2050 (Schindler & Rogers 2009). This set of simulations enabled us to explore potential interactions between ongoing climate change and ongoing geomorphic evolution, including the possibility for restoration, in controlling growth potential in juvenile sockeye salmon. The delta method is an approach that captures underlying short term variability in the climate while accounting for projected change in climate variables

(N. Mantua, Univ. Washington, pers. comm.). The projected change in air temperature by 2050 (+2°C) was added to the observed temperature in 2008. DYRESM simulations were run using these forecasted air temperatures while holding all other meteorological inputs at current conditions to predict lake temperature responses to future air temperatures. Air temperature directly affected lake energy fluxes calculated by DYRESM but is not incorporated into inlet stream water temperatures which were input separately and reflected current climate conditions. These simulations were conducted over the period mid June to late August and the hydrological data were not available to explore scenarios of increasing growing season duration.

Assessment of metabolism and growth

We used the Wisconsin bioenergetics model (Hanson et al. 1997) to assess the metabolic response of juvenile sockeye salmon to alternative thermal regimes. This model uses an energy balance approach where the energy available for growth (G) equals the energy obtained from consumption (C) minus the energy lost to metabolic (respiration) processes (M) and waste (W); $G = C - (M+W)$. Temperature and metabolic scaling of metabolism and consumption were parameterized according to Beauchamp et al. (1989) for sockeye salmon. Rates of consumption for cool and cold water fishes increase with temperature below the optimal consumption temperature (20°C with unlimited access to food) and decrease rapidly above their optimal temperature (as in Thornton & Lessem 1978). Rates of respiration, on the other hand, increase exponentially with temperature (Brett 1971). The scope for growth is greatest at the maximum difference between maintenance and maximum energy intake (Elliot 1976). Thus, maximum growth occurs not at the temperature which produces maximum consumption rates but where the difference between consumption rate and metabolic rate is the greatest. With unlimited food availability, this optimal growth temperature is assumed to be 15°C for sockeye salmon (Brett

1971), but declines at lower feeding rates. The model was used to estimate the proportion of maximum consumption (*pCmax*) to produce the observed growth rate based on the diet composition and temperature conditions. The parameter *pCmax* and observed temperatures were then used by the model to estimate consumption over the course of the simulation period and to calculate average daily ration.

Observed growth

Juvenile sockeye salmon were sampled via beach seine in the littoral habitat of Black Lake from early June to late August in 2010, a year with similar thermal conditions to 2008 (see details under *Bioenergetics modeling scenarios*). The seine (35 m x 4 m, 3 mm bag mesh) was deployed at five sampling sites approximately every seven days. Additionally, pelagic sampling was conducted at the end of August as juvenile salmon typically move offshore by late summer although Black Lake does not have a true pelagic habitat. Pelagic sampling was conducted at night to reduce net avoidance (Narver 1966). A net with a 1.2 m x 1.2 m opening was towed at constant speed between two boats for 10 minutes at five sites in the main lake basin. Sockeye salmon from beach seine and townet sampling were euthanized in a buffered MS-222 solution, measured (fork length) to the nearest mm, and weight from a subsample of fish was taken to the nearest 0.1g. Stomach contents were collected from 10-15 individuals per site for five sampling events and preserved in 95% ethanol for later analysis.

Diet composition

In the laboratory, stomach contents of juvenile sockeye salmon were pooled by site for each sample date. Diets were pooled because fish sampled at a given time may vary greatly in the fullness and digestion stage but this may not reflect persistent differences in consumption. Detection of persistent differences would require the use of other methods that integrate over longer timeframes. Samples were diluted to a known volume and, using a Stempel pipette, consecutive subsamples were enumerated under a dissecting microscope until ~ 400 organisms were obtained (similar to Parr 1972). Zooplankton were either identified to order (copepods) or to genus (Cladocerans). Insects were identified to family or to order. An average number of diet items per fish were calculated by sample date. The taxa groups were then multiplied by food unit values previously established for this system (Parr 1972) to estimate mass-weighted diet proportions.

Model inputs and parameter estimation

Juvenile sockeye salmon *pCmax* and average daily ration were obtained by fitting the bioenergetics model to the growth, diet, and temperature data observed over the summer growing season in 2010. Temperature was monitored quasi-continuously in the main lake basin using a HOBO water temperature logger pro v2 (Onset Corporation). We assume that access to prey is accounted for in the observed growth used to fit the model. Prey energy densities used were 2856 joules g^{-1} wet mass for insects (Chironomids all life stages, Cummins & Wuycheck 1971), 2382 joules g^{-1} wet mass for copepods (average of range summarized in Schindler & Eby 1997), and 1674 joules g^{-1} wet mass for *Bosmina* (Schindler & Eby 1997). Prey energy densities are assumed not to vary throughout the summer. Initial and final weights for the model were obtained from the 2010 juvenile sockeye salmon length-weight regression for the average sized fish on the first and last sampling date (Table 4.1).

Bioenergetics model scenarios

We assessed the effects of alternative thermal regimes on respiration costs and the potential offset of those costs via consumption. We compared simulations in which daily ration was constant to those in which *pCmax* remained constant. Under constant ration scenarios, the daily consumption rate is fixed but the energy allocated to metabolism varies with temperature. Thus, if temperatures increase from initial model fitting, metabolic energy demands increase and lower growth is achieved. On the other hand, because *Cmax* is a function of temperature, using a fixed *pCmax* allows daily consumption rates to also change with temperature. The scope for growth is thus dependent on the rate of change of both consumption and metabolism with temperature. The *pCmax* and constant ration values used were from the model fit to 2010 data. Temperature inputs were mean daily temperature predictions produced by DYRESM for all scenarios for 2008. The observed number of degree days (943.1) and average temperature (12.6°C) were the same during the observed growing season in 2008 and 2010 thus we believe the use of 2010 parameter values to be a reasonable approximation to growth conditions sockeye salmon experienced in 2008. Diet composition and prey energy density were constant across all scenarios.

First, we compared seasonal growth and daily growth rates among lake volume and connectivity scenarios for fish rearing under current and future climate conditions when feeding at a constant ration. We then assessed the response in juvenile sockeye salmon growth across all scenarios when consumption responded to temperature, in other words, a constant *pCmax* was maintained.

Results

Water temperature simulations

Volume and connectivity

Griffiths et al. (2011) showed that increases in lake volume (outlet restoration) had a negligible effect on Black Lake thermal regimes (Figure 4.2a). However, the thermal responses to continued lake volume decline varied with the level of connectivity to cool inlet streams. The removal of one or both Alec River channels from the lake hydrology led to substantially warmer summer lake thermal regimes (Figure 4.2c) in the absence of any climate change.

Climate change

A 2°C increase in air temperature generated an average 1°C increase in water temperature in DYRESM simulations with current volume and connectivity (Figure 4.2b). This translated into an approximately 8% increase in the number of summer degree days, and the expected percent of days with mean temperature exceeding the optimum temperature for sockeye salmon growth (i.e., 15°C degree when feeding at unlimited food supply) increased from 10% to 27% from the baseline year during the 70 simulation period. Future air temperature conditions for all volume-connectivity scenarios resulted in a similar water temperature response, an increase of an average of 1°C between current and future climate conditions (Figure 4.2).

Metabolic and growth assessment

Observed growth

1627 juvenile sockeye salmon length observations were made in 2010. Of those individuals, 1050 were also retained for mass. The length-weight relationship is represented by the following equation: $\log_{10}(\text{mass}) = 3.73*\log_{10}(\text{length}) - 6.25$ ($r^2 = 0.97$, $p=0.0$). Juvenile sockeye salmon in Black Lake on June 9 had a mean length of 35.8 ± 3.2 mm (n=56) and a mass of 0.35 g. Final observed mean length on August 28 was 69.7 ± 5.3 mm (n = 341) with a mass of 4.17 g.

Diet composition

Juvenile sockeye salmon diets were dominated by aquatic insects through early August after which sockeye salmon switched to consuming zooplankton. Chironomids comprised 98% of all insects in the diets. Through early August, the zooplankton present in the diets were primarily calanoid and cyclopoid copepods while late August diets were dominated by *Bosmina*.

The seasonal shift in composition is similar to observations by Parr (1972) from 1968-1970 and Ruggerone (1994) in 1993 (Figure 4.3).

pCmax and ration size estimation

The bioenergetics model estimated that juvenile sockeye salmon were feeding at a *pCmax* of 0.66 over the observed 82 day period. The average estimated daily specific growth rate was 0.031 grams of prey allocated to growth per gram of predator mass (g g^{-1} d^{-1}). The average ration over this period was 0.16 g g^{-1} d^{-1}. The water temperature scenarios were simulated for fewer days (70 days) and began on a later date than the 2010 growth observations. Thus, fish mass estimated by the 2010 model for day 167 was used as the initial mass for all water temperature scenario simulations (Table 4.1).

Metabolic costs of geomorphic evolution, restoration, and climate change

Increased lake level associated with outlet restoration did not alter the metabolic costs for juvenile sockeye salmon from current lake levels under either current or future climate regimes (Figure 4.4a). Metabolic costs increased with warmer thermal regimes associated with the loss of tributary connectivity at current lake levels with the average fish growing 5% less under no connectivity (Figure 4.4b). High connectivity at the current lake level buffered the increased metabolic costs due to the effect of warmer future air temperatures on lake temperature. Growth declines were limited to a 10% decrease with high connectivity to cool inlet streams under future climate conditions rather than a 14-16% decrease (Figure 4.4b). The effect of declining lake volume on metabolic costs depended on connectivity. Cooler lake temperatures associated with high connectivity substantially reduced metabolic costs under both current and future air temperature conditions (Figure 4.4c). Similar increases in metabolic costs due to warmer air temperatures were simulated when connectivity was reduced or lost.

Consumption offsets of seasonal metabolic costs

The differences in growth performance between current and increased lake level scenarios remained negligible in simulations where *pCmax* was maintained (Figure 4.4d). Declines in juvenile sockeye salmon growth associated with loss of tributary connectivity and increased in air temperature (Figure 4.4e) were smaller than in simulations where sockeye salmon maintained a constant ration (above). Growth decreased by only 5% from the baseline (4 m high connectivity) due to increased air temperatures instead of by 10% and decreased growth due to lack of connectivity was limited. Notably, under future climate scenarios, growth decreased only up to 7% instead of up to 16% as was predicted in scenarios with no connectivity and future climate condition.

The final mass achieved showed the greatest variation among shallow lake scenarios (Figure 4.4f). Across all constant *pCmax* scenarios, the greatest decrease in growth occurred in shallow lakes under warmer air temperatures and no inlet connectivity.

Fine scale buffering of daily growth rates

We also evaluated the daily variation in growth rates produced in bioenergetics simulations to assess the effect of different climate and geomorphic conditions on development of potentially stressful conditions at short time scales. Daily growth rates showed substantial variation within scenarios with lower growth rates during warm periods with higher metabolic rates (see Figure 4.2 for temperatures, day numbers 188-197 and 217-225) and in late summer when the diet was dominated by less energy dense prey. While at a seasonal scale there was little effect of increased lake level on juvenile sockeye salmon growth, there were days where growth rates were higher in the restored lake level scenario (Figure 4.5a, d). These days were the warmest of the simulation period (days noted above) indicating fine scale dampening of extreme temperatures. Daily temperature reached a maximum of 15.4°C in the restoration scenario under current climate while in the baseline scenario temperatures reached 16.1°C. The short term buffering under current climate conditions was also apparent under the future air temperature scenario. The declines in daily growth rate from the baseline were dampened with increased lake level (Figure 4.5a, d).

At a current lake level, loss of inlet connectivity coupled with increased air temperatures increased both the median percent decline in daily growth rates as well as the variation in decline among days at a constant ration (Figure 4.5b). Maintaining a constant *pCmax* reduced the median change in growth across all current lake level scenarios (Figure 4.5e). Climate change scenarios, however, still produced higher variation in daily growth rates and all growth rates were lower than the baseline.

The shallow lake scenarios produced the greatest amount of variation within and among scenarios in daily growth (Figure 4.5c, f). Under current climate conditions, median differences in metabolic cost were positive for high connectivity scenarios but negative for reduced and no connectivity (Figure 4.5c). Variation among days was also greatest in the no connectivity scenario, reflecting the increased variability in daily lake temperatures. Consumption reduced the median percent change in daily growth rate from the baseline but the no connectivity scenario had the greatest range of differences from the baseline (Figure 4.5f). Climate change again affected the median and range of differences under the constant ration scenarios (Figure 4.5c). While the median difference was buffered by consumption, the response to climate was highly variable among days and the variability increased with decreasing connectivity (Figure 4.5f).

Discussion

Our simulations showed that increased air temperature coupled to the loss of tributary connectivity had the largest negative effect on juvenile sockeye salmon growth in a shallow Alaskan lake via increased water temperatures. Across all simulations, future climate scenario water temperatures substantially increased metabolic costs which could be partially offset by maintaining a constant feeding rate expressed as a percentage of their physiological maximum rate. High inlet connectivity scenarios showed the least decline in growth for a given lake level due to cooling effects on lake temperature. Thus, maintaining inlet tributary connectivity was the most important factor for maintaining profitable growth conditions in Black Lake under current or future climate regimes.

Further lake level decline acted to magnify metabolic costs for sockeye salmon if connectivity was lost and increased the variability of daily growth rates. Restoration associated with increased lake level, on the other hand, had little effect on seasonal sockeye salmon bioenergetics via changes in water temperature and did not mitigate climate related costs. Restoration, however, did provide fine scale buffering for growth rates on the most extreme warm days by reducing the magnitude of water temperature increases.

The increased metabolic costs found here are consistent with other bioenergetics assessments of climate change impacts. In simulations with fixed rations, young-of-the-year (YOY) lake trout starved under water temperature conditions that were 3°C warmer (McDonald et al. 1996). Alternatively, for these YOY lake trout to achieve baseline growth they would need to consume eight times as much food. Less severe declines in growth occurred for lake trout, yellow perch, and largemouth bass (97%, 80%, and 70% of observed rates respectively) in simulations restricted to baseline consumption under future thermal regimes (Hill & Magnuson 1990).

Our simulations, as well as the studies mentioned above, use model parameters that are species-specific or borrowed from closely related species. These models, therefore, do not account for locally adapted populations that may show variation in thermal optima for a variety of physiological processes. It has been shown that populations of adult sockeye salmon in the Fraser River (British Columbia, Canada) show substantially different temperature optima for aerobic scope (Eliason et al. 2011) with important consequences for migration under changing climate. If this is the case for the suite of physiological processes that effect growth, the negative effects of warmer thermal regimes may be dampened if Black Lake populations had growth optima reflecting adaptations to the relatively warm temperatures in this shallow lake. These species specific parameter models are the best tools at present for assessing the general bioenergetics responses of fish to changes in lake thermal regimes, but assessing local adaption for the range of temperature-dependent physiological processes would provide additional support for maintaining diverse populations of sockeye salmon.

Fish mitigate thermal stress in aquatic environments through behavioral mechanisms when experiencing as little as 1°C increase in water temperature (Crawshaw & O'Connor 1997). In heterothermal environments, behavioral adaptation may reduce exposure to higher temperatures and this may minimize the negative effects of temperature on growth. Comparisons of lake trout and yellow perch growth with a fixed ration under conditions of thermoregulatory or stationary behavior showed that the latter produced greater declines in growth (Hill & Magnuson 1990). In Black Lake, we estimated that a 2°C increase in air temperature would produce a 1°C average increase in water temperature. However, Black Lake mixes throughout the summer season and is lacking in any deep water thermal refugia, similar to many large and wind exposed northern lakes (Schindler & Smol 2006).

Fish can also offset metabolic costs by increasing consumptions rates or consuming more energy dense resources if available. In the scenarios explored here, maintaining a constant proportion of maximum consumption had the potential to offset some of the seasonal costs associated with connectivity loss as well as climate change. While growth is sensitive to prey energy density, our use of a single estimated value of *pCmax* or average ration across all scenarios results in prey energy density simply being a scalar value and does not alter the relative importance of the factors determining growth. We did not explore seasonal changes in diet composition among scenarios because there is no evidence that seasonal diet composition has changed over the past 40 years of rapid environmental change (Figure 4.3). The response of juvenile salmonid growth to temperature conditions is ultimately mediated by food production and availability (Crozier et al. 2010; Edmundson & Mazumder 2001; Rich et al. 2009; Schindler et al. 2005). Both of these mechanisms affect the ability of juvenile sockeye salmon to maintain *pCmax*.

The response of zooplankton and aquatic insects to climate warming appears to be species specific (Adrian et al. 2006) and, thus, assessing sockeye salmon access to prey resources in the future presents a challenge. *Bosmina*, which dominate the late summer zooplankton community in Black Lake, had a large, positive production response to earlier ice-outs and more degree days in the lower Wood River lakes, southwest Alaska, but smaller or negative responses in the upper lakes (Carter 2010). *Daphnia*, although rarely observed in Black Lake (UW-ASP unpublished data), have shown strong positive responses to warming temperatures in large number of lake systems including those in the Wood River lakes (Carter 2010) as well as Europe (Straile & Geller 1998). At a continental scale, *Daphnia* population abundance appears to be greatest when lake temperatures are between 15-20°C (Gillooly & Dodson 2000), and therefore they may be a larger component of future Black Lake zooplankton communities, depending on the planktivory pressures on them. Thus, there is the potential for zooplankton resources to maintain production rates that are sufficient to offset at least some of the increase in juvenile sockeye salmon consumption.

Temperature also has an influential role on the physiology and ecology of aquatic insects. Thus, warming lake thermal regimes may alter timing and duration of emergence, seasonal growth rates, abundance, and body size and fecundity (Ward 1992). High arctic communities have exhibited changes in both the abundance and species composition of chironomid assemblages since 1850 corresponding to warming temperatures and shifts in algal communities (Quinlan et al. 2005). Furthermore, change in water level and the stability of intra-annual water level fluxes strongly effect aquatic insect production (Hall et al. 1999) by altering the availability and stability of littoral habitat. Thus, while we have shown that climate warming and certain aspects of geomorphic evolution will reduce the thermal profitability of juvenile sockeye salmon habitat; parallel increases in invertebrate prey production may offset these losses but have not been quantified.

Furthermore, we have not accounted for the expansion of the growing season with earlier ice break-up and later cooling in the fall. While summer growing conditions in Black Lake may degrade with climate or geomorphic evolution, spring and fall growing conditions may improve and buffer against decreased summer growth. In other southwest Alaska lakes, earlier ice break-ups lead to longer growing seasons, warmer lake temperatures, and increased growth of juvenile sockeye (Schindler et al. 2005). Our modeling scenarios focus on the June- August period because of concerns that if current physiological stress causes early-summer emigrations further lake warming will exacerbate stress and downstream competition in Chignik Lake. The timing, magnitude, and body condition of Black Lake emigrants have changed over the past 4 decades with earlier larger migrations of poor condition fish occurring in the 2000s (Westley et al. 2008). In 2005, a year with one of the warmest springs on record, the fish remaining in Black Lake over the summer grew large but catch rates were very low and it appeared that a large fraction of the population migrated downstream to cooler Chignik Lake (Westley et al. 2008).

Taken together our results suggest that maintaining connectivity to cool inlet streams is more important for maintaining profitable thermal conditions for juvenile sockeye salmon than maintaining lake volume in shallow lakes undergoing rapid geomorphic evolution such as that seen in Black Lake. The benefits of highly connected lake are maintained with increased in air temperature, but as Black Lake shallows it is more likely to experience rapid temperature increases and temperatures above 15°C leading to lower growth rates. When food is limiting, the optimal temperature for growth is lower (< 15°C) and thus stressful conditions will occur at cooler temperatures. Mean summer water temperature was 14°C in 2005 (the maximum mean daily temperature was 17°C), the year in which there was substantial, early emigration of poor condition fish. The potential for behavioral avoidance of suboptimal temperatures in the lake is limited and thus prey production and density dependent effects under alternate scenarios is likely very important. Density and temperature have been shown to have strong interactive effects on growth (Crozier et al. 2010) and these two factors vary within and among years in Black Lake.

The responses of juvenile sockeye salmon to changing climate and geomorphology in high latitude ecosystems are likely to be varied and complex. While substantial progress has been made toward exploring the potential effects of climate warming on lake thermal regimes and fishes (e.g., De Stasio et al. 1996; Stefan et al. 1996; Magnuson et al. 1990), such analyses assume that geomorphic evolution of lakes is slow enough as to be inconsequential. However, in high latitude lakes whose watersheds are either geologically young or unstable, or are characterized by extensive permafrost, we should expect that geomorphic evolution may occur on ecologically relevant time scales in some situations. How such geomorphic changes will interact with ongoing climate change to affect the viability of fish populations remains highly uncertain and models are an effective tool to explore the consequences for sockeye salmon under alternate future scenarios. Given the physiological constraints governed by temperature, we can assess both the importance of ecological factors for juvenile sockeye salmon as well as the potential for policy and management actions to mitigate negative consequences for juvenile sockeye salmon. Such assessments are vital in a region that is critically dependent on the harvest of sockeye salmon.

Table 4.1: Inputs to bioenergetics model for 2010 fit, and fitted parameter values and inputs for scenario simulations.

2010 Model Fit	***Paramter values***
Simulation length	82
Initial Mass (g)	0.35
Final Mass (g)	4.17
pCmax	0.65
Average ration (g g^{-1} d^{-1})	0.16
Estimated Consumption (g)	23.14
Values for Scenario Simulations	
Simulation length	70
Initial Mass	0.54
pCmax	0.66
Average ration	0.16

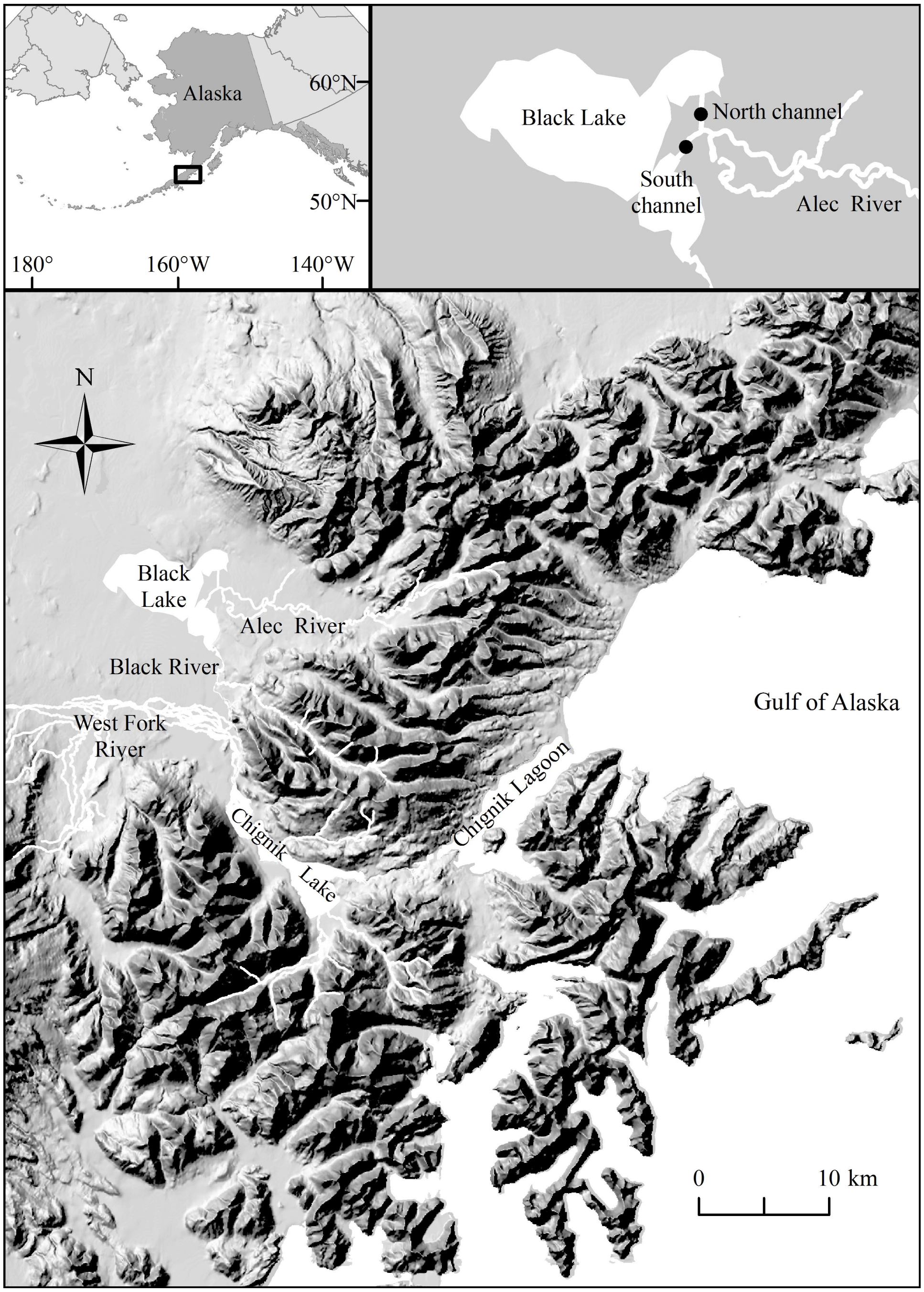

Figure 4.1: Chignik watershed, southwest Alaska, United States (N56°16' W158°50'). Key features of the watershed are indicated. The Alec River carries approximately 80% of the inlet water to Black Lake which flows out to Chignik Lake via the Black River at the southern bay of the lake.

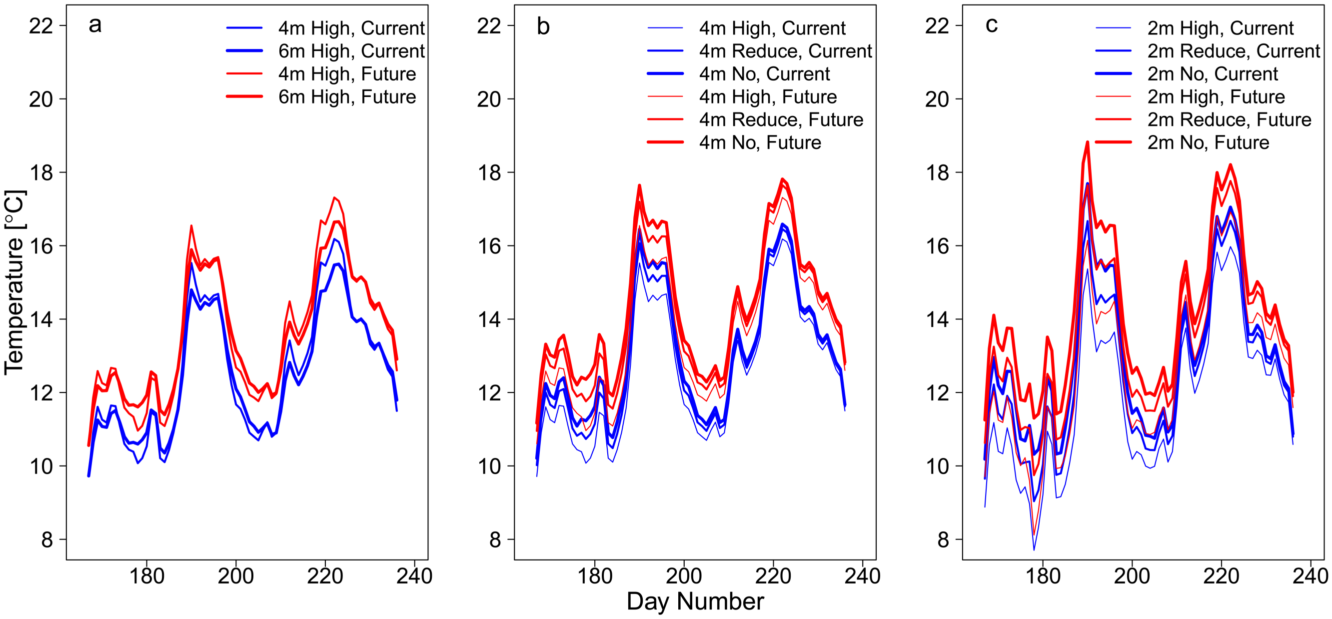

Figure 4.2: DYRESM simulated water temperatures for lake volume (lake level), tributary connectivity, and climate scenarios: a) Current lake level (4m) and restoration lake level (6m) under current and future air temperature conditions (+2°C); b) Current lake level scenarios for scenarios of tributary connectivity (high, reduce, no) under current and future air temperature conditions; and c) further lake level decline (to 2m) under each tributary connectivity and air temperature scenario.

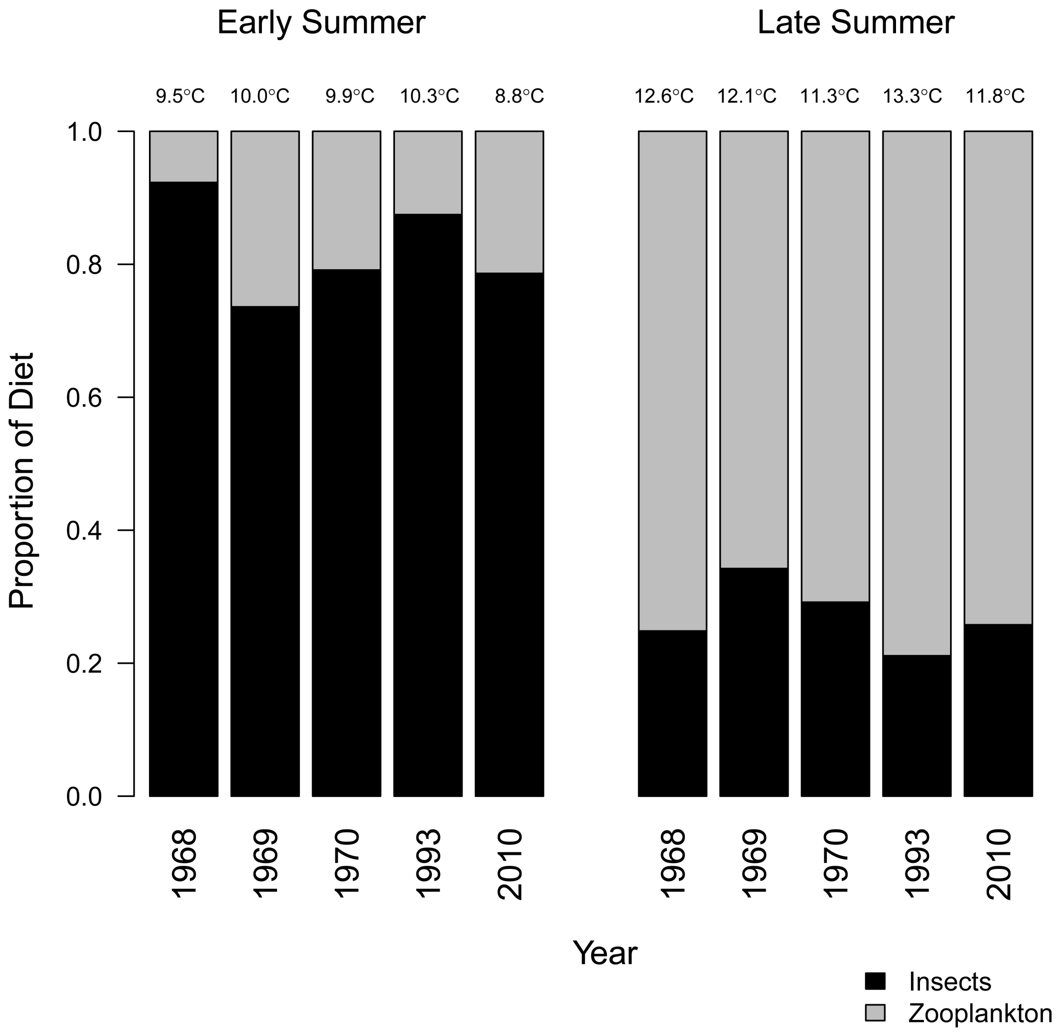

Figure 4.3: Juvenile sockeye salmon diet composition. Early (late June-early July) and late (late August-early September) summer are shown. Historic data were collected by Parr (1972, for 1968-1970 as food units) and Ruggerone (1994, for 1993 as wet mass). Average monthly air temperature is noted above each year with June temperatures used for early summer and August temperatures used for late summer. Chironomids of all life stages dominated the insect category. Early season zooplankton were primarily copepods while late season zooplankton were heavily dominated by *Bosmina.*

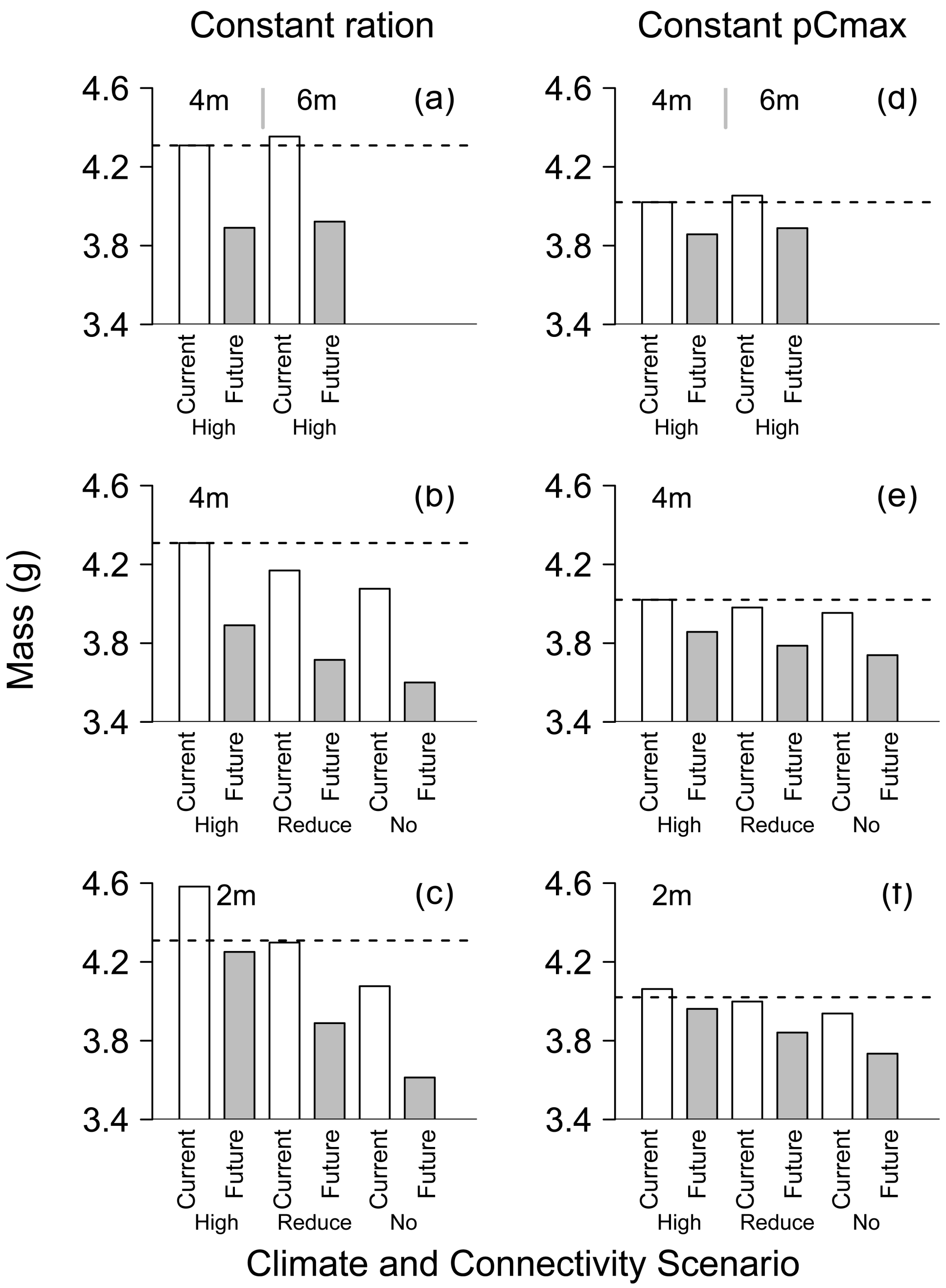

Figure 4.4: Juvenile sockeye salmon mass (g) after the 70-day bioenergetics simulation. Each scenario was conducted a constant ration (a-c) and constant *pCmax* (d-f). Restoration (a, d), tributary connectivity (b, e), and further lake level decline (c, f) are shown. The air temperature scenario (current or future) and the level of inlet tributary connectivity (high, reduce, no) are labeled on the x-axis. Lake level (2m, 4m, 6m) is noted in each plot. The horizontal dashed line indicates growth simulated under the baseline conditions (4m, high connectivity) with either constant ration or constant *pCmax*.

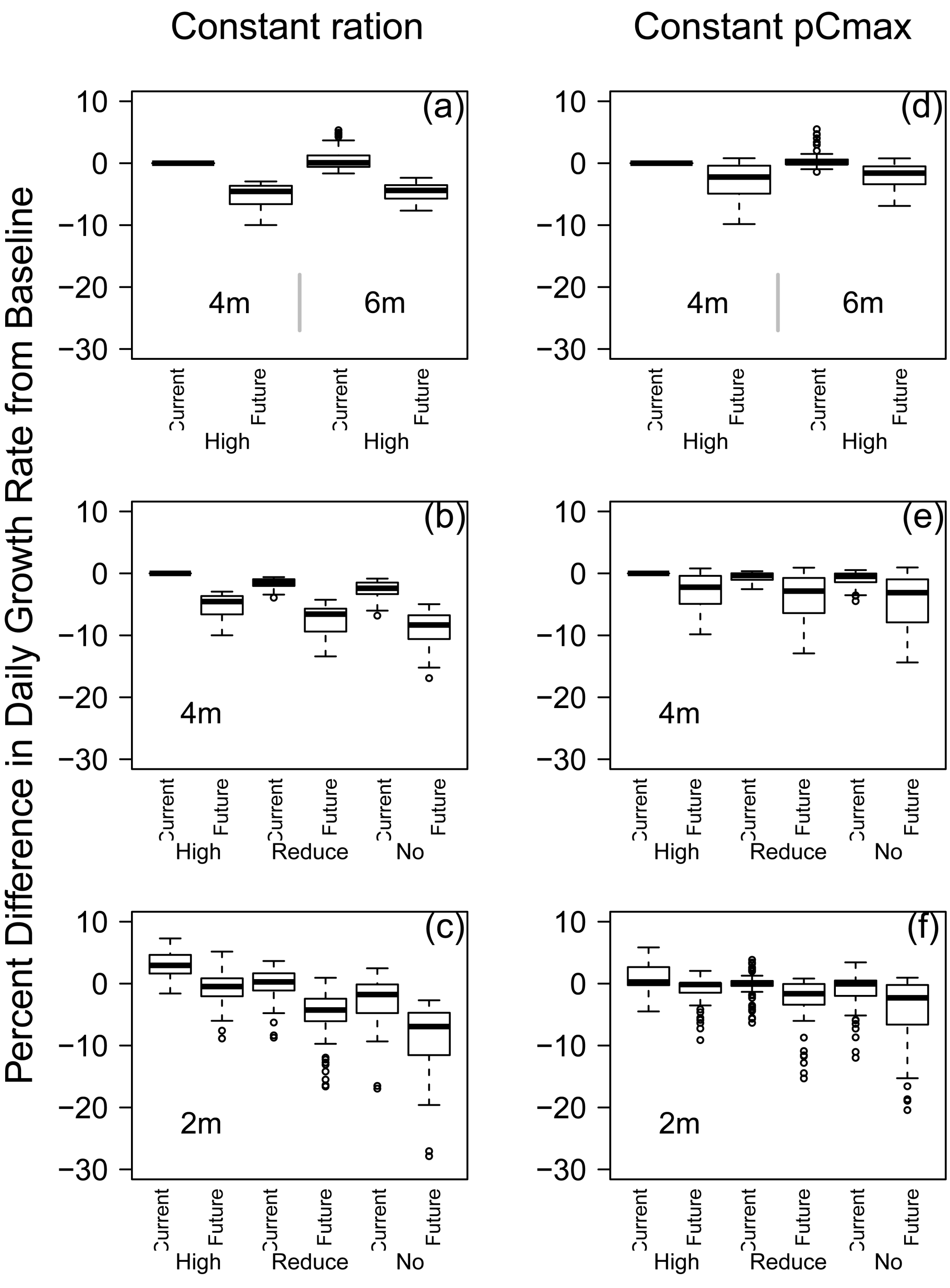

Figure 4.5: Percent difference in daily growth from baseline. The baseline is 4m high connectivity, current climate and the comparisons are shown for fish growth simulated under either constant ration (a-c) or constant *pCmax* (d-f). Scenarios are grouped and labeled as in Figure 4. The thick black line is the median, the box encapsulates the first and third quartiles, and the whiskers indicate ±1.5* IQR.

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Appendix A: Collaborators and Acknowledgements

Chapter 1

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VITA

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