EARLY MARINE GROWTH PATTERNS OF SITUK RIVER STEELHEAD,

ONCORHYNCHUS MYKISS

By

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Abstract

Steelhead *Oncorhynchus mykiss* exhibit complex life-history patterns described by variable freshwater and marine residency periods, maturation patterns, and reproductive characteristics. Over 300 small populations of Steelhead are present in Southeast Alaska, and similar trends in abundance among these populations suggest the influence of population-regulating forces operating on a regional scale. The Situk River, near Yakutat, Alaska, supports the largest known population of Steelhead in Alaska. Stock assessment studies on this river have collected the longest set of biological data and scale samples for Steelhead in the state. For this study, retrospective scale pattern analysis of samples from Situk River Steelhead was synthesized with regional abundance information to investigate patterns in early marine growth among different life-history and demographic groups, as well as to explore linkages between growth, abundance, and marine environmental variables. Positive correlations were identified between freshwater growth, first ocean-year growth, and adult length, while first ocean-year growth was negatively correlated with second ocean-year growth. Early maturing Steelhead were found to have increased first ocean-year growth and reduced adult length relative to later maturing Steelhead, confirming connections between growth and maturation. Correlations in abundance among Southeast Alaska Steelhead populations suggest that marine and climatic drivers may impact these populations in a regionally coherent manner. Correlations among patterns in abundance also varied along a distance gradient: populations located closer to the Situk River were more correlated with the Situk River than more distant populations. Positive relationships between Gulf of Alaska sea surface temperature, North Pacific Gyre Oscillation, and Situk River Steelhead abundance further supported the importance of climate-driven marine conditions to Steelhead productivity. While conservation concerns for Steelhead in Southeast Alaska are currently minimal, proactive investigations into life-history diversity and population linkages may become more relevant with increased marine ecosystem variability related to climate change.

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General Introduction

Steelhead trout *Oncorhynchus mykiss* are an anadromous, broadly distributed salmonid, with a historical native range encompassing much of the west coast of North America from northwest Mexico to the Alaska Peninsula and portions of the Russian Kamchatka Peninsula (Light et al. 1989; Busby et al. 1996; Quinn 2005). Non-anadromous *O. mykiss*, commonly known as Rainbow Trout, co-occur with Steelhead but also have an expanded northerly and southerly distribution that has been further extended by human introductions (MacCrimmon 1971; Quinn 2005). In Alaska, the documented range of Steelhead extends from Dixon Entrance in the Southeast Alaska and north and west around the Gulf of Alaska to Cold Bay on the Alaska Peninsula (Van Hulle 1985), with most populations located in the southeastern portion of Alaska (Harding 2008). Steelhead and non-anadromous Rainbow Trout populations are also found in northeastern Asia, with most populations located on the Russian Kamchatka Peninsula (Light et al. 1989; Quinn 2005).

O. mykiss exhibit a complex suite of life-history patterns across their range, defying simple taxonomic distinctions between Steelhead and Rainbow Trout based on anadromy. Non-anadromous and anadromous forms of *O. mykiss* exist sympatrically in many systems and a high degree of gene flow has been observed between life-history forms (Burgner et al. 1992; Lohr and Bryant 1999; McPhee et al. 2007). The proximate mechanisms regulating anadromy for *O. mykiss* remain unresolved, but river biophysical complexity, aquatic landscape diversity, and local environmental conditions likely operate in concert to influence *O. mykiss* life-history trajectories and habitat use (Narum et al 2008; McPhee et al 2014).

Steelhead are grouped into two general life-history patterns defined by when adults return to freshwater to spawn and their state of sexual maturity upon reentry. In Alaska, ocean-maturing Steelhead return to their natal streams as sexually mature adults in the late winter or spring, typically between March and June, and spawn that spring (Lohr and Bryant 1999; Harding and Coyle 2011). Stream-maturing Steelhead return to freshwater in the late summer and fall, typically between September and November, in a less mature state and overwinter in freshwater before spawning in the spring (Lohr and Bryant 1999; Quinn 2005; Harding 2008). Ocean-maturing Steelhead are generally found in coastal, low-elevation watersheds along the northern portions of their distribution, while the stream-maturing form is more common in the large

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interior watersheds along their southern range (Quinn 2005). Both life-history types co-occur in several rivers in Alaska, with temporally and geographically synchronous spawning and emigration patterns; both ocean- and stream-maturing Steelhead spawn in the spring when water temperatures reach a suitable range of 6-9°C (Harding 2008). Steelhead eggs, deposited in the spring, are smaller than those of fall-spawning Pacific salmon *Oncorhynchus* spp. and produce fry that emerge four to seven weeks post-spawning in late spring and early summer (Lohr and Bryant 1999; Quinn 2005). Among Pacific salmonids, Steelhead can be particularly reliant on freshwater habitats, and typically rear for two to five years in freshwater before migrating to the ocean as smolts (Harding and Coyle 2011). In Alaska, a three-year freshwater rearing period is most common for Steelhead (Harding and Coyle 2011). Adult Steelhead return to their natal rivers to spawn for the first time after spending one to three years at sea (Quinn 2005; Harding 2008). Unlike Pacific salmon, Steelhead are iteroparous, and, although iteroparity varies widely by region, repeat spawning fish have been found to comprise 25 to 33% of a run in Alaska (Lohr and Bryant 1999; Harding 2008).

The status of northerly Steelhead populations in Alaska contrasts with populations along the U.S. West Coast. National Oceanic and Atmospheric Administration (NOAA) Fisheries has identified fifteen distinct population segments (DPSs) of Steelhead in Washington, Oregon, Idaho, and California. Ten of these DPSs have been designated as threatened, one as a population of concern and one as endangered under the US Endangered Species Act (Northwest Fisheries Science Center 2015). The widely accepted causes for declines in Steelhead (and closely related Pacific salmon species) across the southern portions of their range are habitat degradation, hydroelectric infrastructure development, overharvest, and hatchery effects (Ruckelshaus et al. 2002).

Over 300 watersheds in Southeast Alaska are known to support Steelhead stocks, although most are small populations with annual returns of 200 or fewer adults (Harding 2008). Larger populations (greater than 1,000 returning adult Steelhead) may once have returned to the Karta River on Prince of Wales (POW) Island and the Naha River on Revillagigedo Island outside of Ketchikan and the Thorne River, also on POW Island, may still support annual escapements of that magnitude (Harding 2008). The Situk River, near Yakutat, supports the largest known population of Steelhead in Alaska, with average annual emigrating adult counts approximating 9,000 kelts (post-spawn adults) over the past 10 years (Marston et al. 2012).

Available data for Southeast Alaska Steelhead suggest that, while variability exists among systems, most populations have stabilized at abundance levels that allow limited recreational harvest while maintaining stock sustainability (Harding 2008). Steelhead populations in Southeast Alaska persist in a hydrologically and geologically dynamic landscape near the northern extent of the species range, where climate change will likely impact watershed characteristics important to Steelhead (Marston et al. 2012; Shanley and Albert 2014). While Southeast Alaska Steelhead populations have not been as severely affected by anthropogenic disturbance as southerly stocks, the small size of many populations and the lack of stock-specific data to guide management renders them susceptible to overharvest and changes in habitat suitability related to climate and natural environmental variability (Lohr and Bryant 1999; Love and Harding 2009; Shanley and Albert 2014).

The recent history of the Southeast Alaska Steelhead fishery demonstrates the potential vulnerability of Alaska stocks. Since the late 1970s, freshwater sport fishing effort for all species in Southeast Alaska increased steadily to a peak of over 100,000 angler days in 2003 (Harding 2008). Concerns about the sustainability of Southeast Alaska Steelhead fisheries first arose in the early 1990s when managers and the fishing public observed reduced Steelhead abundance across the region and steep declines in Steelhead harvest despite increasing freshwater fishing effort (Harding 2008). In addition, annual Steelhead escapement counts at the Situk River weir in Yakutat declined during the same period (Harding 2008). In 1993, these concerns spurred a reevaluation of Steelhead management by the Alaska Department of Fish and Game (ADF&G), Sport Fish Division. The ADF&G convened a stakeholder committee to develop a survey that was distributed to 1,768 Steelhead anglers to assess public perception of Southeast Alaska Steelhead population health and attitudes towards regulations, fishing preferences, and management goals (Harding 2008). Survey respondents confirmed concerns about declines in Southeast Alaska Steelhead and the need for more restrictive regulations, including preferences for catch-and-release fishing, lowering annual bag limits, and gear restrictions (Harding 2008). In 1994, the Alaska Board of Fisheries (BOF) adopted more restrictive regulations for Steelhead sport fisheries that set a daily bag limit of one Steelhead, an annual limit of two Steelhead, and a 36-inch minimum size limit that was designed to protect approximately 95% of adult Steelhead (Harding 2008). The use of natural bait to catch Steelhead was also prohibited in Southeast Alaska freshwaters from November 16 to September 14 to provide added protection against

catch-and-release mortality; this bait prohibition was subsequently expanded to a year-round restriction in 1997 for the 26 streams with fall runs of Steelhead (Harding 2008). Commercial fishing regulations for the Southeast Alaska region were also modified to prohibit the sale of commercially captured Steelhead by purse seine and gill net permit holders (Harding 2008). In addition to these regulatory changes, the ADF&G recognized the need to consistently monitor Steelhead populations to assess fishery impacts and overall trends in Steelhead abundance in Southeast Alaska. Since 1997, snorkel surveys have been conducted for selected index populations to monitor trends in annual Steelhead abundance and to guide potential management action (Harding 2008).

High levels of sport-fishing effort for Southeast Alaska Steelhead have continued since the implementation of the new regulatory regime. From 1996 to 2013, anglers annually spent an estimated average of 95,000 days pursuing Steelhead in Southeast Alaska according to the ADF&G Statewide Harvest Survey (ADF&G 2016). The effect of conservative regulations and a shift in angler preference for catch-and-release fishing can be seen in reduced recreational harvest, down from historical highs of ≥ 4,000 fish per year in the 1980s, to just ≥ 100 fish annually since the early 1990s (Harding 2008). Trends in total sport fishing catch of Steelhead have fluctuated significantly over the past 20 years from an estimate of just ≥ 5,000 fish in 1995 to ≥ 26,000 fish in 2008 (Harding 2008; ADF&G 2016). Despite consistently high fishing effort, these variable catch rates may reflect the inherent challenge of sport fishing for Steelhead in Southeast Alaska, especially in streams supporting small populations, but also may suggest annual fluctuations in overall Steelhead abundance.

In the early 2000s ADF&G identified a need to generate Steelhead escapement goals for exploited systems in Southeast Alaska. A long-term research plan was designed to estimate stock-specific Steelhead population characteristics that could be combined with detailed habitat mapping to estimate production for Southeast Alaska Steelhead streams based on suitable habitat area available (Love and Harding 2009; Love et al. 2013; D. Love, ADF&G, personal communication). This plan was curtailed due to funding cuts in 2011. Currently, an annual monitoring program of index Steelhead streams is maintained by ADF&G with the goal of achieving peak counts using snorkel surveys to index relative population abundance. Weir studies on the Situk River continue to provide more intensive stock assessment objectives that include enumeration of emigrating kelts, an estimation of sex/length characteristics, and an

assessment of scale-growth and age characteristics of tagged and recaptured adult Steelhead (Marston et al. 2012). Despite conservative regulations many of the small Steelhead populations in Southeast Alaska remain vulnerable to a variety of threats, such as overexploitation, interception in commercial fisheries, hooking mortality and other sport fishing perturbations, and changes to the quality and availability of freshwater and marine habitat (Lohr and Bryant 1999; Love and Harding 2009).

Anadromous fish production is affected by a suite of environmental, ecological, and anthropogenic factors encountered at each phase of their life cycle (McPhee et al. 2009). The geographic and temporal consistency of Pacific salmonid spawning migrations back to natal watersheds has allowed for an in-depth understanding of factors regulating survival and recruitment in freshwater ecosystems. The ecological processes regulating salmon and Steelhead growth, recruitment, and ultimately survival in the marine system are inherently more difficult to investigate.

Data on ocean distribution and movement of Steelhead collected since 1955 from salmon fisheries catch records and International North Pacific Fisheries Commission (INPFC) research vessels describes a distinct seasonal distribution pattern for Steelhead in the North Pacific Ocean (Light et al. 1989). In spring (March to May), Steelhead are found in the central North Pacific Ocean and southern Gulf of Alaska (GOA) from 42 to 52°N latitude tapering westward to 150°E longitude (Light et al. 1989; Welch et al. 2000). During summer (June to August), Steelhead move north and west in the GOA, with greatest densities, ranging just south of the Aleutian archipelago to 42°N latitude and extending from 140 to 180°W longitude. However, some Steelhead have also been found in the far western waters of the Sea of Okhotsk (Light et al 1989; Welch et al. 2000). Fall and winter distributions are less well defined due to limited sampling, but the greatest Steelhead densities in the fall (September to November) appear to remain just south of the Aleutian Islands with a contracted westward distribution (Light et al. 1989). In winter, Steelhead appear to move south and east to coastal regions between 44 to 58°N latitude (Light et al. 1989). These distributions describe a general seasonal marine migration pattern for Steelhead in the North Pacific, where fish move north and westward from spring to summer, retreating south and eastward through fall and winter (Light et al. 1998). No clear distinction in marine movement patterns has been found for different Steelhead populations or life-history types, suggesting all North American Steelhead follow this general migration pattern (Light et al.

1989). However, Quinn and Myers (2005) suggested that Steelhead from coastal streams in the GOA have more northerly and westerly marine distribution than Steelhead from both inland Columbia River basin populations and from coastal Oregon and California populations.

Juvenile Steelhead also appear to follow this general migration pattern and broadly occupy the GOA and Central North Pacific Ocean. Ocean age-0 Steelhead move rapidly offshore from their natal streams and estuaries in the spring (Quinn and Myers 2005), and are found in the greatest abundance in the central and western GOA in summer and fall (Light et al. 1989). The rapid offshore movement of juvenile Steelhead differs from other Pacific salmon species that use productive coastal and shelf marine habitats during their early marine residency (Burgner et al. 1992), and has important implications for understanding the factors that influence their marine ecology.

During marine residency, Steelhead encounter a dynamic environment shaped by the basin-scale circulation occurring in the GOA and inter-annual patterns climatic variability. Circulation in the GOA is defined by the large-scale cyclonic flow of the broad Alaska Current along the Southeast Alaska coast and the stronger Alaskan Stream south of the Aleutian Islands (Combes et al. 2009). This basin-wide cyclonic circulation motivates upwelling in the center of the Alaska Gyre, while Ekman transport drives this upwelled, nutrient-rich surface water towards the coast of Alaska (Stabeno et al. 2004; Mundy 2005). Wind-induced onshore nutrient transport, most prominent during winter months, coincides with mesoscale (10 km) anticyclonic eddy flows occurring along the Alaska current that advect nutrient (iron)-rich freshwater runoff across the shelf to contribute to offshore, interior gyre productivity (Combes et al. 2009). The relative strength of offshore upwelling and coastward transport of upwelled waters are a function of the position and intensity of the Aleutian Low pressure system that varies both seasonally and interannually. Stronger coastal downwelling conditions have been observed during periods with a more intense Aleutian Low, which also spurs the generation of stronger anticyclonic eddies (Combes et al. 2009).

Coherent patterns of climatic variability may serve as proxy measures of changes in GOA productivity. The El Niño Southern Oscillation (ENSO) and North Pacific Gyre Oscillation (NPGO) interact with the Aleutian low pressure system to broadly influence North Pacific marine ecosystems at annual, decadal, and interdecadal time scales (Di Lorenzo et al. 2008;

Wolter and Timlin 2011). The basin-wide geographic scale at which these climatic indices affect the GOA also align with seasonal marine distribution patterns of Steelhead.

Linkages between patterns of marine climate variability and North Pacific salmonid production were initially recognized through correlation and time series analysis of retrospective commercial fishery data and records of Pacific basin climate indices (Beamish and Bouillon 1993; Hare and Francis 1994; Mantua et al. 1997). Broad coherence between marine climate regimes and geographically specific Pacific salmonid abundance trends suggest the importance of marine climatic conditions to anadromous fish survival and recruitment (Mantua et al. 1997). The influence of marine conditions appears to be time lagged by species-specific marine residence periods (i.e., two to three years for sockeye salmon *O. nerka* and one year for pink salmon *O. gorbuscha;* Mantua et al. 1997), suggesting ocean conditions impact juvenile salmonids most during early portions of their marine life cycle. Understanding the processes that regulate salmonid growth and survival in the ocean informs long-term sustainable fishery management and the protection of Pacific salmonid biodiversity. These concerns grow evermore relevant as the North Pacific environment responds to the continued effects of climate change.

The analysis of fish scale patterns is a well-established anatomical method to estimate age and assess growth patterns for salmonid species. Scale pattern analysis uses the deposition of concentric ridges of overlapping circuli, which have been found to coincide with somatic fish growth (Fukuwaka 1998; Peyronnet et al. 2007; Seamons et al. 2009). Patterns of tightly spaced circuli are associated with slower growth during freshwater portions of the anadromous fish life cycle and cold winter periods, while widely spaced circuli correspond to more rapid summer growth and marine growth (Das 1994). Pairing these two intervals of circuli formation characterizes annual growth, and fish age can be estimated by counting bands of tightly spaced circuli, known as annuli (Das 1994). Regular patterns of circulus periodicity and width can be used to infer variation in the ecological, environmental and physiological factors that regulate fish growth (Das 1994). Bands of reabsorbed and disrupted circuli preceding an annulus, associated with energetically stressful spawning events, are preserved on scales of iteroparous fish, and provide a record of reproductive history (Love, in press).

Retrospective scale pattern analysis is well suited to the study of Steelhead in Alaska. Small and remote Southeast Alaska Steelhead populations challenge traditional stock assessment methods and more intensive growth studies that require multiple recaptures of individual fish

(Farley et al. 2007). The collection of scale samples is relatively inexpensive, non-invasive, and does not require sacrificing the fish (Beakes et al. 2014), which is crucial for the study of small but prominent Southeast Alaska Steelhead populations. The establishment of standardized Steelhead scale aging and measurement methodologies for Southeast Alaska populations can provide foundational information on age composition and provide support the further study of growth and life-history patterns (Love, in press).

The overall goal of this study was to assess how scale-derived growth measurements from adult Steelhead can be utilized to better understand the early marine growth patterns of Southeast Alaska Steelhead and investigate linkages between Steelhead marine growth, abundance, and climate-driven ocean conditions. The Situk River, near Yakutat, Alaska, supports the largest known population of Steelhead in the state. The high productivity and unique accessibility of the Situk River Steelhead fishery has led to its recognition as a world-class recreational fishing opportunity. The acknowledged biological and economic value of this fishery led to formalized assessment methods beginning in 1988 utilizing an aluminum picket weir located on the lower river (Bain et al. 2003). Consistent biological sampling protocols for Steelhead were initiated in 1990, with a target of 10-15% of the run sampled annually at the weir for sex, length, condition, and scale collection (Bain et al. 2003). Steelhead kelts were also implanted with Passive Integrated Transponder (PIT) tags during 2000-2011, and tagged Steelhead were sampled for sex, length, scars, and scales (Marston et al. 2012).

Data collected over the past 20 years from the Situk River provides a unique opportunity to investigate the marine ecology of Southeast Alaska Steelhead and examine potential climate impacts on Steelhead growth and abundance. We conducted a retrospective analysis of Steelhead scale samples collected on the Situk Riverby ADF&G from 1999 to 2013, excluding 2002 through 2004 when scale samples were not available. Analysis of adult Steelhead scales from the Situk River allowed for marine age estimation, quantification of growth during various life-history periods, and characterization of repeat spawning behavior. Data from ADF&G Steelhead snorkel surveys suggest a region-wide pattern of above-average Steelhead abundance between 2003 and 2007 among nearly all index streams surveyed (Harding and Coyle 2011; Marston et al. 2012; Coyle 2013). This regionally coherent abundance pattern may suggest linkages between Southeast Alaska Steelhead populations and implicates climate-driven marine processes as influential factors in Southeast Alaska Steelhead survival and recruitment. To date, Southeast

Alaska Steelhead research and management efforts have necessarily focused on population monitoring, habitat conservation, and sport fishery maintenance, but have not undertaken more mechanistic investigations into Steelhead marine ecology and the effects of climatic variability on Steelhead populations in Alaska.

Chapter one of this thesis estimates marine age and quantifies freshwater and marine growth from Situk River Steelhead scales. A mixed-effects modeling approached was used to assess relationships among freshwater growth, early marine growth, and overall adult Steelhead length, as well as to test for differences in early marine growth between different Steelhead demographic and life-history groups. The second chapter describes abundance correlations among Southeast Alaska Steelhead populations and examines how interannual patterns in Situk River Steelhead early marine growth relate to conditions in the GOA and region-wide trends in Steelhead productivity. This study addresses population-specific demographic data foundational to effective population monitoring and management, as well as describing concordance among Southeast Alaska Steelhead population abundance trends. These investigations may lead to more robust population assessment and monitoring protocols for Steelhead in Alaska that incorporate climate-driven marine variability into the long-term tracking of stock demography, life history, and abundance.

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Chapter 1 Interactions between marine growth and life-history diversity in Situk River Steelhead *Oncorhynchus mykiss*[1]

1.1 Abstract

Steelhead (anadromous Rainbow Trout) *Oncorhynchus mykiss* exhibit complex patterns of life-history diversity described by variable freshwater and marine residency periods, maturation patterns, and reproductive characteristics. Life-history complexity can stabilize populations against perturbations by allowing for differential utilization of freshwater and marine resources and by dispersing the risk of mortality among different cohort groups. The Situk River, near Yakutat, Alaska, supports the largest known population of Steelhead in Alaska and stock assessment studies on the Situk River have collected the longest running set of biological data and scale samples for Steelhead in the state. Retrospective scale pattern analysis was used to examine patterns in early marine growth and compare growth among different life-history and demographic groups of Situk River Steelhead. Positive correlations were identified between freshwater growth, first ocean-year growth, and adult length, while first ocean-year growth was negatively correlated to second ocean-year growth. Second-ocean year growth was also more variable than first-ocean year growth or adult length. Early-maturing Steelhead were found to have increased first ocean-year growth, decreased second ocean-year growth, and decreased adult length compared later maturing Steelhead. This pattern suggests a critical period for life-history divergence in Steelhead during their first year at sea, when faster growing fish mature earlier. Early maturation leads to allocating energy away from somatic growth to gamete development earlier, which could explain slower second ocean-year growth in early maturing individuals. Our results suggest that scale-pattern analysis is a useful tool to investigate the early marine ecology of Southeast Alaska Steelhead and inform on the ongoing conservative management of this important sport fish.

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[1] Catterson, M. R., D. C. Love, T. M. Sutton, and M. V. McPhee. Interactions between marine growth and life-history diversity in Situk River Steelhead *Oncorhynchus mykiss*. Prepared for submission to Transactions of the American Fisheries Society.

1.2 Introduction

Steelhead, the anadromous form of Rainbow Trout *Oncorhynchus mykiss*, are a highly valued sport fish that contributes to prominent recreational fisheries in the Pacific Northwest, British Columbia, and Alaska. In recent years, Steelhead populations in Washington, Oregon, and California have suffered significant declines associated with the cumulative impacts of habitat degradation, hydroelectric development, fishery harvest, and hatchery effects (Ruckelshaus et al. 2002; Augerot 2005; Good et al. 2005). However, more remote and northerly regions in British Columbia, Alaska, and eastern Russia persist as strongholds for healthy populations of wild Steelhead (Augerot 2005). Alaska Steelhead populations are distributed widely across the southeastern and southcentral regions of the state, with the majority located in the coastal streams of Southeast Alaska (Harding and Coyle 2011). Most Southeast Alaska Steelhead populations are small, consisting of 200 or fewer adults, but several populations with escapements ranging into the thousands can be found near Yakutat and on Prince of Wales Island (Coyle 2014).

Steelhead spend two to five years rearing in freshwater before migrating to the ocean (Harding 2008), which is the longest freshwater rearing period exhibited by anadromous members of the genus. During this freshwater phase, the physiological and genotypic characteristics of juvenile Steelhead interact with biotic and abiotic ecosystem features to influence fitness, growth, and the propensity for anadromy expressed by individuals (McPhee et al. 2014; Sloat and Reeves 2014; Kendall et al. 2015). The species *O. mykiss* encapsulates the continuum of Pacific Ocean salmonid anadromous life-history strategies through the sympatric occurrence of anadromous and non-anadromous forms, gene flow between forms, and the production of offspring expressing either form (McPhee et al. 2007; Sloat and Reeves 2014; Kendall et al. 2015). Hodge et al. (2016) identified 38 unique life-history categories displayed by *O. mykiss*, varying in freshwater and ocean-rearing periods, maturation, and reproductive characteristics. While this complex of life-history strategies diversifies the suite of ecological forces that may impact the survival of individual fish and regulate the productivity of a population (Kendall et al. 2015), life-history diversity also buffers populations against variability by creating asynchronous population dynamics that disperse mortality over space and time (Hilborn et al. 2003; Moore et al. 2014). This 'portfolio effect' of salmonid biodiversity has been identified in stock complexes of Pacific salmon (Hilborn et al. 2003; Schindler et al. 2010) and

Steelhead populations (Moore et. al 2014). The stabilizing effect of life-history complexity may also support the persistence of small, otherwise vulnerable Alaska Steelhead populations.

While Steelhead management opportunities are primarily limited to freshwater environments, a better understanding of relationships between juvenile growth and life-history complexity in both freshwater and marine ecosystems may help inform ongoing management strategies to preserve biodiversity. The small size and remote location of many Alaska Steelhead populations challenges intensive research on their ecology and population dynamics, but available information on index populations of Southeast Alaska Steelhead across the region indicates relatively stable abundance trends in recent years (Harding and Coyle 2011). These small populations are protected by conservative sport fishing regulations designed to allow angling opportunity while conserving stocks. However, a lack of stock-specific information, potential overexploitation in recreational and subsistence fisheries, unknown levels of interception in commercial fisheries, and changes to marine and freshwater habitat quality are tangible threats to Southeast Alaska Steelhead (Lohr and Bryant 1999; Love and Harding 2009). Much remains unknown about basic Southeast Alaska Steelhead ecology and population dynamics, and the ecological processes regulating Southeast Alaska Steelhead growth, survival, and recruitment remain largely unstudied.

Retrospective scale-growth analysis is a particularly well suited method of evaluating growth patterns for Southeast Alaska Steelhead because it is relatively non-invasive and less costly and labor intensive than alternative methods of fish growth assessment (Beakes et al. 2014), and provides information about growth over the entire lifespan of the fish. Scale growth analysis has been broadly applied to evaluate juvenile growth patterns in anadromous fishes. Relationships between growth, maturity, and life-history patterns have been investigated using scale growth increment analysis for chum salmon *O. keta* (Morita and Fukuwaka 2006), coho salmon *O. kitsuch* (Beamish and Mahnken 2001; Fisher and Pearcy 2005), sockeye salmon *O. nerka* (Farley et al. 2007; Ruggerone et al. 2007; Martinson et al. 2008), pink salmon *O. gorbuscha* (Cross et al. 2009), Chinook salmon *O. tshawytscha* (Ruggerone et al. 2009a, b; McPhee et al. 2016; Graham 2016), Atlantic salmon *Salmo salar* (Peyronnet et al. 2007; McCarthy et al. 2008; Friedland et al. 2009), sea (brown) trout *Salmo trutta* (Marco-Rius et al 2012; Marco-Rius et al. 2013) and Steelhead *O. mykiss* (Daugherty et al. 2003; Quinn et al. 2011; Friedland et al. 2014; Hodge et al. 2016).

Complex patterns of juvenile growth observed across anadromous salmonid species reflect the diversity of specific life-history strategies employed by these fish to exploit freshwater and marine habitats. Ruggerone et al. (2009a, b) used scale growth analysis to identify positive correlations between freshwater growth and first-year marine growth in Chinook salmon, while subsequent marine growth was also found to be related to previous years' growth. However, Marco-Rius et al. (2012) identified a compensatory growth pattern in juvenile anadromous brown trout, described by a negative relationship between freshwater growth and growth occurring after migration to the marine environment. The relatively large size of juvenile Steelhead when they first enter the ocean (Love et al. 2013) and their rapid offshore migration (Burgner et al. 1992; Quinn 2005; Quinn and Myers 2005) suggests they may immediately utilize abundant marine resources for growth and development. As such, we hypothesized positive relationships among juvenile Steelhead freshwater growth, marine growth, and adult fish length.

While similarly complex relationships have been found between growth and life-history diversity, negative relationships between the age at which life-history transitions occur and growth conditions are common across a broad range of taxa (Day and Rowe 2002). A pattern of faster-growing individuals within a population exhibiting earlier age at maturity is characteristic of anadromous salmonids (Vollestad et al. 2004; Morita and Fukuwaka 2006). We hypothesized that earlier maturing Steelhead will have increased early marine growth, and female Steelhead will show reduced late marine growth as they dedicate energy towards reproductive development.

This study explored relationships between juvenile freshwater and marine growth and the relative influence of each on life-history diversity of Steelhead once they enter the marine environment. Using adult Steelhead scale samples collected from the Situk River, Alaska between 1999 and 2012, we performed retrospective scale-growth pattern analyses with a mixed-effects modeling approach to evaluate relationships among freshwater growth, early marine growth, and adult size in Steelhead with complex life-history characteristics. Specifically, our objectives were to: 1) estimate marine age and quantify juvenile freshwater and marine growth from adult Steelhead scales; 2) assess correlations among juvenile growth increments and adult length at capture; and 3) determine how growth patterns differ among different life-history and demographic groups of Steelhead. These investigations may support more in-depth population

assessment and monitoring protocols for Steelhead in Alaska that incorporate juvenile growth into the long-term tracking of stock demographic, life-history, and abundance characteristics.

1.3 Study Site

The Situk River is located approximately 16 km southwest of the remote coastal village of Yakutat, Alaska (Figure 1.1). It is a relatively small river, with a mean summer discharge ranging between 5.7 and 8.5 m^3/s (Gubernick and Paustian 2007), and a total watershed area of 397 ha (Marston et al. 2012). Originating in two headwater lakes (Mountain and Situk Lake) and fed by two tributaries (the West Fork and the Old Situk rivers), the mainstem Situk River flows 29 km into the Gulf of Alaska via Situk-Ahrnklin Lagoon (Figure 1.1). From its headwater lakes to the ocean, the Situk River drops approximately 500 m in elevation and is characterized by slow, meandering rifle-pool channels, passing through old growth Sitka Spruce *Picea sitchensis* timber stands and muskeg meadows. The Situk River joins with the Ahrnklin River, Seal Creek, Lost River, and several smaller streams in a tidally influenced lagoon before exiting into the Gulf of Alaska.

For its size, the Situk River is among the most productive rivers in Alaska, supporting the largest known population of Steelhead in Alaska and significant populations of all five North American Pacific salmon, Dolly Varden *Salvelinus malma*, non-anadromous Rainbow Trout, and eulachon *Thaleichthys pacificus*. Historically, about 450,000 Pacific salmon *Oncorhynchus* spp. return to Situk River and contribute commercial, subsistence, and sport fisheries (Thedinga et al. 1993). The unusually high salmonid productivity of the Situk River has been attributed to its stable hydrologic regime and high base flow, mediated by two headwater lakes and substantial groundwater inflow (Thedinga et al. 1993). An abundance of complex low gradient rifle-pool habitat and significant food availability create a diversity of high quality spawning and juvenile rearing habitat for salmonids (Thedinga et al. 1993). The Situk River is an important economic driver for the nearby community of Yakutat, with over 200,000 salmon harvested in the Situk River commercial fisheries in 2015 (Zeiser and Woods 2016). The Situk River also supports an important sport fishery, accounting for an average of 16% annually of all the freshwater sport fishing effort in Southeast Alaska since 1996 (ADF&G 2016). The Steelhead sport fishery in the Situk River is the largest in the region, with an average of 67% of the Southeast Alaska Steelhead catch occurring in this system since 1996 (ADF&G 2016). From 2002 to 2008, angler

catches of Steelhead averaged 12,600 fish annually, while the average catch of other salmonids in the Situk River exceeded 50,000 fish (Marston et al. 2012). Although subsistence salmon fisheries in the Situk River are important to the community of Yakutat, the subsistence harvest of Steelhead remains small.

1.4 Methods

1.4.1 Steelhead sampling

Various methods have been used by the ADF&G and U.S. Fish and Wildlife Service (USFWS) to enumerate salmon and Steelhead in the Situk River since the 1950s, with reliable counts of Steelhead beginning in the early 1990s (Bain et al. 2003). The current aluminum bipod and picket weir structure, with a 10-m floating polyethylene resistance board section, stretches 40 m across the Situk River, at a location approximately 1.9 km upstream from the lower landing (Marston et al. 2012). Steelhead kelts (post-spawn adults) are counted as they move downstream using an underwater video system, which allows personnel to remotely count Steelhead in a nearby cabin and eliminates the need for any presence on the weir during counting periods. An aluminum picket trap and holding pen is constructed on the downstream side of the weir in the deepest section of water adjacent to the floating weir section to capture and sample a portion of the run each year.

Age, sex, and length sampling protocols at the Situk River Steelhead weir have evolved over the duration of operation in response to changes in project objectives (Bain et al. 2003), but a target of 5% of the run has been sampled in recent years (Marston and Power 2016). The weir is in operation from early May to mid-June. Sampling occurred two nights each week, with sample size goals calculated by multiplying the fish counted since the last sampling event by the fixed proportion set in the operational plan at 5% (Marston and Power 2016). Early weir studies observed diel variation in emigration, with older fish moving downstream earlier in the evening (Johnson and Jones 1998). To account for this variation, Steelhead were sampled after midnight on the first weekly sampling event and prior to midnight on the second event (Marston et al. 2012). Captured Steelhead were sampled for sex and standard length (SL), incidence of wounds was noted, and each fish was assigned a color classification of bright, medium, or dark (Marston et al. 2012). Four scales were taken from each side of the fish from the preferred area above the

lateral line on a diagonal between the posterior end of the dorsal fin and the anterior end of the anal fin. All scales were immediately affixed to gum cards labeled with date, species, river system, and sampler information (Marston 2014). Due to changes in project objectives, the regular collection of scales from sampled Steelhead was halted in 2014.

Beginning in 2000, a subsample of selected Steelhead kelts were implanted with 20-mm passive integrated transponder (PIT) tags. In an attempt to maximize the accuracy of age determinations, marine age-2 Steelhead, returning to spawn for the first time, were targeted for tagging and sampling (Marston et al. 2012). Criteria for PIT tagging required fish to be a total length of 750 mm or less, have a "bright" color classification, and lack of any significant wounds or body fungus growth (Marston et al. 2012). All PIT tag-implanted Steelhead were characterized by sex, length, wounds, and color, and eight scales were collected from the preferred area (Marston 2014). A PIT tag antenna was attached to the upstream weir trap opening so that all emigrating Steelhead kelts passed through the reception field during normal counting and sampling. A tagged Steelhead passing through the antenna field would have its tag code recorded, and the PIT tag reader would emit an audible tone via a speaker system allowing weir personnel to remotely close the trap doors and capture the fish (Marston et al. 2012). Recaptured PIT-tagged Steelhead were sampled again for sex, length, and scales, and scored for color and wounds.

1.4.2 Scale measurement

Acetate impressions of scales were made from the original scale gum cards for long-term storage and archiving of scale samples at the ADF&G scale laboratory in Douglas, Alaska. Historical ADF&G operational plans and project reports for the Situk River Steelhead weir indicate scale samples were collected as early as 1994 (Johnson and Jones 1998). All available Situk River Steelhead scale samples were collected and centralized, including acetate scale impressions and scale gum cards that had yet to be pressed. Scale samples suitable for inclusion in this analysis required corresponding sex, length, and sampling date information. Significant centralizing, cataloging, and error checking of data was completed to ensure all available scale samples with corresponding data were utilized. Scale samples and data from 1999 through 2012, excluding 2002 through 2004 when samples and/or data were unavailable, were used in this

study. This initial data and sample organization occurred before any of the scale samples were visually assessed for quality and usefulness (Love et al. 2012).

High-resolution digital scale images of acetate impressions were made using a microfiche scanner (Indus®, Salem, Wisconsin) and electronic imaging software following procedures outlined by Hagen et al. (2001). Scale images were consistently calibrated using a 22-mm optical lens and stored in Tagged Image File (.tif) format with 8-bit depth, 400-dpi resolution, and 3360 x 4426 pixels. Each digital image was archived in the ADF&G Mark, Tag and Age (MTA) Lab database with a unique filename containing pertinent meta-data of species, river origin, year sampled, fish age, sex, and inventory number.

Scale-growth pattern analysis of adult Steelhead scales is complicated by diverse Steelhead life-history patterns and iteroparity (Seamons et al. 2009). Damaged, scarred, or regenerated scales may obscure the area around the scale focus and confound accurate life-history and age analysis. Irregular regions of scale reabsorption associated with feeding cessation and spawning can also obscure the record of circuli and annuli formation. Scale reabsorption associated with illness or starvation during marine residency may lead to the false identification of spawning checks (Love, in press). Moreover, inconsistent or ambiguous circuli patterns resulting from homogeneity in the environmental and physiological mechanisms that regulate scale formation and growth may inflict an inherent subjectivity to scale analysis methods. These challenges informed our scale aging and measuring protocols.

An initial round of quality control was completed during digitization to ensure that only scales suitable for analysis were scanned into the database. Scale-selection criteria were adapted from ADF&G MTA Lab scale scanning protocols to ensure consistent and accurate measurement could be made while tolerating certain unique characteristics of Steelhead scales. Scale assessment occurred in two stages: an initial visual assessment during the scanning process and a more rigorous appraisal of scanned scale images considered for measurement. This assessment methodology was appropriate because none of the Situk River Steelhead scales had been previously aged and all age estimates were made from scanned scale images. Four to eight scales were collected from each individual Steelhead during sampling, which allowed additional suitable scale samples to also be scanned and potentially utilized to verify age assignments. All scales that were scanned and added to the ADF&G digital image archive met the following criteria: 1) the scale was from the correct species and additional sample data were available; 2)

clear circuli were visible along the longitudinal axis for a majority of the scale area; 3) annuli were visible and not obscured or damaged; 4) the focus and outer edge of the scale were visible and well defined; and 5) regeneration did not obscure annuli or focus. All scale quality assessments were based solely on the quality of the scale image and not the complexity of scale patterns. Any scale that did not meet these criteria was excluded from further consideration.

ImagePro® Plus 7.0 (Acton, Massachusetts) software and an unpublished macro developed by ADF&G (D. Oxman, ADFG, personal communication) were used to estimate marine age from digitized scale images following methods described by Love et al. (2013). The scale focus, freshwater-saltwater transition (i.e., smolt check), annuli, and spawning/stress checks were identified along the longest axis of the anterior half the scale and marked digitally on each image (Figure 1.2). Marine age, defined as the number of years spent at sea following the initial juvenile freshwater emigration and smoltification period, was estimated by counting the annuli from the smolt check to the outer edge of the scale. Three blind and independent age readings were completed by the same reader for each sampled scale; if none of the age estimates agreed, the sample was considered unreadable and omitted from further analysis unless an additional scale from the same fish was independently aged to verify modal age estimate (Love et al. 2013). The modal age of the three or four successful scale-age readings was considered to be the most precise age and was reported. The age designation used followed Koo (1962), where the first integer denoted years spent in freshwater, followed by a decimal, then the second integer denoted years spent in saltwater prior to spawning. Additionally, an "s1" was used to denote the occurrence of reabsorption of annuli in a stress or spawning check and an additional year of marine growth (Love, in press). For example, a Steelhead with an estimated age of X.2s1 spent an unknown number of years rearing in freshwater, two years in the ocean prior to returning to spawn, then survived another year at sea and returned to spawn again.

ImagePro® software and the ADF&G macro were also used to measure digitized scale images following general procedures synthesized from Ruggerone (2009a), Quinn et al. (2011), and Love et al. (2013), and all scale increment data was archived in the ADF&G MTA Lab, Oracle ® Database in Juneau, Alaska. Measurement occurred along the longest axis of the anterior half the scale, with circuli identified as the dark rings and annuli identified as densely spaced circuli associated with slower winter growth. Each circulus growth increment was measured in millimeters from the outermost edge of one circulus to the outer edge of the next

adjacent circulus, and annual growth zones were quantified as the sum of the individual circuli increments occurring beyond the outer edge of the preceding annulus and ending at the outer edge of the annulus of the growth zone being measured. For each scale, all individual circuli were measured from the scale focus to the outer edge of the scale. This allowed for the quantification of the entire freshwater zone (FW) as the distance from the scale focus to the outermost edge of the smolt check, the first ocean-year growth zone (SW1) as the distance from the smolt check to the first marine annulus, and second-ocean year growth zone (SW2) as the distance from the first marine annulus to the second marine annulus. Peyronnet et al. (2007) suggested that different measurement types vary in their usefulness as proxies for fish growth, because poor growth conditions may result in no circuli deposition or the possible reabsorption of existing circuli. Therefore, two types of growth measurements were quantified for each growth zone: circuli count and cumulative inter-circuli distance or width. All scale measurements were normalized to a mean of zero, allowing for direct statistical comparisons of different measurement types. The quantification of individual freshwater annual zones was not attempted in this study due to the difficulty in identifying freshwater annuli (the freshwater growth zone was small and compressed relative to the marine portion of these adult Steelhead scales).

1.4.3 Aging accuracy, estimated bias, and precision

Validation is necessary to demonstrate that an aging technique is accurate (Beamish and MacFarlane 1983). Validation of scale aging accuracy requires use of methods developed from scales taken from known-age fish or recaptures of previously marked fish for the life-history stage of interest (Campana 2001). Although known-age freshwater and first-ocean marine samples were not available for Situk River Steelhead scales, PIT-tag recaptures of adult Steelhead initially tagged at Sitkoh Creek as juveniles provided a useful proxy for ocean-growth characteristics of recaptured adult scales (Love, in press). Prior to aging Situk River Steelhead scales, the lead author first practiced reading adult scales using known ocean-age samples from Sitkoh Creek, thus establishing age estimation technique based on true values in a reference collection. A small sample (n = 10) of PIT-tagged and recaptured Situk River Steelhead was also available to assess aging accuracy and to allow for partial (marine) age validation of repeat spawners since the number of years between adult kelt tagging and recapture were known. PIT-

tagged and recaptured Situk River Steelhead scales and scale-aging methods based on validated scale morphological characteristics from Sitkoh Creek provided the most accurate method possible in the absence of known-age Situk samples.

Measures of systematic differences (bias) and precision in methods used are required to evaluate that age readers remain consistent in their age interpretations (Campana et al. 1995). Love (in press) also provided standardized procedures for aging Steelhead scales so that consistent aging results could be obtained thus limiting bias and minimizing variability (improving precision). Pairwise age-bias plots (Campana et al. 1995) comparing each of the three aging reads made for each scale's modal age were constructed to identify any occurrence or direction of bias occurring during age estimation (Figure A.1.1). For all age estimates obtained, the precision or reproducibility of repeated measurements were assessed using coefficient of variation (CV), which was quantified as the ratio of the standard deviation over the mean for each age estimate (Campana 2001):

$$CV_j = 100 \times \frac{\sqrt{\frac{\Sigma_{i=1}^{R}(X_{ij} - X_j)^2}{R-1}}}{X_j},$$

where CV_j was the age precision estimate of the jth Steelhead, X_{ij} was the ith age estimate of the jth Steelhead, X_j was the mean age estimate of the jth Steelhead, and R was the number of times age was estimated for each Steelhead. The CV_j was averaged across all Steelhead to assess the general consistency of the aging method and stratified by Steelhead marine age to assess variability in age estimates related to the ocean age of the Steelhead sampled (Table A.1.1).

1.4.4 Relationships between growth zones

A mixed-effects modeling approach was used to assess relationships between FW growth, SW1 growth, SW2 growth, and adult length at capture. Separate linear mixed-effects models were fit for each measure of growth with preceding growth measurements included as explanatory variables (Table 1.1). Smolt year (calendar year of emigration from freshwater) was included as the random term to allow models to incorporate greater similarity in growth patterns among individuals experiencing the same growth year (McPhee et al. 2016). Smolt year was used to index growth because uncertainty in assigning freshwater age limited our ability to assign individuals to brood year. We only included data from smolt years with minimum sample size of

10 fish, which led to the exclusion of eleven individuals originating from smolt four years: 1995, 1996, 2001, and 2002. To evaluate the appropriate random-effects model structure, we compared linear models with no random effect, models with a random effect affecting the intercept only, and models with a random effect affecting both the intercept and slope using Akaike's information criterion corrected for small sample sizes (AICc) after Zuur et al. (2009). This preliminary analysis suggested that a random-intercept model structure was preferable to a model with no random effect and models with random intercepts and slopes.

We evaluated the assumptions of the linear mixed-effects models and assessed potential outliers with a combination of graphical residual assessment and statistical tests. Assumptions of constant variance, normality, and independence in residuals were assessed graphically with residual plots against corresponding fitted values and specified explanatory variables. The independence assumption was further evaluated with autocorrelation function (ACF) and partial autocorrelation function (PACF) plots. Normal Q-Q probability plots were used to further assess normality and the presence of potential outliers. The Shapiro-Wilk test and the Durbin-Watson test were used to supplement graphical assessments of residual normality and independence respectively. Potential outliers and their influence were identified and evaluated with residual plots and Cooke's distance. No violations of modeling assumptions were identified for any of the fitted models. All statistical analyses were completed using the open source statistical program R (Version 3.1.2, R Core Team 2014). Additionally, we compared among-individual CVs of FW, SW1, and SW2 growth increments, total scale radius, and adult length to assess differences in the variability of growth among different life-history periods.

1.4.5 Life-history and demographic growth differences

A mixed-effects modeling approach was also used to compare SW1 and SW2 growth, and adult length, between Steelhead of different life-history and demographic groups. Separate random linear mixed-effects models were fit for each measure of growth with age at maturity and sex included as explanatory variables and smolt year included as the random effect (Table 1.1). As in previously described analyses, a random-effects model structure comparison using AICc supported the use of the random-intercept structure. Previously described sample-size criteria and model assumption testing procedures were also used in these models to determine that the models conformed to assumptions of normality, constant variance, and independence.

1.5 Results

1.5.1 Age estimation and validation

A total of 525 Steelhead sampled over 11 years (1999-2012, excluding 2002-2004 for which samples were not available) had scales suitable for analysis (Table 1.2). We identified 356 of the scales as lacking a spawning check and thus were categorized as first-time spawners, while 169 scales contained a spawning check and were categorized as repeat spawners. Among the first-time spawning fish, saltwater age-2 and saltwater age-3 were the dominant age classes, representing 36% and 31% of the samples respectively (Table 1.2.) Repeat-spawning fish were found to have saltwater ages -3 to -6 (Table 1.2.) All sampled Steelhead, first-time and repeat spawners, returned to spawn for the first time after two or three years.

Age estimates of all ten scale pairs from PIT tagged and recovered fish matched the interval between sampling events, corroborating marine age estimation (Table 1.A-1). Age-bias plots (Figure 1.A-1) illustrate that minimal aging bias was evident for saltwater age-2 and -3 Steelhead, saltwater age-4 estimates were biased slightly low, and saltwater age-5 fish were underestimated most frequently.

The average CV of all samples was 5.4%, and age-specific CVs ranged from zero to 18.02% (Table 1.2). The CVs of dominant age classes were below the average for the entire sample. Repeat-spawning Steelhead that spent three years at sea before spawning were found to have the largest CVs, reflecting the complexity of their scale patterns. Two fish were estimated to have spent two years at sea before returning to spawn, then successfully spawning four times before being sampled (actually five times because they are sampled immediately after spawning). These uncommon older Steelhead had CVs of zero, indicating they were aged consistently in each of the three scale reads.

1.5.2 Growth measurement types

Growth zone widths and circuli counts were found to be highly correlated. For the FW growth zone, the correlation was 0.8, for the SW1 and SW2 growth zones the correlation was 0.9, and for the entire scale the correlation was also 0.9. Because both measurement types provided essentially the same measure of growth, it was not informative to include both in our analyses, so only growth zone width measurements were modeled

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1.5.3 Relationships between growth zones

Growth during the first year at sea (SW1) increased with freshwater (FW) growth (Figure 1.3). The significant positive relationship between FW growth and SW1 growth explained 9% of the variance in SW1 growth (Table 1.3). Growth during the second year at sea (SW2) decreased with SW1 growth, but was unrelated to FW growth (Figure 1.4). The significant negative relationship between SW1 growth and SW2 growth explained 8% of variance in SW2 growth (Table 1.3). Adult length increased with FW, SW1, and SW2 growth (Figure 1.5). The significant positive relationship between SW1 growth and length explained 19% of the variance in length, and the significant positive relationship between SW2 growth and length explained 30% of the variance in length (Table 1.3).

Situk Steelhead SW2 growth CV (22.7%) was greater than SW1 growth CV (17.3%), and adult fish length measurements (10.4%) and total scale radius (14.0%) had reduced CVs compared to previous freshwater and saltwater growth CVs (Figure 1.6). Freshwater growth CV (19.2%) was also greater than SW1 CV (Figure 1.6).

1.5.4 Life-history and demographic growth differences

Growth and size comparisons between age at maturity and sex are summarized in Table 1.4 and Figure 1.7. Later-maturing Steelhead (those returning to spawn for the first time after three years at sea) had reduced SW1 growth compared to earlier maturing Steelhead. No significant difference in SW1 growth was seen between males and females. These later-maturing Steelhead were also found to have increased SW2 growth compared to earlier maturing Steelhead, but there was no significant difference in SW2 growth between male and female Steelhead. Adult length of later-maturing Steelhead was greater than that of earlier maturing Steelhead, while male Steelhead exhibited slightly increased adult length compared to female. No differences were identified in FW growth between early and later-maturing Steelhead, or between male and female Steelhead

1.6 Discussion

This study provided foundational information on patterns of juvenile freshwater and marine growth for Southeast Alaska Steelhead. Fish that grew more in freshwater tended to show enhanced growth during their first year at sea, while fish that grew more slowly during the first marine year appeared to show compensatory growth during the second marine year. A review of salmonid growth studies by Marco-Rius et al. (2012) determined that the majority of studies considered found no significant relationship between smolt size and marine growth, and negative correlations occurred more frequently than positive ones. However, the single study that specifically considered Steelhead growth relationships (Johnsson et al. 1997) found a weakly positive correlation between freshwater pre-smolt growth and marine post-smolt growth that was consistent with our results. Fish that grew more during their first year at sea tended to show reduced growth during their second year at sea, and they also tended to mature earlier, suggesting that interactions between growth and maturity resulted in initially faster-growing fish diverting energy from somatic growth to gamete development. This relationship between growth and maturity is consistent with findings for Pacific salmonids (Quinn 2005) and Atlantic salmon *Salmo salar* (Hutchings and Jones 1998; Jonsson and Jonsson 2007). Additionally, increased Steelhead SW2 growth CV compared to SW1 growth CV suggests that SW2 growth was more variable as a cohort diverges into early and later-maturing life-history forms, with differential investments in somatic or reproductive growth.

Steelhead exhibit a different early marine migratory pattern (Burgner et al. 1992) and bio-energetic strategy than other Pacific salmon species by moving rapidly offshore during their first year at sea and foraging on a more dispersed but higher energy prey base of juvenile fishes and squid (Atcheson et al. 2012a). Atcheson et al. (2012b) identified distinct differences in prey composition of ocean age-0 Steelhead relative to older Steelhead, with ocean age-0 Steelhead consuming more larval and juvenile fish species, while older Steelhead consumed more squid. Steelhead in Alaska typically spend three years rearing in freshwater before emigrating to the ocean (Harding 2008), which allows them to attain a relatively large body size upon ocean entry. Their large ocean age-0 size, early marine strategy of rapid offshore migration, and utilization of high-energy prey (fish and squid) allow Steelhead to achieve SW1 growth not observed for Pacific salmon species until their second year at sea (Atcheson et al. 2012a). These migratory

and foraging patterns of juvenile Steelhead may help explain the positive FW-SW1 growth relationship we observed because larger individuals have a competitive advantage in the consumption of dispersed fish and squid prey during their first year at sea (see also Ruggerone et al. 2009 for a similar interpretation of a positive FW1-SW1 relationship in yearling-smolt Chinook salmon from western Alaska). Our data show a pattern of diminished SW2 growth for these larger, faster-growing fish, which may reflect their switch to allocating energy resources to reproductive development rather than somatic growth. Slower-growing Steelhead may delay maturation, allowing them to increase in size and compensate for preceding differences in growth.

First- and second-ocean year growth models described a relatively small amount of the variation, suggesting that many factors other than previous growth affect early marine growth. Freshwater growth and first and second-ocean year growth were all positively correlated with adult fish size, but second ocean-year growth was the best predictor of adult fish length, suggesting that diverging energy allocation to somatic growth or gamete development occurring during the second ocean-year for Steelhead is important to help us understand adult growth patterns. Similar results have been found for anadromous brown trout (*Salmo trutta*; Marco-Rius et al. 2012), suggesting that Steelhead adult length is affected by interactions between marine growth rates and maturity, while the influence freshwater growth is mediated through its relationship to first ocean-year growth.

The critical size and period hypothesis describes two phases of growth-mediated differential mortality for juvenile anadromous salmonids, the first occurring as size-selective predation upon ocean entry and the second as physiologically-based mortality of individuals unable to reach a critical size before their first winter at sea (Beamish and Mahnken 2001). Despite their relatively large size as smolts and rapid early marine growth, size-selective sources of mortality may still impact Situk River Steelhead during the marine phase of their life history, so the growth patterns described in this study are the product of juvenile Steelhead early marine ecology and differential mortality related to size. Reduced scale radius and adult length CV may also be explained by differential mortality that constrained total adult growth patterns of individual Steelhead that survived to return to their natal stream. An inherent limitation of this study is that all samples were collected only from adult Steelhead that survived to return to their

natal stream, so growth patterns identified here represent a small portion of the original juvenile cohort and offer little insight into how growth relates to juvenile mortality.

We found significant differences in marine growth between Steelhead that spent two and three years at sea before returning to spawn. Earlier-maturing (ocean age-2) Steelhead grew more in first year at sea, while later-maturing Steelhead (ocean age-3) grew more in their second year at sea. Further, later maturing Steelhead also had greater adult length. Earlier-maturing Steelhead also exhibited slightly increased freshwater growth, but the difference was not statistically significant. These results match our expectation that earlier-maturing Steelhead exhibited increased early marine growth, while later-maturing Steelhead grew more in the later portions of their ocean residency period and attained increased adult size. This relationship between marine growth and age at maturity has been demonstrated for Atlantic salmon (Hutchings and Jones 1998; Jonsson and Jonsson 2007), while Vollestad et al. (2004) found that the proportion of coho and Chinook salmon maturing early and returning as jacks was primarily related to smolt size and not early marine growth in hatchery populations. The relationship between growth and age at maturity is likely impacted by both environmental conditions and genetic thresholds (Day and Rowe 2002). The mechanisms directing patterns of anadromy in Steelhead are complex and likely variable among populations, but the relationships we identified between marine growth and maturity reflect the acknowledged plasticity of Steelhead life-history (Kendall et al. 2015). Differences in growth patterns among male and female Steelhead in our study were less clear. There was no difference in first- and second-marine year growth between male and female Steelhead, but male Steelhead had slightly greater adult length compared to females. These results again reflect the complexity of Steelhead life history patterns and the variety of other environmental and physiological factors not considered in this study that affect individual growth patterns.

We can offer two general findings that were true of all Steelhead considered in this study. Among the large body of research that has retrospectively quantified fish growth from scale samples, a variety of growth measurement types have been analyzed. In this study, we found scale zone width measurements and circuli counts very similar measures of growth for all life-history periods and demographic groups of Steelhead. Additionally, the mixed-effects modeling approach resulted in improved model performance (reduced AICs and increased R^2 values) compared to simple linear models and a significant contribution of the random effect smolt year

term in all growth zone models (Zuur et a. 2009). This suggests that significant differences in marine growth and overall fish size among smolt year cohorts were present and significantly improved our understanding of marine growth patterns.

The measurement of annual growth increments depends on accurate and precise identification of scale annuli, and interpretation of analyses that utilize these measurements require correctly assigning them to a particular year or life-history period. While absolute age-validation methods were somewhat limited for adult scale samples in this study, established Steelhead aging protocols and precision assessment tools such as coefficient of variation and age-bias plots provide quantitative measures of confidence (Campana et al. 1995). While no formal *a priori* standard of precision has been agreed upon, a literature review by Campana (2001) suggests that CVs below 7.6% are sufficient to support further analysis and an informal target CV of 5% is sought by many researchers. Average age-specific CV values in this study ranged from 0.0 – 18.2%, but for dominant age classes of 2SW and 3SW, the average CVs were 4.69% and 4.04%, respectively. Age-bias plots corroborate these findings, indicating minimal aging bias for dominant age classes, but some underestimation of older age fish. Difficulties in aging scales from older individuals were an expected result as these scales contain complex annuli and circuli patterns that may be obscured or disrupted by scale reabsorption at the spawning check. Scale samples from tagged and recaptured fish provide an additional level of validation, confirming our age estimates for the period of time between capture events. Our estimates of age and repeat spawning rates also matched those found in previous Southeast Alaska Steelhead scale analysis studies (Harding and Coyle 2011; Love et al. 2012, 2013).

Our inability to estimate freshwater age prevented our marine growth models from accounting for differences in growth related to freshwater age. Given the acknowledged complexity of the freshwater rearing period for juvenile Steelhead (ranging from two to five years in our study region; Harding 2008), it is likely that freshwater growth and residency duration impacted subsequent marine growth patterns and life-history variation. Overall study design and age validation protocols could be improved by tagging and collecting scales from rearing juvenile Steelhead in freshwater, so that the length of time at liberty could be maximized for recaptured adults (Campana 2001). This sampling protocol would allow for the validation of growth-increment periodicity with the known absolute age of the recaptured fish for both the freshwater and marine portions of their life history, and several other Southeast Alaska Steelhead

studies have utilized methods similar to this approach (Love et al. 2012, 2013). These studies have been synthesized into a reference collection of known-age Southeast Alaska Steelhead scales that will aid in the detection of biases in future research of this type (Campana 2001; Love, in press). Additionally, future studies could synthesize freshwater growth measurement methodologies from this study with scales from juvenile Southeast Alaska Steelhead to define the quantitative relationship between freshwater age and freshwater growth. This research would provide a validated methodology to estimate total Steelhead age from adult Steelhead scales and provide increased insight into relationships between growth and life-history diversity that impact juvenile Steelhead ecology and subsequent recruitment, and survival.

Current ADF&G Situk River Steelhead stock assessment objectives focus on abundance monitoring and the tracking of fish sex and length characteristics (Marston and Power 2016). This information facilitates management that is responsive to changes in stock characteristics and fishery effects. Conservative Situk River Steelhead recreational fishing regulations and popular catch-and-release angling practices have maintained relatively stable stock characteristics while allowing for continued high levels of recreational fishing activity (Marston and Power 2016). This combination of population monitoring and conservative regulations has effectively managed this important fishery (Harding and Coyle 2011), but is limited in its consideration of how changing marine and freshwater aquatic habitats may impact Steelhead in Alaska. Scale-increment analysis offers an underutilized source of information on patterns of Steelhead marine growth and may be expended to more fully investigate patterns of freshwater juvenile growth. Furthermore, scale-increment analysis is well suited to Steelhead research because it is relatively non-invasive and affordable compared to alternative sampling methods (Love, in press). The standardized collection of scales from Situk River Steelhead should continue to support ongoing studies that increase our understanding of Steelhead early marine ecology, life-history diversity, and growth dynamics that may be both novel and informative to Southeast Alaska Steelhead management. Incorporating metrics of juvenile Steelhead growth into population monitoring protocols would provide more in-depth baseline information on relationships between growth and life-history diversity that may inform management in the face of unpredictable environmental change. Among Southeast Alaska Steelhead populations, the Situk River provides a unique opportunity to increase our understanding of the population regulating processes of a

completely wild and healthy stock as climate-related changes to terrestrial and aquatic ecosystems begin to impact fish populations.

1.7 Figures
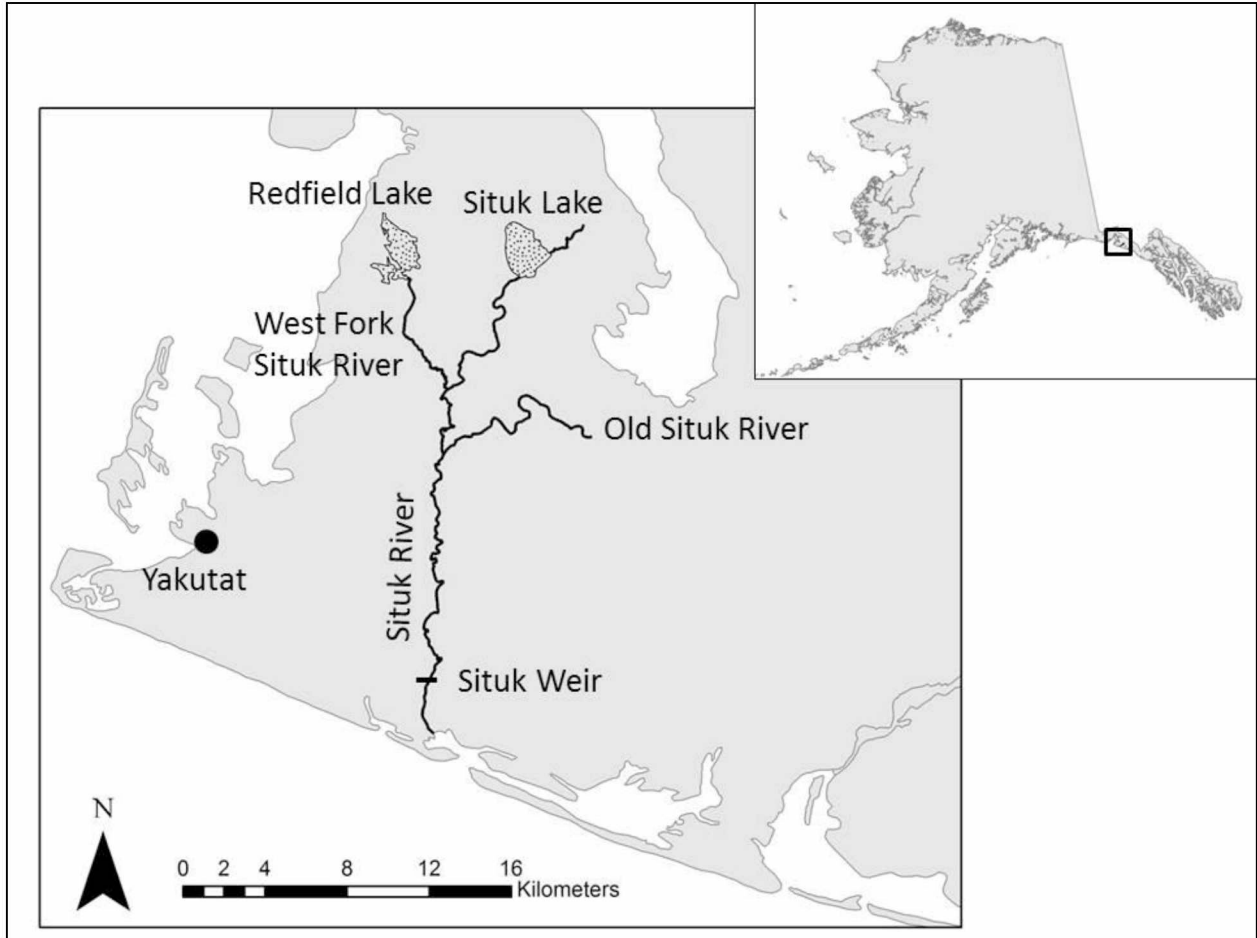
Figure 1.1: Map of the Situk River, showing the location of the weir and the neighboring village of Yakutat.
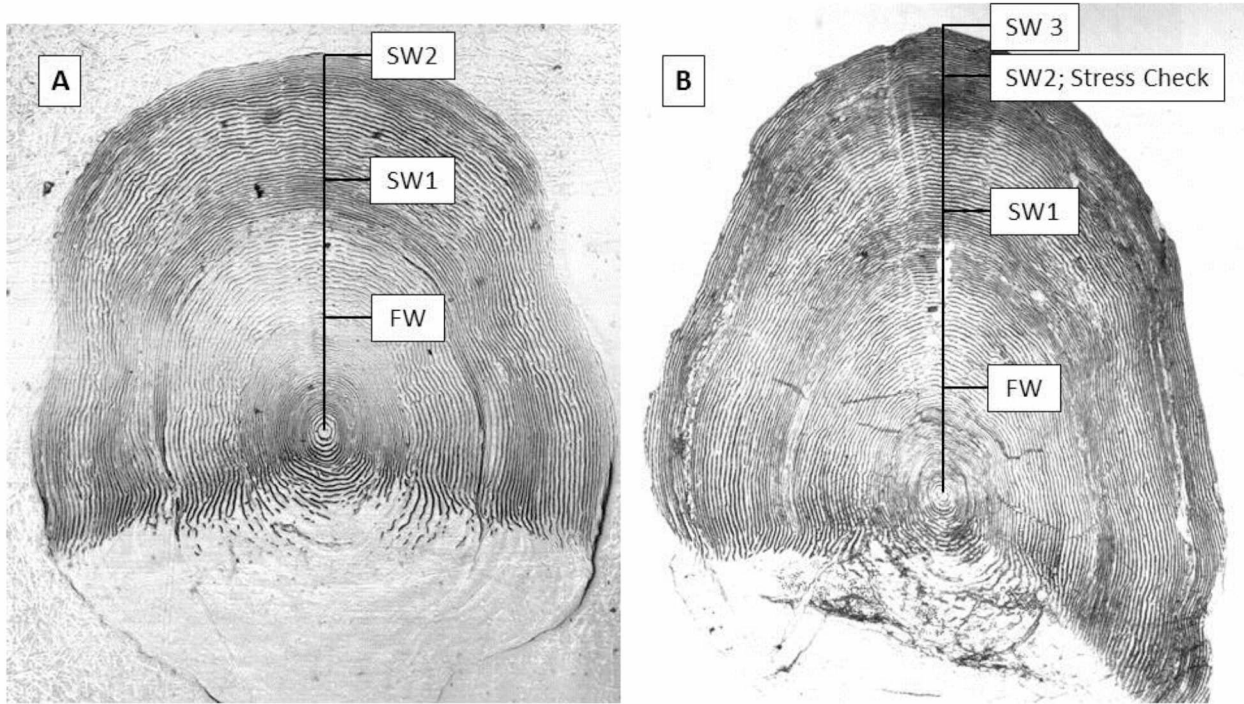
Figure 1.2: Annotated age X.2 (A) and X.2s1 (B) Steelhead scales from the Situk River displaying freshwater (FW) and the first (SW1), second (SW2), and third (SW3) ocean-years of growth. Scale B also contains a spawning check that indicates the stress of an energetically costly spawning event, denoted by the "s" in the age designation.
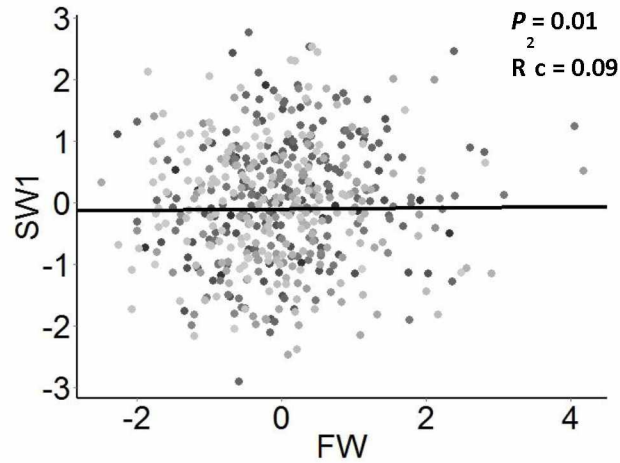
Figure 1.3: Relationship between freshwater growth (FW) and first-ocean year growth (SW1). The black line is the fitted relationship from the linear mixed-effect regression model between the growth variables (fixed effect), with different smolt years (random effect) designated by point shade. P-value and conditional coefficient of determination (R^2c) were obtained from the linear mixed-effect regression model.
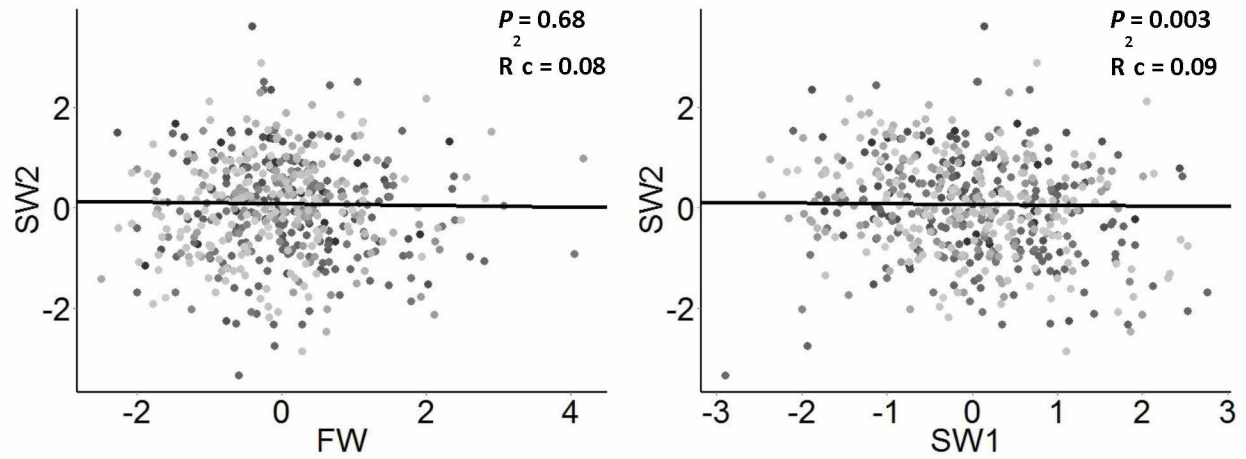
Figure 1.4: Relationships of first-ocean year growth (SW1) and freshwater growth (FW) with second-ocean year growth (SW2). The black lines are fitted relationships from the linear mixed-effect regression model between the growth variables (fixed effect), with different smolt years (random effect) designated by point color. P-value and conditional coefficient of determination (R^2c) were obtained from the linear mixed-effect regression model.
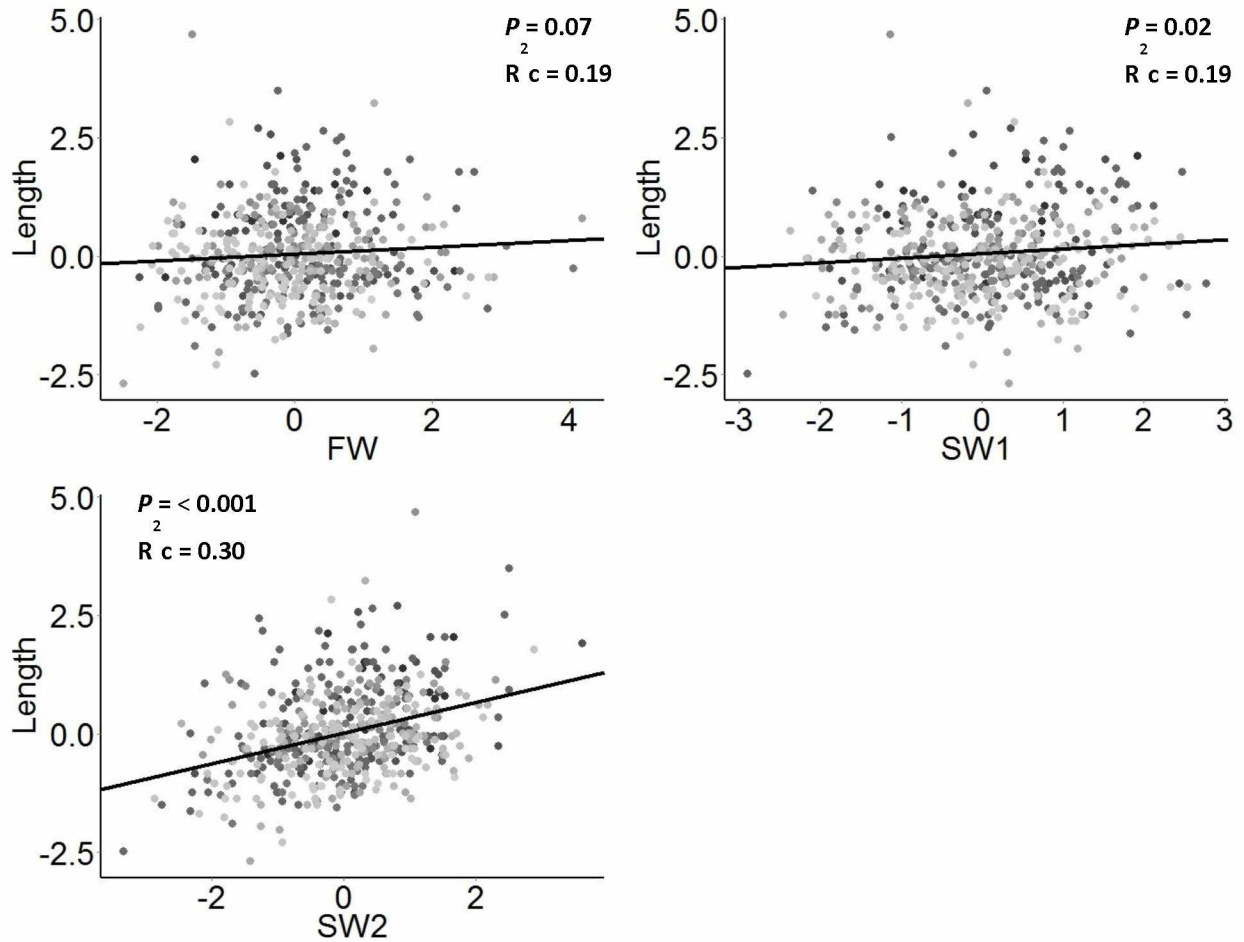
Figure 1.5: Relationships of freshwater growth, first-ocean year growth (SW1), and second-ocean year growth (SW2) to adult length (Length). The black lines are model fitted relationships from the linear mixed-effect regression between the growth variables (fixed effect), with different smolt years (random effect) designated by point color. P-value and conditional coefficient of determination (R^2c) were obtained from the linear mixed-effect regression model.
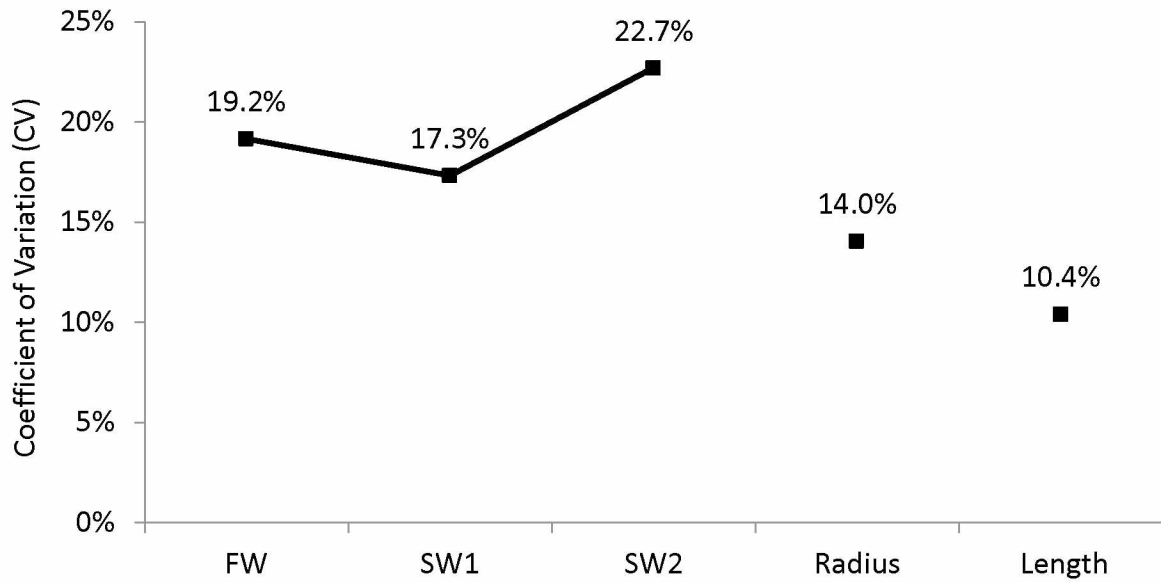
Figure 1.6: Coefficient of variation (CV) of scale growth increments for freshwater, first-ocean year, and second-ocean year growth zones, as well as CV of total scale radius, and adult length at capture.
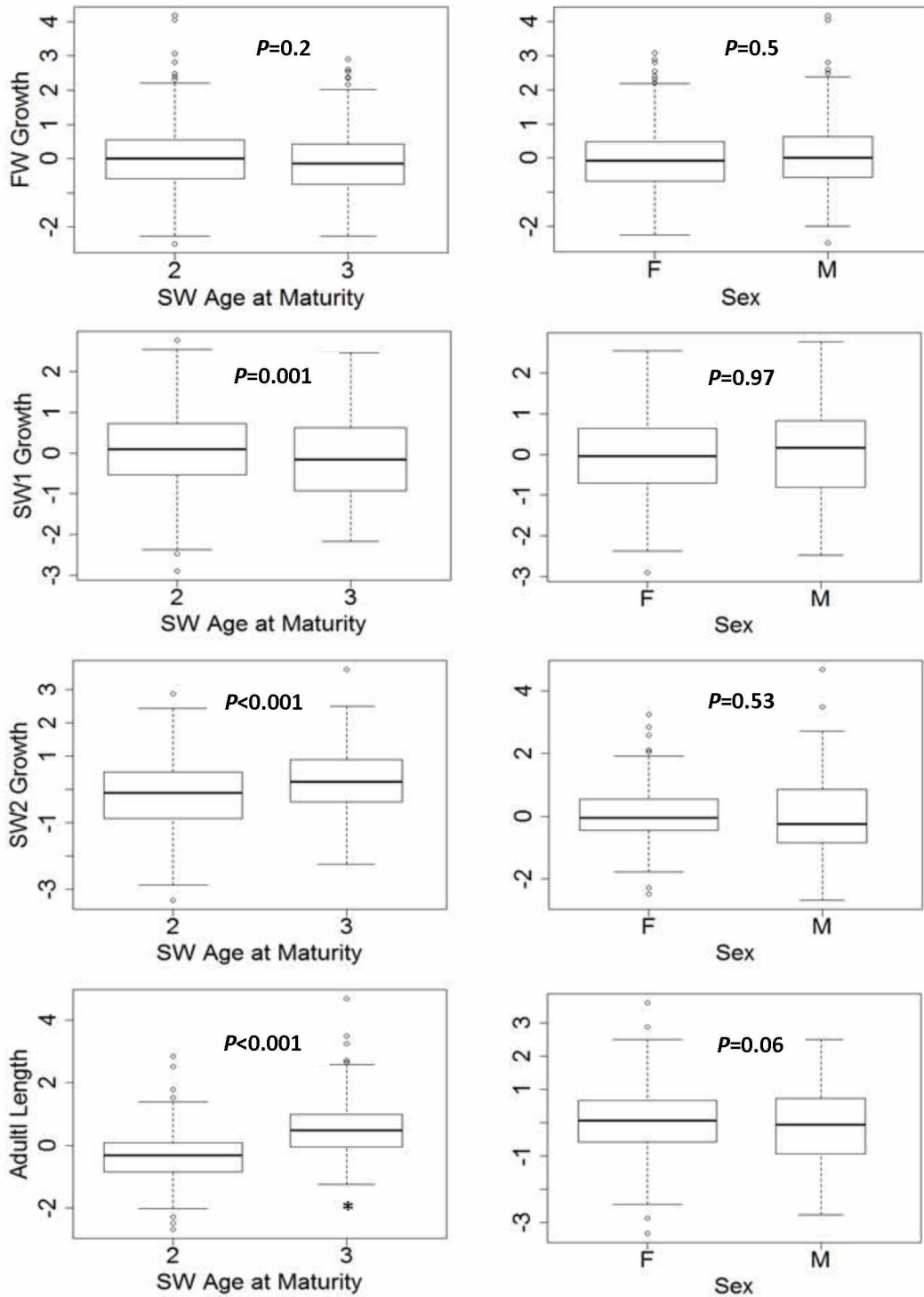
Figure 1.7: Comparison of FW growth, SW1 growth, SW2 growth, and adult length between saltwater age-2 and -3 Steelhead, and male and female Steelhead. In each boxplot the box identifies the upper and lower quartiles of the data; the horizontal line identifies the median, and the whiskers are equal to the upper and lower quartiles +/- 1.5 · interquartile range (IQR). *P*-values were obtained from linear mixed-effect regression models each growth variable.

1.8 Tables

Table 1.1: Structure of all models of growth measurements and adult length, including fixed and random effects.

Dependent Variable	Independent Variable	Random Effect
Growth Zone Relationship Models		
SW1 Width	FW Width	
SW2 Width	FW Width	
SW2 Width	SW1 Width	Smolt Year
Adult Length	FW Width	
Adult Length	SW1 Width	
Adult Length	SW2 Width	
Demographic and Life-history Group Growth Models		
FW Width	SW Age at Maturity + Sex	
SW1Width	SW Age at Maturity + Sex	
SW2 Width	SW Age at Maturity + Sex	Smolt Year
Adult Length	SW Age at Maturity + Sex	

Table 1.2: Summary of assessed Steelhead scales by saltwater age, repeat-spawning status (where 's' indicates a spawning event; e.g., X.2s1 indicates 2 years at sea, followed by a spawning check, followed by an additional year of marine growth), percent female, sample size (N), and average of the coefficient of variation in an individual's age estimates (CV) by estimated saltwater age.

Years at Sea	Age	% Female	N	Average CV
2	X.2	54	192	4.69
3	X.2s1	84	99	4.42
3	X.3	73	164	4.04
4	X.2s1s1	100	22	5.26
5	X.2s1s1s1	100	4	4.33
4	X.3s1	79	33	18.02
5	X.3s1s1	82	9	12.37
6	X.2s1s1s1s1	89	2	0.00
Total			525	5.41

Table 1.3: Mixed-effects model results describing relationships between growth zone increments and previous growth of individual Steelhead. Marginal coefficient of determination (R^2m) quantifies the proportion of variance explained by fixed effects, while conditional coefficient of determination (R^2c) describes the proportion of variance explained by both fixed and random effects.

Dependent Variable	Independent Variable	Model					
		β	Standard Error	t	P	R^2m	R^2c
SW1	FW	0.11	0.04	2.57	0.01	0.01	0.09
SW2	SW1	-0.13	0.04	-3.00	0.003	0.02	0.08
SW2	FW	-0.02	0.04	-0.42	0.68	0.00	0.08
Adult Length	FW	0.07	0.04	1.80	0.07	0.01	0.19
Adult Length	SW1	0.10	0.04	2.41	0.02	0.01	0.19
Adult Length	SW2	0.32	0.04	8.95	< 0.001	0.12	0.30

Table 1.4: Mixed-effects model results comparing growth increments between saltwater age 2 and 3 Steelhead, and male and female Steelhead. Marginal coefficient of determination (R^2m) quantifies the proportion of variance explained by fixed effects, while conditional coefficient of determination (R^2c) describes the proportion of variance explained by both fixed and random effects.

Dependent Variable	Independent Variable	Model					
		β	Standard Error	t	P	R^2m	R^2c
FW Width	SW Age at Maturity (3)	-0.12	0.09	-1.28	0.20	0.01	0.07
	Sex (Male)	0.07	0.10	0.69	0.50		
SW1 Width	SW Age at Maturity (3)	-0.31	0.09	3.3	0.001	0.02	0.11
	Sex (Male)	-0.004	0.10	-0.04	0.97		
SW2 Width	SW Age at Maturity (3)	0.39	0.09	4.26	< 0.001	0.04	0.11
	Sex (Male)	-0.06	0.10	-0.63	0.53		
Adult Length	SW Age at Maturity (3)	0.83	0.08	10.80	< 0.001	0.19	0.27
	Sex (Male)	0.15	0.08	1.92	0.06		

1.9 References

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1.10 Appendix 1

Table A.1.1 Summary of PIT-tagged and recaptured samples collected from Situk River Steelhead.

| Tag Code	Implant				Recovery				Sample Year Interval	Assigned Age Interval
	Date Tagged	Sex	Length	SW Age	Date Recovered	Sex	Length	SW Age		
985120028265770	6/12/2007	F	715	3	6/5/2009	F	840	5	2	2
985120027810379	6/16/2008	F	630	2	6/8/2009	F	750	3	1	1
985120028260527	6/4/2009	F	725	2	5/25/2010	F	740	3	1	1
985120020950831	6/23/2010	F	730	2	5/27/2011	F	750	3	1	1
985120020954077	5/31/2010	F	680	2	6/3/2011	F	720	3	1	1
985120018374590	6/23/2010	F	725	2	6/5/2011	F	620	3	1	1
985120023632554	5/27/2010	F	780	3	6/12/2011	F	780	4	1	1
985120020944184	6/5/2011	F	670	2	6/6/2012	M	745	3	1	1
985120018376520	6/5/2011	F	810	3	6/12/2012	F	850	4	1	1
985120020966696	6/7/2011	F	665	2	6/15/2012	F	685	3	1	1
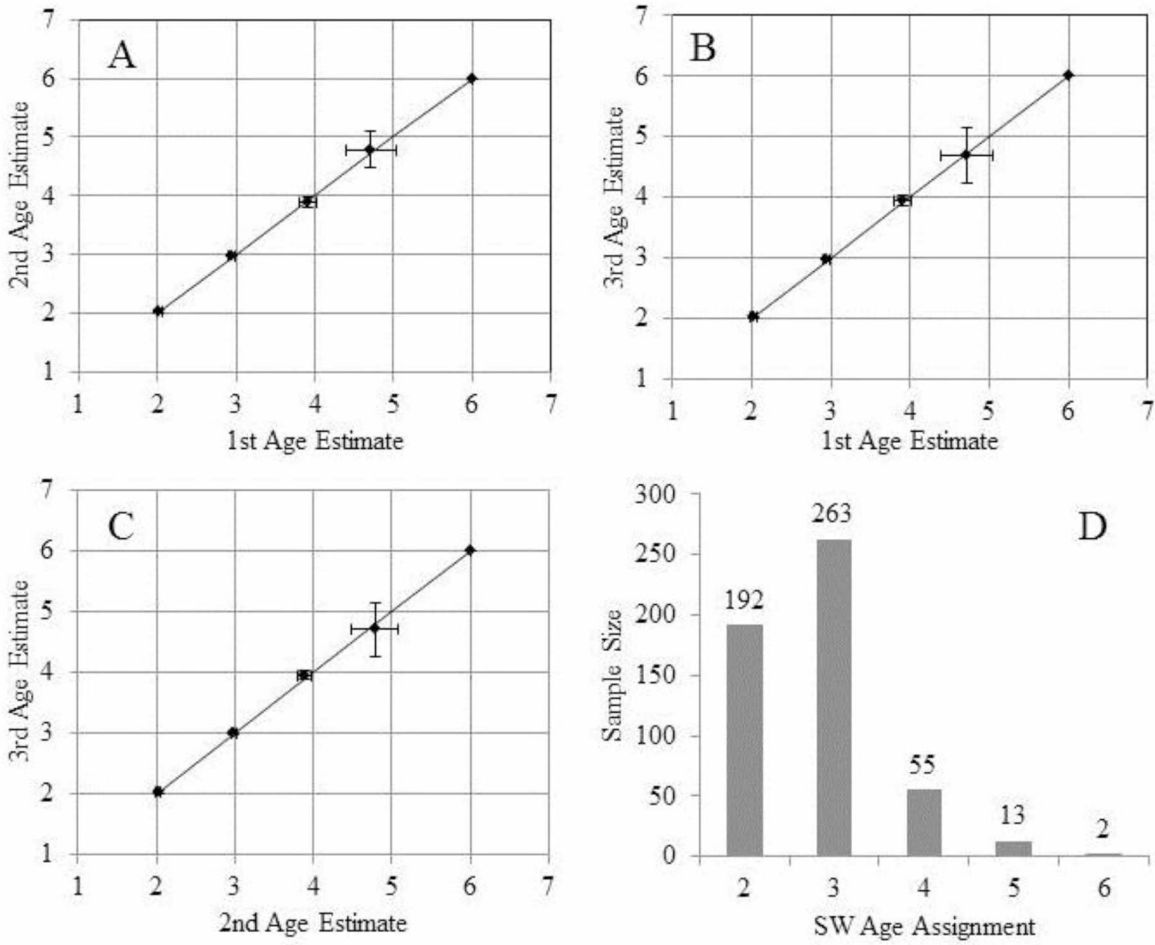
Figure A.1.1 (A-C) Age-bias plots depicting pairwise comparisons of each set of age estimates for all 525 scales assessed. Error bars represent the 95% confidence interval about the average age assigned during each round of age estimation, and a 1:1 equivalence line is also provided as reference. (D) Sample sizes of each age class.

Chapter 2 Relationships of Situk River Steelhead *Oncorhynchus mykiss* growth and abundance with regional climate and Steelhead abundance patterns.[2]

2.1 Abstract

Common trends in abundance among Southeast Alaska Steelhead *Oncorhynchus mykiss* populations suggest the influence of population-regulating forces operating on a regional scale. Twenty years (1997-2016) of abundance information from eleven Southeast Alaska Steelhead populations was combined with scale-derived early marine growth measurements and pertinent marine climate variables to assess regional abundance correlation patterns and relationships among Steelhead growth, abundance, and ocean conditions. Strong abundance correlations between Situk River Steelhead and regional Steelhead abundance trends were found to vary along a distance gradient, whereby populations located closer to the Situk River had higher abundance correlations than more distant populations. Across the region, populations located closer to each other were more strongly correlated, however a Mantel test of the relationship between abundance correlation and distance matrices for Southeast Alaska Steelhead populations was not statistically significant (r = -0.21, P = 0.9, df = 10). Positive relationships between Gulf of Alaska sea surface temperature, North Pacific Gyre Oscillation, and Situk River Steelhead abundance further support the importance of ocean conditions to Steelhead productivity. An improved understanding of the spatial structure of Southeast Alaska Steelhead populations and the influence of climate-driven ocean conditions on Steelhead productivity should improve ongoing management, research and conservation efforts.

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[2] Catterson, M. R., D. C. Love, T. M. Sutton, and M. V. McPhee. Relationships of Situk River Steelhead *Oncorhynchus mykiss* growth and abundance with regional climate and Steelhead abundance patterns. Prepared for submission to Transactions of the American Fisheries Society.

2.2 Introduction

Interactions between atmospheric and oceanographic systems drive lower trophic-level productivity, which fuel complex ecosystem dynamics occurring in the North Pacific that impact commercially and ecologically important fish species (Hare and Francis 1994; Francis et al. 1998; Stabeno et al. 2004; Combes et al. 2009). Linkages between patterns of marine climate variability and North Pacific salmon production were initially identified through correlation and time series analysis of retrospective commercial fishery data and records of Pacific basin climate indices (Beamish and Bouillon 1993; Hare and Francis 1994; Mantua et al. 1997). Broad coherence between marine regimes and Pacific salmonid abundance trends suggest the importance of marine conditions to anadromous fish survival and recruitment (Hare and Francis 1994; Mantua et al. 1997). Additionally, the influence of marine conditions appears to be time-lagged by species-specific marine residence periods, suggesting that ocean conditions impact juvenile salmonids the most during the early portions of their marine life cycle (Mantua et al. 1997).

The critical size and period hypothesis describes how early marine mortality may occur (Beamish and Mahnken 2001). As juvenile salmonids enter the marine environment, they may encounter an initial period of size-selective predation occurring immediately upon ocean entrance, followed later by a period of growth-mediated mortality where juvenile fish unable to reach a critical size cannot satisfy the metabolic requirements needed to survive their first winter at sea (Beamish and Mahnken 2001). This hypothesis emphasizes the importance of early marine growth to avoid predation and reach sizes that enable increased feeding opportunities. Evidence of the importance of early marine growth to anadromous fish survival and recruitment has been described for Pacific salmon *Oncorhynchus* spp. (Beamish and Mahnken 2001; Farley et al. 2007; Ruggerone et al. 2009), Steelhead *O. mykiss* (Bond et al. 2008; Friedland et al. 2014), and Atlantic salmon *Salmo salar* (Friedland et al. 2009; Peyronnet et al. 2007; McCarthy et al. 2008). Correlations between early marine growth rates, increased survival or recruitment, and favorable ocean thermal conditions exist for Steelhead (Friedland et al. 2014) and sockeye salmon *O. nerka* (Ruggerone et al. 2009), suggesting that early marine growth may be a physiological link between marine conditions, salmonid survival, and recruitment.

Consideration of the unique characteristics of Steelhead marine migration and life-history is important to understanding the ecological processes that drive Steelhead productivity. Juvenile Steelhead exhibit a marine migration and distribution pattern that broadly spans the GOA and Central North Pacific (CNP) region. Unlike some closely related and sympatric salmon species, juvenile Steelhead migrate rapidly from natal freshwaters to offshore summering areas of the central and western GOA (Light et al. 1989; Burgner et al. 1992). Tagging and marine sampling information indicates that there is little stock-specific differentiation in marine migration and distribution for populations ranging along the coast of North America (Burgner et al. 1992). Steelhead have been found to occupy near-surface depths during the majority of their marine residence period (Burgner et al. 1992; Nielsen et al. 2011), but they may also descend to moderate depths and exhibit diel vertical migration patterns (Walker et al. 2000).

The broad marine distribution pattern, preference for near-surface depths, and interacting bio-energetic temperature and prey preferences suggest that Steelhead rely on ocean conditions shaped both by large and small-scale climate features occurring across the GOA and CNP (Atcheson et al. 2012a,b). Spatial and temporal changes occurring in dynamic marine environments that may affect juvenile Steelhead growth and survival can be quantified by several key ocean climate indices. El Niño Southern Oscillation (ENSO)-driven climatic variability has also been shown to influence anadromous fish populations in the North Pacific (Costello et al. 1998). Early returns of Bristol Bay sockeye salmon, increased weight of mature Fraser River sockeye salmon, and lower than expected coho salmon *O. kisutch* returns in Oregon have all been attributed to warm ENSO phases (Mysak 1986; Johnson 1988). The North Pacific Gyre Oscillation (NPGO) index tracks fluctuations in salinity, nutrients, and chlorophyll driven by variation in regional and basin-scale patterns of wind-driven upwelling and horizontal advection (Di Lorenzo et al. 2008). These oceanographic characteristics provide the foundation of the marine food web, shaping planktic marine ecosystem dynamics that support higher trophic level populations like salmon and Steelhead (Di Lorenzo et al. 2008). The North Pacific Index (NPI) characterizes changes in the intensity of the Aleutian Low (AL) pressure system, which impacts sea surface temperature variation over short time scales, with these linkages being most apparent during winter months (November- March) when most SST variability occurs (Trenberth and Hurrell 1994). These indices provide interrelated measures of the primary oceanographic processes that drive lower trophic level productivity and form the foundation of the marine food

web. Steelhead marine distribution and overall productivity are shaped by physiological requirements to optimize growth and preferences for high energy density prey species, both of which are significantly influenced by interacting atmospheric and marine climate systems (Kaeriyama et al. 2004; Atcheson et al. 2012a,b).

Steelhead populations across Southeast Alaska have exhibited similar trends in abundance in recent years (Marston et al. 2012). Correlations in Southeast Alaska Steelhead abundance may indicate the shared response of individual population dynamics to forcing factors common among watersheds across the region. For anadromous salmonids that are not significantly impacted by anthropogenic forces, these factors are likely driven by climate or marine conditions and may explain some of the trends in Steelhead growth and abundance (Mueter et al. 2005; Jorgensen et al. 2016). Specifically, we expect that favorable ocean conditions for juvenile salmonid growth experienced during positive phases of the ENSO cycle and years of warmer sea surface temperatures in the GOA and CNP could lead to increased marine survival of Situk River Steelhead and increased adult abundance in freshwater (Mysak 1986; Mantua et al. 1997). Similarly, we expect that high NPGO measures would indicate increased offshore upwelling and more coastal eddy activity leading to higher productivity in GOA waters that would be favorable for juvenile Steelhead growth, survival and ultimately spawning fish abundance (Di Lorenzo et al. 2008; Jeffrey et al. 2017). In contrast, we expect positive NPI values would indicate decreased Aleutian Low pressure activity, and both decreased upwelling and coastal eddy activity, which would decrease productivity in the GOA leading to decreased growth, survival and abundance for juvenile Steelhead (Trenberth and Hurrell 1994). We expect increased early marine growth may improve juvenile Steelhead marine survival and lead to increased Situk River Steelhead abundance (Beamish and Mahnken 2001; Friedland et al. 2014).

The degree to which Southeast Alaska Steelhead populations, including the Situk River, exhibit synchronous abundance trends informs our understanding of the factors regulating these small and potentially vulnerable stocks. Spatial patterns of abundance synchrony may further describe the scale and relative importance of climate- or marine-forcing factors and contribute to our understanding of population connectivity and interaction (Jorgensen et al. 2016). This study combines the longest available time series of Alaska Steelhead abundance and biological samples collected from the Situk River with abundance monitoring information for other

Southeast Alaska Steelhead populations, in order to test the hypotheses outlined above regarding the potential role of climate and the marine environment in mediating patterns of abundance and growth for Southeast Alaska Steelhead. Our specific objectives were to: 1) identify correlations in abundance among regional Steelhead populations, including any spatial correlation structure; and 2) assess relationships between Situk River Steelhead early marine growth, Steelhead abundance, and specific measures of marine conditions that characterize the GOA and North Pacific ecosystem.

2.3 Methods

2.3.1 Steelhead abundance

The Situk River, located at the northern extent of Southeast Alaska and ~15 km southwest of the coastal village of Yakutat, supports the largest known population of Steelhead in Alaska (Figure 2.1). Abundance of Situk River Steelhead is enumerated each spring through an Alaska Department of Fish and Game (ADF&G) stock assessment project that counts post-spawning kelts as they emigrate downstream through a weir on the lower river. The ecological importance and economic value of the Situk River Steelhead fishery led to formalized assessment efforts beginning in 1988, and Steelhead counts have occurred annually at this lower river weir operation (Marston and Power 2016). However, complete emigrant Steelhead counts are only available since 1995 (Bain et al. 2003). Individual Steelhead are counted as they pass downstream through the weir using underwater video cameras, and biological sampling protocols have collected sex, length, and condition information as well as scale samples since 1990 (Bain et al. 2003).

Regional Southeast Alaska Steelhead abundance information was obtained from annual ADF&G surveys of Steelhead index streams across the region (Figure 2.1) (P. Fowler, ADF&G, personal communication). Standardized snorkel survey methodology has been used since 1997 to enumerate peak Steelhead abundance in selected reaches of established index streams (Fowler 2016). The survey was not designed to count an entire spawning population, but instead to capture the peak abundance index count that is comparable across years to provide in-season run information and allow for long-term abundance trend monitoring (Fowler 2016). Peak abundance was defined as a high count that is bracketed temporally between lower counts and was targeted

based on run timing information from previous weir studies and local area knowledge (Fowler 2016). Variation in run timing, poor weather, or other unexpected conditions may prevent the achievement of peak counts; in these cases, "high" counts were utilized and qualified as such (Fowler 2016).

Twenty years (1997-2016) of abundance index information from 11 Southeast Alaska streams was incorporated in our analysis (Figure 2.2). We also calculated an average annual Steelhead abundance trend for the Southeast Alaska region by averaging peak or high counts of seven index streams (Peterson, Ford Arm, Sitkoh, Pleasant Bay, and Petersburg Creeks, and the Harris and White Rivers) for which we had data for all 20 years (Figure 2.2).

2.3.2 Steelhead growth

The systematic collection of scales from Situk River Steelhead was conducted from 1994 to 2014 (Johnson and Jones 1998; Marston 2014). A minimum of four scale samples were collected from each side of the fish from the preferred area above the lateral line on a diagonal between the posterior end of the dorsal fin and the anterior end of the anal fin. Biological sampling occurred twice weekly, and a representative and proportional sample of the entire run was accomplished by sampling 5% of the fish that had passed since the last sampling event (Marston and Power 2016). This fixed sampling fraction method allowed for the achievement of minimum annual sample sizes to meet project objectives during years of low returns (Marston and Power 2016).

All available Situk River Steelhead scale samples were catalogued and matched with corresponding sex, length, and sampling date information to create a set of scale samples and data from the years 1999 through 2012, excluding 2002 through 2004 for which data and samples were not available. High-resolution digital scale images of acetate impressions were made using a microfiche scanner (Indus®, Salem, Wisconsin) and electronic imaging software following procedures outlined by Hagen et al. (2001). Scale images were consistently calibrated using a 22-mm optical lens and stored in Tagged Image File (.tif) format with 8-bit depth, 400-dpi resolution, and 3360 x 4426 pixels.

A two-stage quality control assessment ensured that only suitable scales were utilized for analysis. The following criteria were met by all scanned scales used in age assessments: (1) the scale was from the correct species and additional sample data were available; (2) clear circuli

were visible along longitudinal axis for majority of scale area; (3) annuli were visible and not obscured or damaged; (4) the focus and outer edge of scale were visible and well defined; and (5) regeneration did not obscure annuli or focus. All scale-quality assessments were based solely on the quality of the scale image and not the complexity of scale patterns.

ImagePro® Plus 7.0 (Acton, Massachusetts) software and an unpublished macro developed by ADF&G (D. Oxman, ADF&G, Personal Communication) were used to estimate marine age and measure growth from digitized scale images. Aging procedures followed methods described by Love (in press) to identify the scale focus, freshwater-saltwater transition (i.e., smolt check) annuli, and spawning/stress marks along the longest axis of the anterior half the scale and marked digitally on each image (Figure 2.3). Marine age, or the number of years spent at sea following the initial juvenile freshwater emigration and smoltification period, was estimated by counting annuli from the smolt check to the outer edge of the scale. Three blind and independent age readings were completed by a single reader for each sampled scale; if none of the age estimates agreed, the sample was considered unreadable and omitted from further analysis unless an additional scale from the same fish was available and independently aged to verify a modal age estimate (Love et al. 2013). The modal age of the three or four successful scale-age readings was considered to be the most precise age (Love, in press).

Scale measurement protocols followed procedures synthesized from Ruggerone et al. (2009), Quinn et al. (2011), and Love (in press). Measurements occurred along the longest axis of the anterior half the scale, with circuli identified as the dark rings and annuli identified as densely spaced circuli associated with slower winter growth. Each circulus was measured from the outermost edge of one circulus to the outer edge of the next adjacent circulus, and annual growth zones were quantified as the sum of the individual circuli widths occurring beyond the outer edge of the preceding annulus and ending at the outer edge of the annulus of the growth zone being measured. All annual marine growth zones were measured for each scale, but the quantification of freshwater annual zones was not attempted due the difficulty in identifying freshwater annuli.

Marine age estimates were used to index all growth measurements to smolt year by back-calculating from the year sampled; this allowed for the identification of the years that SW1 and SW2 growth occurred. We calculated annual averages of SW1 growth occurring during 1997-2000 and 2003-2010 and SW2 growth occurring during 1998-2001 and 2004-2011. Years with

less than ten growth measurements were excluded from this analysis, yielding twelve years of growth data for each measure.

2.3.3 Marine environmental variable selection

Potential marine explanatory variables were selected to describe the major atmospheric and oceanic processes that are the foundation of the marine ecosystem in the GOA and the North Pacific Ocean (Mundy 2005). The rapid and broadly ranging offshore migration of juvenile Steelhead into the GOA and CNP guided our selection of measures of marine conditions. Potential variables considered included: (1) large-scale climate patterns with global influence: El Niño-Southern Oscillation (ENSO); (2) basin-scale atmospheric and oceanographic systems: North Pacific Index (NPI) and North Pacific Gyre Oscillation (NPGO); and (3) geographically and temporally specific measures of sea surface temperature (SST) for the GOA and the CNP that align with Steelhead marine distribution and early marine growth periods (Table 2.1).

The ENSO is a coupled ocean-atmosphere phenomenon originating in the equatorial the Pacific Ocean that has been shown to influence global climate variability on seasonal and interannual time scales (Wolter and Timlin 2011). A warm ENSO phase is characterized by a relaxation of the Walker circulation pattern in tropical Pacific Ocean, where dominant westward surface winds weaken, leading to decreased coastal upwelling in the eastern Pacific and anomalously warm temperatures (Sarachik and Cane 2010). Cold ENSO phases display the opposite pattern of strong Walker circulation with greater westward surface winds driving increased cold water upwelling in the eastern Pacific and generally cold temperatures throughout the region (Sarachik and Cane 2010). Warm ENSO phases are also characterized by an expansion of persistent precipitation across the equatorial Pacific, while during cool phases the region of precipitation contracts significantly to the west (Sarachik and Cane 2010). Tropical ENSO patterns have been shown to influence wind and weather patterns in the North Pacific through atmospheric teleconnections, resulting in anomalously warm SSTs in the GOA and Bering Sea (Overland et al. 2001). The Multivariate El Niño Southern Oscillation Index (MEI) quantifies the ENSO phenomenon as the first unrotated principal component of six marine climate variables: sea-level pressure, zonal and meridional surface wind components, sea-surface temperature, surface air temperature, and cloudiness (Wolter and Timlin 2011). A MEI value is computed separately for 12 bi-monthly seasons and standardized by season and to a long-term

reference period to ensure comparability over time (Wolter and Timlin 2011). This index is available online through the National Oceanic and Atmospheric Administration (NOAA) at fttp://www.esrl.noaa.gov/psd/enso/mei/table.html; our analysis used the average of the 12 bi-monthly values to characterize ENSO on an annual scale.

To directly describe the thermal environment that juvenile Steelhead experience during their first year at sea, we obtained SST data for the Gulf of Alaska (GOA SST) and the larger Central North Pacific (CNP SST) from the NOAA, Earth System Research Laboratory (ESRL) website (http://www.esrl.noaa.gov/psd/data/timeseries/). This online platform allows for the extraction of monthly SST time series data from their National Centers for Environmental Prediction (NCEP) Reanalysis Dataset for geographically specific areas based on latitude and longitude (Kalnay et al. 1996). We defined these geographic areas for the GOA (56.2-50.5° N, 195-135° W) and CNP (56.2-46.7° N, 180-135° W) based on the ocean distribution of Steelhead inferred from salmon fisheries catch records and International North Pacific Fisheries Commission (INPFC) research vessels (Light et al. 1989; Atcheson 2012b). Temperature data were limited to the inferred juvenile Steelhead first marine critical period (Quinn 2005) by calculating an average of monthly SST values for each marine region from April through September.

The NPGO is the second empirical orthogonal function (EOF) of Northeast Pacific sea-surface temperature and height anomalies (Di Lorenzo et al. 2008). Positive phases of the NPGO correspond to an intensification of both the Alaskan Coastal Current and the California Current that create conditions favorable for upwelling in the Alaskan Gyre and downwelling in the Alaska Coastal Current (Di Lorenzo et al. 2008). Index values for the NPGO have been computed monthly from January 1950 to the present and are available online at http://www.o3d.org/npgo/npgo.php. We averaged the 12 monthly values for each year to provide an annual average NPGO index value.

The NPI provides an area-weighted measure of sea-level pressure variation occurring on interannual and decadal time scales in the North Pacific (Trenberth and Hurrell 1994). Atmospheric changes described by NPI are typically expressed in SST variation one to two months later owing to ocean surface heat fluxes and mixing patterns (Trenberth and Hurrell 1994). The National Center for Atmospheric Research provides NPI Data (Trenberth and Hurrell 1994) and is updated regularly at https://climatedataguide.ucar.edu/climate-data/north-pacific-

np-index-trenberth-and-hurrell-monthly-and-winter. Monthly NPI values were averaged to create annual measures of NPI variation for our analysis.

Multicollinearity was an inherent characteristic of several of the marine climate explanatory variables that we considered in our modeling approach. We identified highly correlated variables ($|r| > 0.7$) as candidates for exclusion (Dormann et al. 2012) We excluded highly correlated variables from further analysis based on how temporally or geographically appropriate they were in describing the marine environment utilized by juvenile Steelhead. Correlation analysis demonstrated that GOA SST and CNP SST were highly correlated ($r = 1.0$). The CNP SST variable was eliminated because the area specified for the GOA SST data set more precisely encompasses the geographic region thought to be occupied by first ocean-year Steelhead (age 0) based on historical tagging and survey data (Light et al. 1989; Atcheson 2012b). Variance inflation factors (VIFs) were also calculated for our reduced set of explanatory variables, and all VIFs were below 3 indicating minimal collinearity in these variables (Zuur et al. 2009). The structure of models testing relationships between marine conditions, abundance, and marine growth included the explanatory variables of GOA SST, ENSO, NPGO, and NPI (Table 2.1).

2.3.4 Statistical analysis

Two patterns in abundance were tested to explore potential spatial structure in abundance trends among Southeast Alaska Steelhead populations: 1) relationships among all Southeast Alaska index populations and 2) relationships between Southeast Alaska index populations and the Situk River population. Abundance correlations were quantified using Pearson correlation coefficients (Zuur et al. 2009) and distance between Steelhead populations was measured as the putative marine migratory pathway between rivers using the Google Earth path distance tool.

The relationship between all pairwise abundance correlations and pairwise geographic distances for eleven Steelhead populations (ten Southeast Alaska index populations and the Situk River) were assessed using the Mantel test. To further examine spatial relationships in abundance correlations we organized all eleven Southeast Alaska Steelhead populations into northern ("North") and southern ("South") stock groupings based on a latitudinal division (Figure 2.1) identified by Malick et al. (2015), to be associated with contrasting relationships between pink salmon productivity and spring phytoplankton bloom timing along the eastern GOA shelf. We

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compared the direction and strength of abundance correlations within and between stock groupings.

The relationship between Situk River Steelhead and other Southeast Alaska Steelhead populations was tested with linear least-squares regression of Situk River abundance against a regional average of the abundances of 7 Southeast Alaska populations (Table 2.2). To assess potential spatial structure of abundance correlations between Southeast Alaska populations and the Situk River, correlations between the Situk River and each of the 10 other Southeast Alaska populations were plotted against their geographic distances from the Situk River. This relationship was not tested statistically due to the limited sample size (n = 10).

A linear least-squares regression modeling approach was also used to test relationships among Situk River Steelhead abundance, growth, and marine conditions (Table 2.2). Models testing relationships between growth and abundance or marine explanatory variables incorporated two- and three-year lags to align explanatory variables with the first critical year of juvenile marine residency (Table 2.2). These lags were based on dominant Southeast Alaska Steelhead marine age classes of two and three years (Harding et al. 2008). We also attempted to more precisely apply temporal lags to our models testing relationships between Situk River Steelhead abundance and early marine growth by creating separate data sets of growth measurements from marine age-2 and -3 Steelhead and modeling abundance by growth measurements of each individual marine age class separately with the appropriate temporal lag.

Selection of final models that included multiple explanatory variables was based on Akaike's information criterion bias-corrected for small sample size (AICc). Models minimizing AICc were considered the best representations of the data, but models with a ΔAICc with two of the minimum AICc were considered suitable alternatives and were thus reported (Burnham and Anderson 2002).

Linear regression modeling assumptions and the potential occurrence of outliers were evaluated with a combination of graphical residual assessment and statistical tests (Zuur et al. 2009). The assumptions of constant variance, normality, and independence in residuals were assessed graphically with residual plots against corresponding fitted values and specified explanatory variables. The independence assumption was further evaluated with autocorrelation function (ACF) and partial autocorrelation function (PACF) plots. Normality and the occurrence of potential outliers were further assessed with QQ probability plots. Shapiro-Wilk and Durbin-

Watson tests were selectively used to support graphical assessments of residual normality and independence respectively. Potential outliers and their influence were identified and evaluated with residual plots and Cooke's distance. Graphical assessment of residual plots suggested no major violations of the homogeneity, normality, and independence linear modeling assumptions for abundance or growth models in this study. The Shapiro-Wilk normality test supported our assumption of residual normality, and ACF and PACF plots confirmed the validity of the independence assumption and a lack of temporal autocorrelation. Several potential outliers were identified in abundance models, but they were not removed because Cooke's distances suggested that they were not overly influential and they represented valid data points during years of high Situk River Steelhead abundance. Residual analysis of marine growth models was challenged by small sample sizes, but statistical test results supported our conclusions that linear modeling assumptions were not violated. All statistical analyses were completed using the open source statistical program R (Version 3.1.2, R Core Team 2014).

2.4 Results

2.4.1 Regional abundance correlations

Abundance relationships among all Southeast Alaska Steelhead populations exhibited a trend of declining correlation with increasing distance apart, however the Mantel test of the relationship between correlation and distance matrices was not statistically significant ($r = -0.21$, $P = 0.9$). The average abundance correlation among Steelhead populations within the northern group and within the southern group both exceeded the average correlation between northern and southern groups (Figure 2.4). Additionally, abundance correlations increased with distance apart among pairs of populations within the same northern or southern group, while abundance correlations decreased with distance apart for population pairs in different groups (Figure 2.4).

A significant positive relationship ($r = 0.78$, $P < 0.001$) was identified between Situk River Steelhead abundance and the regional average Southeast Alaska Steelhead abundance (Figure 2.5). Correlations in abundance between the Situk River and other Southeast Alaska populations nominally decreased for streams that were farther from the Situk River ($r = -0.65$; Figure 2.6), but limited sample size precluded the statistical testing of this relationship.

2.4.2 Abundance models

Models of the abundance of Situk River Steelhead indicated a role for marine environmental conditions, although the amount of variability in abundance explained by these models was modest. The marine explanatory model of Situk Steelhead abundance at a three-year lag, which included positive relationships with GOA SST and NPGO, minimized AICc and explained 28% of the variability in abundance data (Table 2.3; Figure 2.7).

The marine explanatory model of abundance at a two-year lag, which included a positive relationship with GOA SST, was within two AICc units of the AICc minimizing model and explained 21% of the variability in abundance (Table 2.3; Figure 2.8). The addition of the FW growth variable to the best marine explanatory model (with a three year lag and including GOA.SST and NPGO as explanatory variables) produced a higher AICc (ΔAICc = 4.71) value compared to the model without the FW term. Similarly, the addition of a SW1 growth variable to the best marine explanatory model (with a three year lag and including GOA.SST and NPGO as explanatory variables) produced a higher AICc value (ΔAICc = 5.87) compared to the model without the SW1 term.

Our attempt to more precisely apply temporal lags in models of Situk River Steelhead abundance including early marine growth as an explanatory variable did not produce consistent or significant correlations between abundance and early marine growth for Steelhead spawning after two or three years at sea. More directly, we specified the relationships to be tested by using growth measurements explicitly lagged to abundance based on marine age, but this approach reduced already small sample sizes by more narrowly defining the data. The two-year lag model was limited to seven years of data, while the three-year lag model used only eight years of data.

2.4.3 Marine growth models

Growth occurring during the first year at sea (SW1) was not related to marine explanatory variables. The SW1 growth model that minimized AICc was the null model (an intercept-only model that included no marine explanatory variables). Growth during the second year at sea (SW2) growth increased with NPI (Table 2.3; Figure 2.9). These models were challenged by small sample sizes (12 years) which limited their statistical power and also made evaluation of modeling assumptions difficult.

2.5 Discussion

Understanding the spatial structure of fish populations and the mechanisms through which populations may interact is fundamental to management and conservation efforts, especially for vulnerable or threatened species. The strong positive relationship between Situk River Steelhead abundance and Southeast Alaska regional abundance describes region-wide coherence in Steelhead populations among diverse watersheds. This result supports the hypothesis that climate-driven processes act broadly on Steelhead across Southeast Alaska to influence the dynamics of individual populations and define a region-wide trend. A spatial pattern in abundance correlations was also identified, where populations located closer to the Situk River were more highly correlated with Situk River abundance. Synchrony among neighboring populations may suggest some level of population connectedness whether mediated through shared exogenous drivers (e.g., ocean survival, climate, or geology) or through direct interactions in a meta-population system (Mueter et al. 2005; Jorgensen et al. 2016).

An interesting result of our study was that abundance correlations were greater within northern and southern population groupings than between population groupings, regardless of geographic distance. This observation suggests that Steelhead might be affected by the same geographic shift in marine conditions between northern and southern regions of the Alexander Archipelago implied by the results of Malick et al. (2015), for the effects of spring bloom phenology on salmon survival, and by Mueter et al. (2002, 2005) and Su et al. (2004) for relationships between salmon productivity and SST. The mechanisms underlying this divergence are not well understood but could be related to the transition between upwelling (southern) and downwelling (northern) domains in the GOA (Ware and McFarland 1989; Mueter et al. 2005). However, this geographic break is also associated with the outlet of the Stikine River, a transboundary drainage whose substantial freshwater discharge could influence the early marine movements of Steelhead moving north and west toward the GOA from rivers included in the southern stock grouping.

The importance of marine climate to regional Steelhead population coherence was supported by the positive relationship between Situk River Steelhead abundance and GOA SST and NPGO at two- and three-year lags. Warmer sea surface temperatures and increased North Pacific Ocean gyre activity may have created more favorable conditions in the GOA that allowed

juvenile Steelhead to survive the early marine critical period and return to spawn in greater numbers two and three years later (Mueter et al. 2005). The amount of variation explained by these models was relatively small and the models persistently underestimated the prominent period of increased Steelhead abundance observed over 2004-2007. The addition of freshwater and early marine growth information to these models did not explain any additional variation in Steelhead abundance, although doing so limited statistical power due to small sample sizes. It is not surprising that many other factors could contribute to abundance trends, such as freshwater habitat conditions, predator and prey dynamics, and anthropogenic influences. It is also possible that micro- or meso-scale variation across marine-rearing habitats is important but not captured by the macroscale environmental variables available for analysis (T. Sutton, University of Alaska Fairbanks, pers. comm.).

Our finding of a positive correlation between SST and Steelhead abundance contrasts with Friedland et al. (2014), who identified a negative correlation between return rates and SST for Steelhead from the Keogh River, British Columbia. Given the aforementioned potential geographic transition in environmental conditions between the northern and southern portions of the Alexander Archipelago, this result is not surprising. A number of ecological pathways could be hypothesized to link the thermal conditions of juvenile Steelhead marine habitat to overall population productivity and these relationships may differ by species and even stock. Martins et al. (2012), in a synthesis of existing research on how climate may impact sockeye salmon phenology, growth, and survival, found that responses to thermal conditions vary among and within stocks, and the mechanisms through which temperature impact salmon at sea are still poorly understood. Further, studies of pink salmon *O. gorbuscha* and coho salmon in Southeast Alaska have also demonstrated that linkages between salmon productivity and marine environmental conditions vary among populations and along latitudinal gradients (Malick et al. 2009; 2015). The complexity and annual variability of nearshore and offshore marine oceanographic processes and ecosystem dynamics in the GOA may ensure that these relationships are variable over time and space.

Analyses of relationships between early marine growth and marine climatic variables were challenged by relatively small sample sizes (12 years). We did not detect relationships between SW1 growth and marine explanatory variables, but SW2 growth did increase with the NPI. The positive relationship between SW2 growth and NPI contrasts with our expectation that

increased NPI would lead to less favorable GOA growing conditions for juvenile Steelhead and decreased marine growth. The relationship between SW2 growth and marine conditions is further complicated by the compensatory nature of SW2 growth as it relates to SW1 growth and maturation described in Chapter 1 of this study. Thomson et al. (2012) found that low years of Fraser River sockeye salmon returns coincided with years of positive NPI and a weakened winter Aleutian Low Pressure system. While their study did not specifically consider marine growth, the authors suggested that ocean conditions encountered during years of high NPI values led to reduced food availability and decreased survival (Thomson et al. 2012). Again, it is important to note that marine and climate-driven processes impacting more southerly anadromous fish populations may not impact Southeast Alaska Steelhead in the same manner. The inconsistent results of marine growth models in our study and short time series of data available to describe complex relationships between Steelhead growth and oceanographic processes warrant a conservative interpretation of the relationship that we identified between SW2 growth and NPI.

Previous studies demonstrated the importance of freshwater growth to subsequent early marine growth for anadromous salmonids (e.g., Johnsson et al. 1997; Ruggerone et al. 2009) Freshwater growth was found to be significantly positively correlated with subsequent first ocean-year growth for Yukon River Chinook salmon *O. tshawytscha* (Ruggerone et al. 2009; McPhee et al. 2016) and Ward (2000) described the importance of freshwater growth and initial smolt size to Keogh River Steelhead marine survival and return rate. However, after an abrupt decline in productivity in the Keogh River, the relationship between smolt size and marine survival disappeared (Ward 2000, Welch et al. 2000), and adult return rate may be better explained by post-smolt growth periods occurring after the first month at sea (Friedland et al 2014). From these contrasting findings we may infer that the relative importance of growth occurring in freshwater or during the first year at sea may vary depending on marine conditions or other unknown ecological considerations. Given our small sample sizes and the inability to estimate freshwater age, growing conditions in fresh water were not incorporated into our growth models for this analysis. We included total FW growth in our abundance model as a measure of size at ocean entry, but this model did not prove informative and was limited by small sample size. Additional information on Steelhead freshwater spawning and rearing habitat conditions may also help explain periods of increased Steelhead productivity that occurred from 2004 to 2007 across the Southeast Alaska region.

We did not detect strong relationships between growth and climate-driven marine environmental variables. Bioenergetic modeling suggests that juvenile Steelhead marine growth can vary significantly depending on interacting biotic (i.e., prey quality and quantity) and localized abiotic (i.e., thermal conditions) marine ecosystem components (Atcheson et al. 2012a, b). Regardless of whether temperature impacts are direct or indirect, the relationship between temperature and growth is not likely linear. As for other anadromous salmonids, Steelhead likely exhibit size- and life stage-specific optimal temperature ranges that maximize growth efficiency, outside of which somatic growth is more metabolically costly (Atcheson et al. 2012a). As highly migratory marine predators, Steelhead may move or change their feeding patterns in relation to the thermal ocean conditions and the availability of high quality prey such as squid or fish (Atcheson et al. 2012a). Welch et al. (1998) synthesized historical longline, gill net, and trawl survey data to describe well-defined thermal limits of Steelhead ocean distribution, which can be observed in the narrow longitudinal band of Steelhead occurrence that stretches broadly across the North Pacific. The strong thermal constraint of the Steelhead marine distribution may indicate that Steelhead actively seek out preferred SSTs and their growth may vary along other biological and ecological gradients occurring within that preferred thermal environment.

Another important consideration is that all growth data were collected from adult Steelhead that survived to maturity and returned to the Situk River. As a result the growth patterns we have described are only representative of Steelhead that successfully overcame marine mortality events and therefore were not necessarily representative of all the physical and biological conditions juvenile Steelhead may encounter in their first two years at sea. The assessment of relationships between growth and survival require stock-specific metrics of marine survival or recruitment (Freidland et al. 2014), or samples from Steelhead collected longitudinally during their marine residency period (Farley et al. 2007), which is extremely difficult to achieve for a single population.

Steelhead from the Situk River exhibit complex patterns of anadromy characterized by variation in freshwater and marine rearing duration and spawning migration timing (Harding 2008, Chapter 1). Both stream- and ocean-maturing life-history types occur within the Situk River population, but the mechanism by which that divergence occurs is unknown and we were unable to differentiate life history type in our scale samples. Due to our inability to reliably estimate freshwater age for Situk River Steelhead, which typically ranges from two to five years

(Harding 2008), we were unable account for differences in freshwater residency in our analyses. Steelhead life history variation is related to energy allocation, reproductive development, marine-residency duration, and other physiological processes that directly interact with marine growth patterns (Kendall et al. 2015). The complex life history characteristics exhibited by Situk River Steelhead complicate investigations of causal mechanisms affecting growth and survival.

Current Southeast Alaska Steelhead management objectives are necessarily focused on collecting abundance index information that allows managers to monitor populations and take responsive regulatory action to protect the sustainability of individual Steelhead populations or the regional Southeast Alaska Steelhead stock complex (Fowler 2016). Conservative sport fishing regulations ensure that exploitation of Southeast Alaska Steelhead remains low and relatively consistent over time, but much remains unknown about the processes driving Steelhead productivity in these systems. An improved understanding of the spatial component to Southeast Alaska Steelhead population structure would help define the appropriate management unit for future regulatory actions, research programs, or conservation efforts (Jorgensen et al. 2016). An improved understanding of how marine conditions relate to Steelhead abundance may allow managers to disentangle sources of mortality in systems that receive heavy sport fishing pressure, like the Situk River, and better inform ongoing conservative management efforts. Research that works to identify linkages between Southeast Alaska Steelhead productivity and available measures of marine climatic conditions also provides an additional level of information to help managers evaluate abundance trends and potentially anticipate future changes. The apparent impact of marine conditions on juvenile Steelhead during their first ocean critical period may support some basic forecasting capacity for managers tracking adult abundance observed two or three years later. Continued research that incorporates scale-derived growth measurements from other Southeast Alaska populations may improve the statistical certainty of these analyses and help validate some of the observed patterns. Collection and analysis of scales from known stream and ocean-maturing Steelhead may also offer insight into how growth relates to life-history diversity and help us further disentangle relationships between growth and abundance. While current conservation concerns are minimal, changes occurring in the marine ecosystem related to global climate change may increase the relevancy of such proactive investigations to ensure the long-term sustainability of Southeast Alaska Steelhead populations.
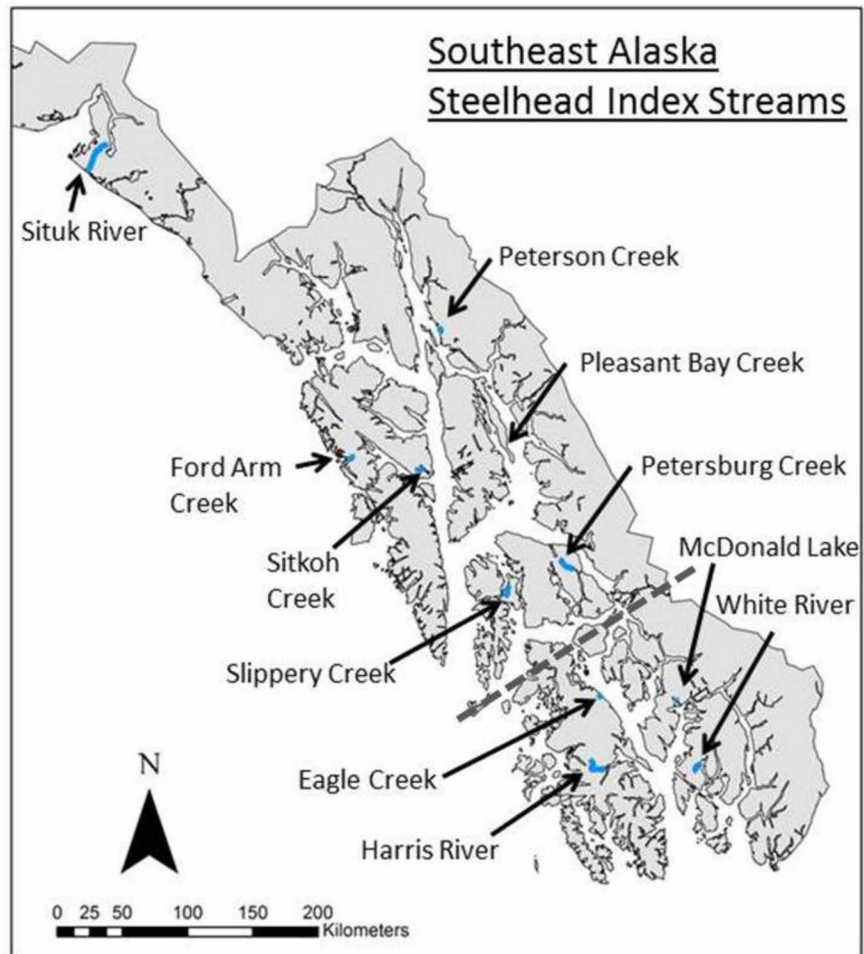
2.6 Figures

Figure 2.1: Map of eleven Southeast Alaska Steelhead streams, including the Situk River. Gray dotted line depicts the North-South dividing line for correlational grouping analysis.
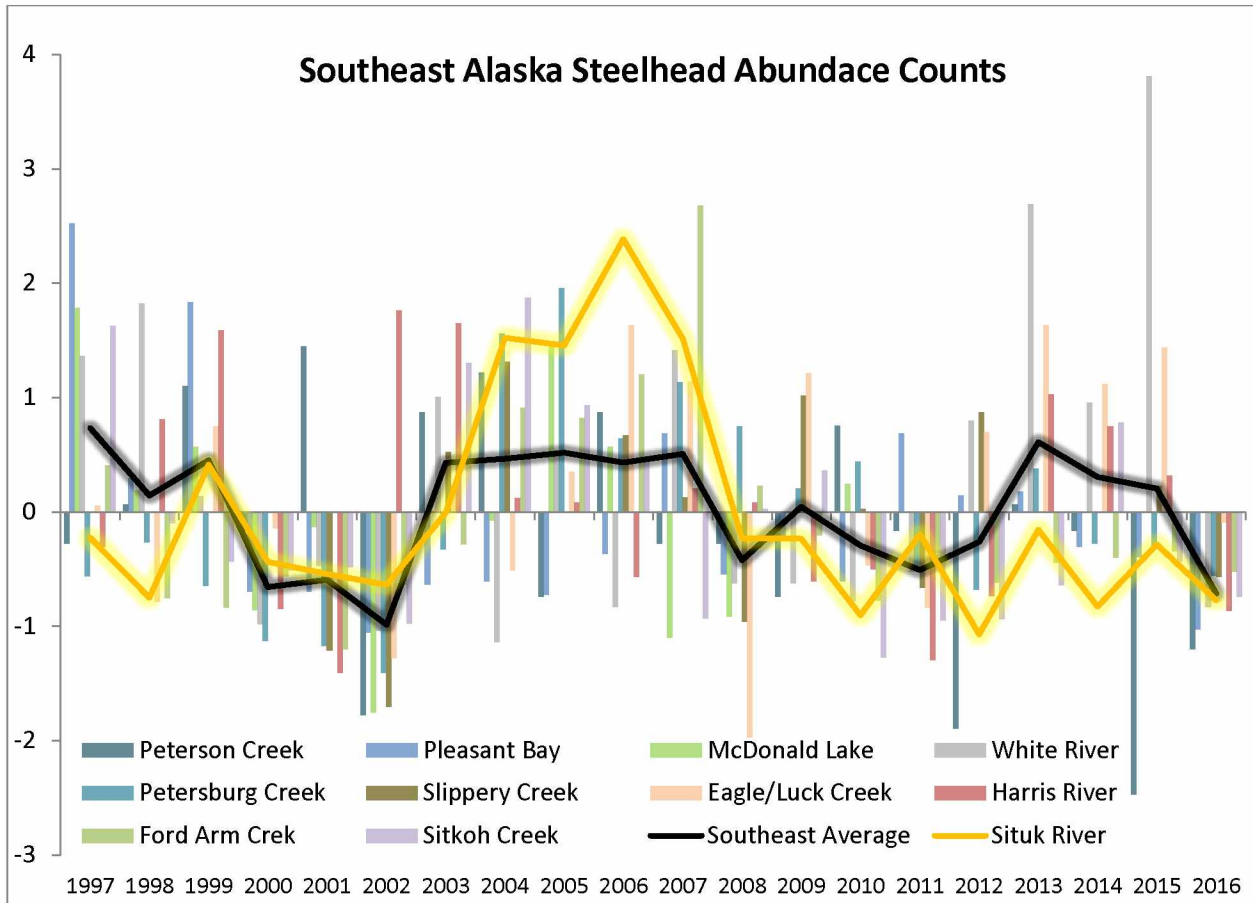
Figure 2.2: Normalized Steelhead abundance counts from snorkel counts of ten Southeast Alaska Steelhead index streams for the years 1997-2016. The annual regional average of Southeast Alaska index counts (in black) is included along with the Situk River Steelhead weir count (in yellow).
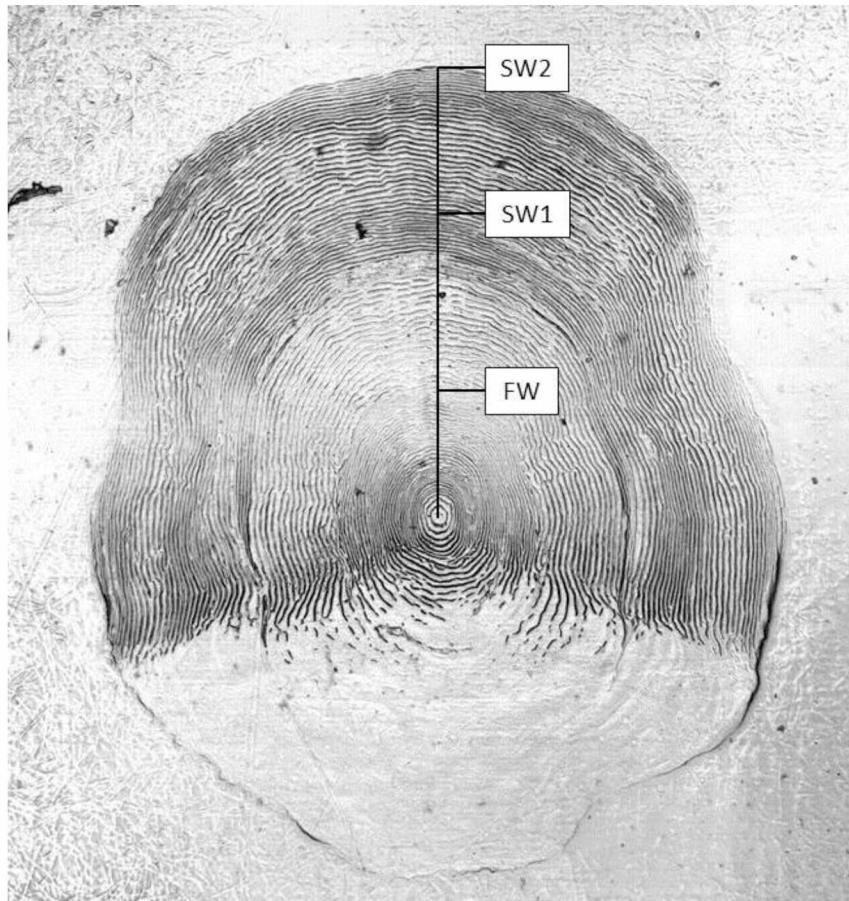
Figure 2.3: Annotated X.2 Steelhead scale from the Situk River displaying freshwater (FW), first (SW1), and second (SW2) years of marine growth.
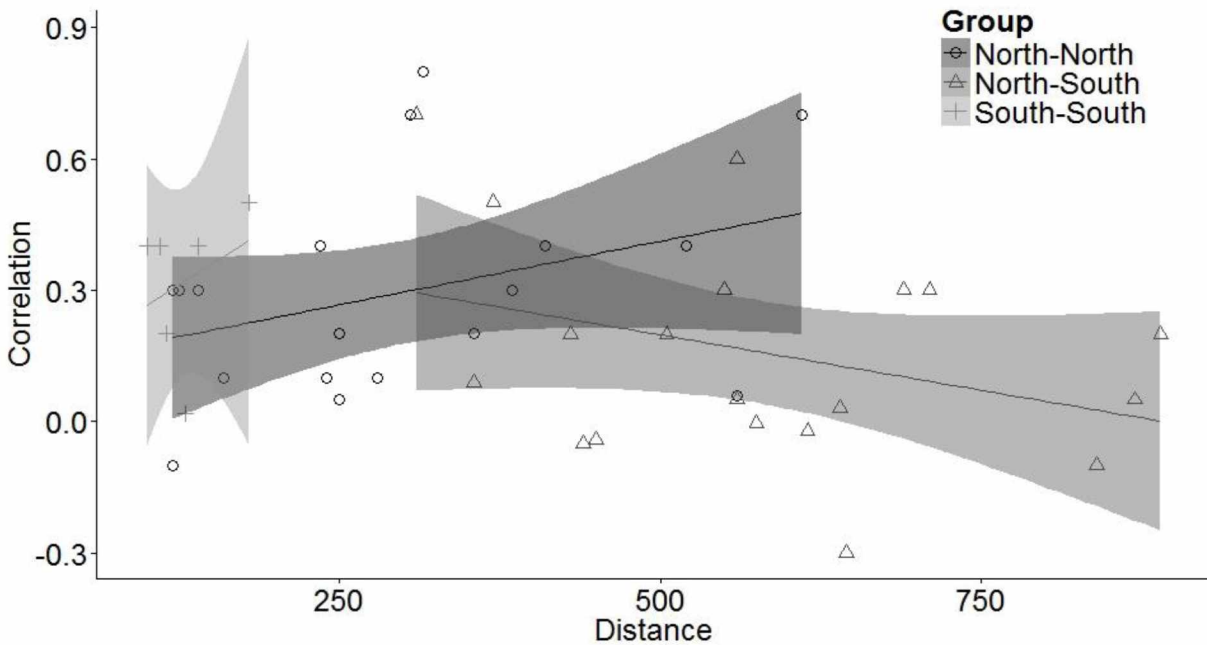
Figure 2.4: Linear relationships between pairwise abundance correlations and pairwise geographic distances for all individual index Southeast Alaska Steelhead populations and the Situk River. Relationships are grouped into three categories based on the locations of each population: relationships among Northern populations (North-North), relationships among Southern populations (South-South), and relationships among Northern and Southern populations (North-South).
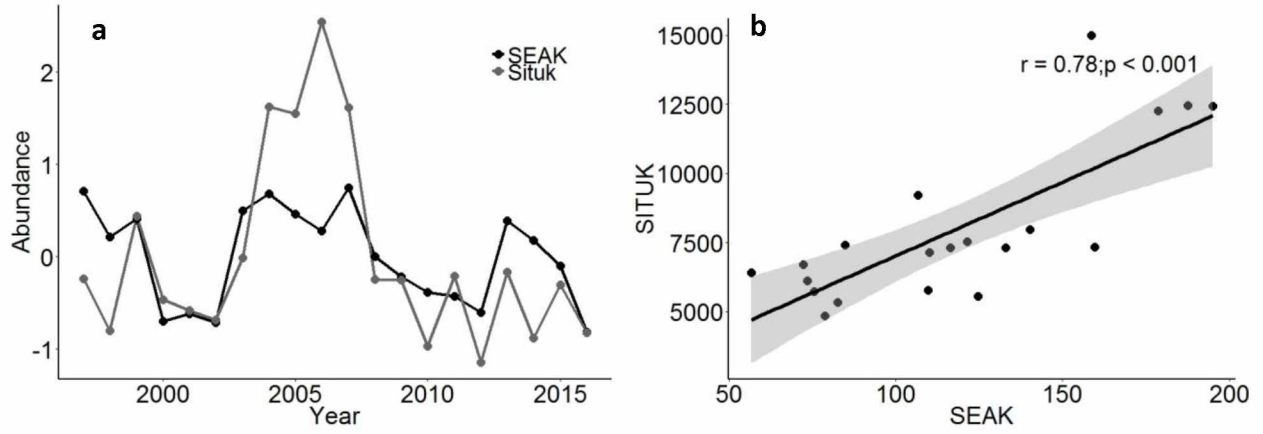
Figure 2.5: Time-series (a) and scatterplot (b) of the relationship between Southeast Alaska Steelhead abundance and Situk Steelhead abundance. The line in (b) represents a locally weighted scatterplot smoothing (LOESS).
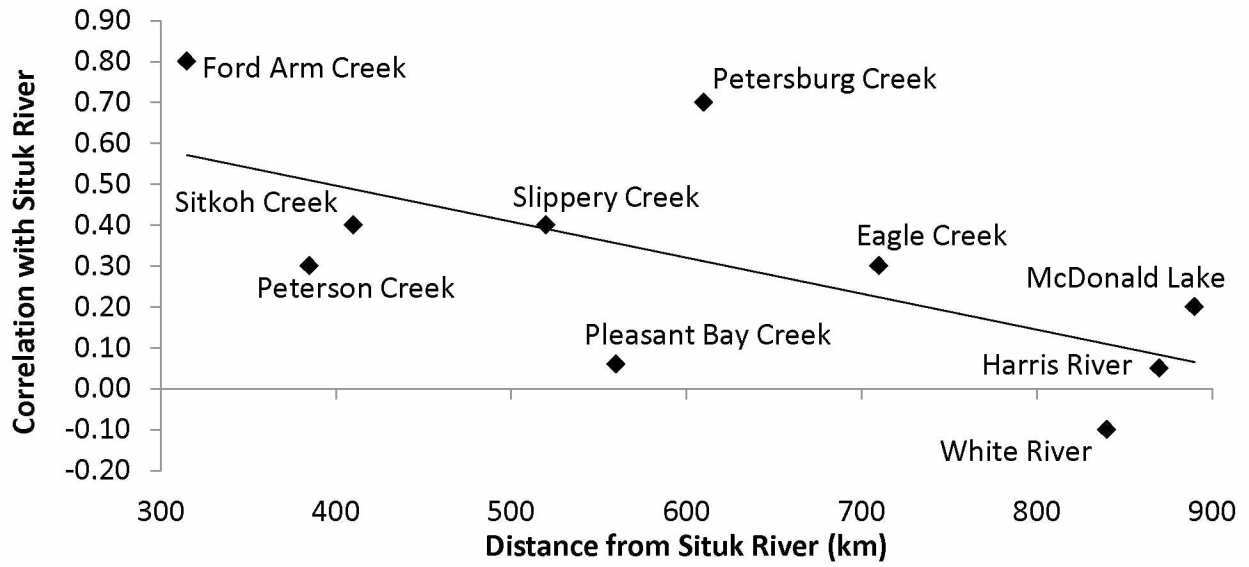
Figure 2.6: Spatial pattern of correlations of individual Southeast Alaska Steelhead population abundance index counts and Situk River Steelhead abundance.
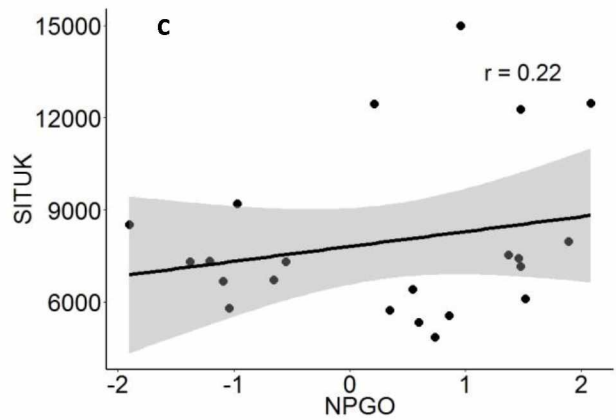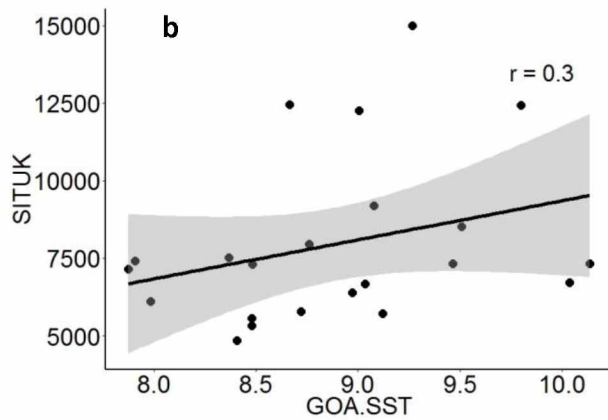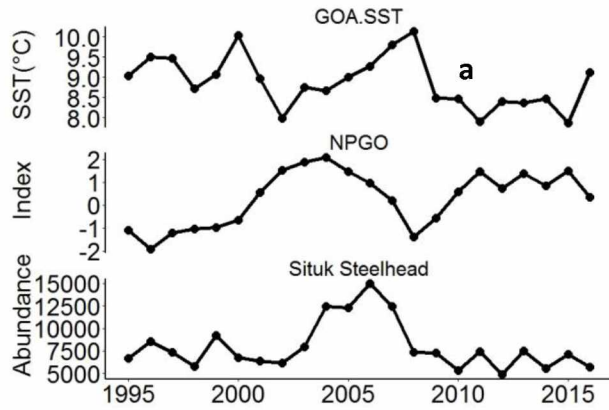
Figure 2.7: Time series (a) and scatterplots of the relationships between Situk River Steelhead abundance at a three-year lag and (b) GOA SST; (c) NPGO. The lines in (b) and (c) represent locally weighted scatterplot smoothing (LOESS).
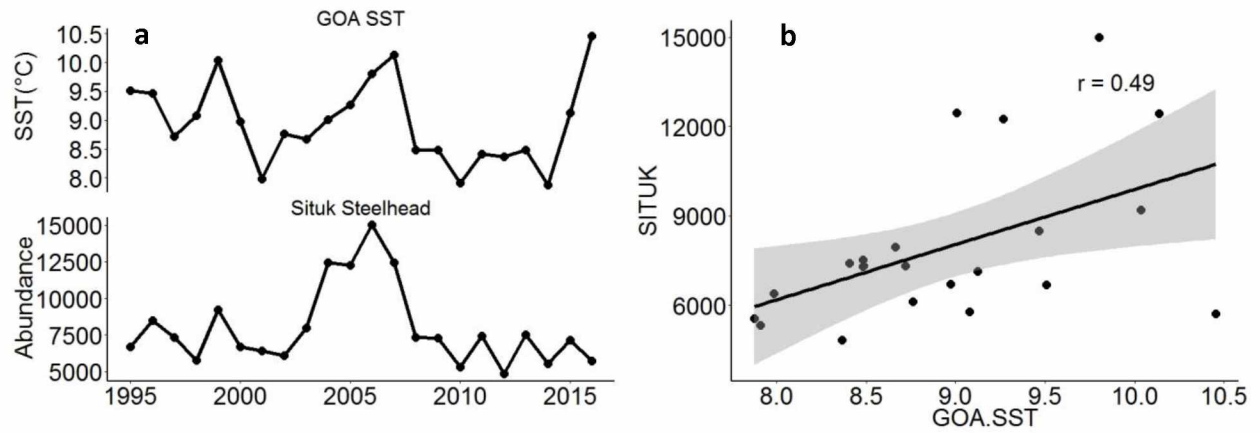
Figure 2.8: Time series (a) and scatterplot (b) of the relationship between and GOA SST and Situk River Steelhead abundance at a two-year lag. The line in (b) represents a locally weighted scatterplot smoothing (LOESS).

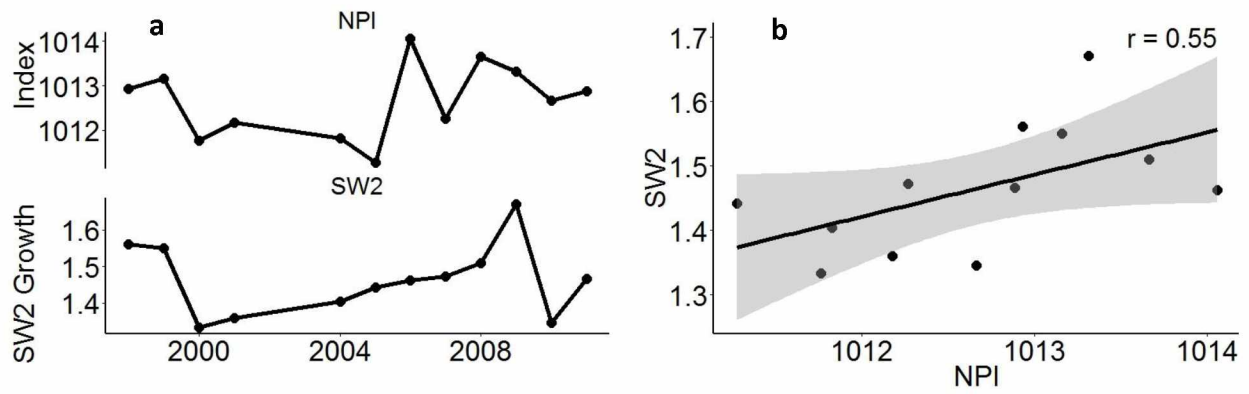Figure 2.9: Time series (a) and scatterplot (b) of the relationship between second-ocean year growth (SW2) and the North Pacific Index (NPI). The line in (b) represents a locally weighted scatterplot smoothing (LOESS).

2.7 Tables

Table 2.1: Marine environmental variables hypothesized to influence Steelhead growth that were considered in exploratory analysis.

Variable	Geographic Scale	Time Period	Source
El Nino Southern Oscillation (ENSO)	Pacific Ocean	Annual Average	Wolter and Timlin 2011, MEI, ESRL, NOAA
North Pacific Index (NPI)	North Pacific Ocean	Annual Average	Trenberth and Hurrell 1994, National Center for Atmospheric Research
North Pacific Index (NPI) North Pacific Gyre Oscillation (NPGO)	North Pacific Ocean North Pacific Ocean	Annual Average Annual Average	Trenberth and Hurrell 1994, National Center for Atmospheric Research Di Lorenzo et al. 2008
Central North Pacific Sea Surface Temperature (CNP SST)	56.2 - 46.7 N. Lat., 180.0 - 135.0 W. Long.	April-Sept. Average	NCEP Reanalysis, ESRL, NOAA
Central North Pacific Sea Surface Temperature (CNP SST)	56.2 - 46.7 N. Lat., 180.0 - 135.0 W. Long.	April-Sept. Average	NCEP Reanalysis, ESRL, NOAA
Gulf of Alaska Sea Surface Temperature (GOA SST)	56.2 - 50.5 N. Lat., 195.0 - 135.0 W. Long.	April-Sept. Average	NCEP Reanalysis, ESRL, NOAA

Table 2.2: Full Steelhead abundance and growth model structure, lag, and sample size of data available for each modeling scenario.

Model Structure	Lag	Sample Size
Abundance Correlations		
Southeast Alaska Abundance Correlations = $\alpha + \beta1 \cdot$ Distance between Southeast Alaska Populations + ε	N/A	11 Populations
Situk Abundance = $\alpha + \beta_1 \cdot$ Average Southeast Alaska Abundance + ε	N/A	20 Years: 1997- 2016
Abundance Models		
Situk Abundance = $\alpha + \beta_1 \cdot$ GOA.SST + $\beta_2 \cdot$ ENSO + $\beta_3 \cdot$ NPGO + $\beta_4 \cdot$ NPI + ε	2 and 3 Years	22 Years: 1995-2016
Situk Abundance = $\alpha + \beta1 \cdot$ GOA.SST + $\beta2 \cdot$ NPGO + $\beta3 \cdot$ FW Growth + $\beta4 \cdot$ SW1 Growth + ε	2 and 3 Years	12 Years: 1999-2002, 2005-2012
Marine Growth Models		
SW1 Growth = $\alpha + \beta1 \cdot$ GOA SST + $\beta2 \cdot$ ENSO + $\beta3 \cdot$ NPGO + $\beta4 \cdot$ NPI + ε	N/A	12 Years: 1997-2000, 2003-2010
SW2 Growth = $\alpha + \beta1 \cdot$ GOA SST + $\beta2 \cdot$ ENSO + $\beta3 \cdot$ NPGO + $\beta4 \cdot$ NPI + ε	N/A	12 Years: 1998-2001, 2004-2011

Table 2.3: Parameter estimates (and SE) for models describing relationships between Situk River Steelhead abundance, Southeast Alaska (SEAK) Steelhead abundance, Situk Steelhead first and second ocean-year growth (SW1, SW2), and marine explanatory variables. Only models minimizing Akiake's information criterion bias corrected for small sample sizes (AICc) and those within ΔAICc < 2 of the best model are shown. Cases where no parameter estimates for marine explanatory variables are given indicates that the null model had the lowest AICc.

| Response | Lag | ΔAICc | Intercept | Explanatory Variable | | | | R^2 |
				GOA.SST	NPGO	ENSO	NPI	
Situk Steelhead Abundance	3 Year	0.00	-19157.4 (9010.9)	2999.6 (1000.8)	1480.3 (531.4)	---	---	0.28
	2 Year	0.39	-8640.4 (6553.5)	1853.6 (729.7)	---	---	---	0.21
Situk Steelhead SW1 Growth	N/A	0.00	---	---	---	---	---	N/A
Situk Steelhead SW2 Growth	N/A	0.00	-64.77 (32.12)	---	---	---	0.065 (0.032)	0.23

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General Conclusion

Steelhead (anadromous Rainbow Trout) *Oncorhynchus mykiss* occupy a relatively small but important niche in Alaska fisheries. They are highly valued as a sport fish and have been the subject of significant management action taken in the mid-1990s to support the long-term conservation of small and potentially vulnerable Southeast Alaska Steelhead populations (Lohr and Bryant 1999; Harding and Coyle 2011). Studies of Steelhead production on Sitkoh Creek and Big Ratz Creek in Southeast Alaska were completed as part of larger Alaska Department of Fish and Game (ADF&G) effort to define escapement targets for these populations (Love and Harding 2009; Love et al. 2013). These management-focused research efforts were curtailed in 2011 due to funding limitations, and current management efforts are focused abundance monitoring of index Steelhead populations across the region (Fowler 2016). More intensive studies on the Situk River have enumerated emigrating kelts, monitor population sex and length characteristics, and have assessed scale-growth and age characteristics of tagged and recaptured adult Steelhead (Marston et al. 2012). In contrast to the well-studied Steelhead from the Keogh River, British Columbia (Friedland et al. 2014), relationships between early marine growth, ocean conditions, and survival have not been studied in Southeast Alaska prior to the research described in this thesis.

Southeast Alaska Steelhead populations have exhibited coherent trends in abundance in recent years (Marston et al. 2012). Covariance in abundance of geographically proximate Southeast Alaska Steelhead populations may suggest direct connections through a meta-population system or shared responses to exogenous influences likely related to climate-driven and marine processes (Mueter et al. 2005; Jorgensen et al. 2016). In this study, we characterized a spatial component to abundance correlations among Southeast Alaska Steelhead populations, where more proximal Steelhead populations were more strongly correlated, and populations located closer to the Situk River were more strongly correlated with the Situk River. We also identified positive relationships between Gulf of Alaska (GOA) sea surface temperature (SST), North Pacific Gyre Oscillation (NPGO), and Situk Steelhead abundance. These relationships provide evidence that large-scale marine climate patterns may be useful in better understanding regionally coherent trends Southeast Alaska Steelhead abundance (Mueter et al. 2005; Friedland et al 2014). Greater coherence in abundance of populations within northern and southern stock

groupings than between groupings suggested that Steelhead populations are influenced by a similar geographic transition that affects other Pacific salmon populations in the Gulf of Alaska (Malick et al. 2015 and references therein), although the nature of this transition remains unclear.

Investigations into the underlying ecological mechanisms linking climate to Steelhead abundance trends necessitate finer scale measurements that describe Steelhead physiological processes and relevant environmental or ecological drivers (Atcheson et al. 2012). The critical size and period hypothesis suggests that growth-mediated differential mortality occurring during the early marine period of the anadromous fish life cycle may regulate year class strength (Beamish and Mahnken 2001). To better understand Steelhead marine growth patterns we used scale-derived growth measurements from Situk River Steelhead to examine relationships among growth occurring during different life history periods, and to assess how growth may differ among Steelhead of different life history groups. We characterized positive correlations between freshwater, first-ocean year growth, and adult length, while first ocean-year growth was negatively correlated to second ocean-year growth for Situk River Steelhead. We also found that earlier maturing Steelhead had increased first ocean-year growth and decreased adult length compared to later maturing Steelhead. These results describe the importance of freshwater growth to subsequent marine growth and pin-point a well-known interaction between growth and maturity in salmonids, demonstrating that growing Steelhead divert energy from somatic growth to gamete development during their second year at sea. These results describe for Situk River Steelhead the interrelated processes of freshwater and marine growth, maturation, and reproduction, which are the components of complex Steelhead life-history patterns (Hodge et al. 2016). This life history diversity further complicates the identification of ecological mechanisms regulating Steelhead abundance (Kendall et al. 2015), and may have contributed to the inability of our retrospective scale-pattern analysis to identify relationships between Situk River Steelhead abundance and growth.

This thesis demonstrated the utility of scale-pattern analyses to expand our understanding of the relationships among growth, abundance, and climate-driven marine conditions for Southeast Alaska Steelhead. However, we were limited by the resolution of data available on Steelhead marine distribution and on measures of climatic variability in the North Pacific Ocean. Selected marine-climate indices were useful in describing general environmental trends but may have lacked resolution in describing variation important to Steelhead. Finer-scale and temporally

stratified data on Steelhead marine migration patterns and the environmental conditions they experience would provide more insight into the ecologically important processes impacting Steelhead productivity (Mueter et al. 2005; Atcheson et al. 2012).

Small Southeast Alaska Steelhead populations persist in dynamic freshwater and marine environments that are sensitive to climate change and resource development (Shanley and Albert 2014). Southeast Alaska Steelhead resiliency may be directly related to the complexity of their life history patterns and interconnections with other proximate Steelhead populations (Kendall et al. 2015; Hodge et al. 2016). Additionally, Southeast Alaska Steelhead populations have not been significantly impacted by fisheries harvest, habitat degradation, or enhancement activities (Lohr and Bryant 1999; Love et al. 2013), making them useful research subjects in the study of how changing climate may impact anadromous fish populations. All of the data and samples used in this study were collected for other stock monitoring and assessment research on Southeast Alaska Steelhead. We were able to opportunistically apply newly standardized Steelhead scale aging and measurement methodologies to this existing data set and scale collection to address our specific research objectives. Future research should continue to build on this work by applying our methods to other scale collections from Southeast Alaska Steelhead populations, evaluating whether populations that share region-wide abundance trends are also similar in their growth patterns and marine ecology. Future investigations into regional abundance trends may also expand on our findings of the spatial component to Southeast Alaska Steelhead abundance synchrony. With longer time series, multivariate analyses of abundance correlations may expose latent trends and grouping patterns among Southeast Alaska Steelhead abundance that provide further insight into the mechanisms underlying these population correlations (Jorgensen et al 2016). These insights may prove important as we seek to conserve vulnerable anadromous fish populations under changing climate conditions.

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