Manuscript title: Spatial variation in age-specific growth of female Chinook salmon

Authors: Lorna I. Wilson*[1,2], Milo D. Adkison[1,2], Richard E. Brenner[2,4], Ellen M. Yasumiishi[3], Megan V. McPhee[1]

*Corresponding author, lorna.wilson@alaska.gov

Author affiliations

1. College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena Loop Road, Juneau, AK, 99801, U.S.A.
2. Headquarters Office, Alaska Department of Fish and Game, 1255 W. 8th Street, Juneau, AK 99811-5526, U.S.A.
3. National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratories, 17109 Point Lena Loop Road, Juneau, AK 99801, U.S.A.
4. Present address: National Marine Fisheries Service, Alaska Regional Office, 709 W. 9th St., Room 420, Juneau, AK 99802-1668, U.S.A.

Lorna Wilson Orcid ID: 0000-0002-0812-0811
Richard E. Brenner Orcid ID: 0000-0001-7209-9757
Ellen M. Yasumiishi Orcid ID: 0000-0003-4095-0409
Megan V. McPhee Orcid ID: 0000-0001-9614-4137

Abstract

While declines in size, age at maturity, and productivity in Chinook populations have been documented in several large-scale comprehensive studies, changes in growth phenology that might underly these phenomena have examined 1-2 populations at a time. We measured growth in fresh water (FW) and in the 1st through 4th year in salt water (SW1–SW4) from >17,000 scales sampled from 14 populations across Alaska, 1966–2015. We examined correlations between increments within brood years, populations, and ages at maturity and estimated population-level growth and differences in growth for fish that matured at age 5 vs. age 6. Growth generally declined with additional years at sea. SW1 growth was above average for Bering Sea populations and below average for Gulf of Alaska populations, particularly in Cook Inlet. SW2 growth was clinal, decreasing from southeast to northwest. SW3 and SW4 growth varied regionally (Cook Inlet and Prince William Sound > Bering Sea > Southeast). Fish that matured at age 5 had higher incremental growth than those that matured at age 6 and these differences increased with each increment. Populations with greater age 5 than 6 SW1 growth had greater SW2 growth and populations with greater age 5 than 6 SW3 growth had greater SW4 growth. Within brood years, FW growth was positively correlated with SW2 growth, but high SW2 growth was negatively correlated with SW4 growth. Our results highlight the need for research on mechanisms linking Chinook salmon growth and maturation in a rapidly changing climate, with potential negative consequences for demography.

Keywords

body growth; fish scales; maturation; population variation; Pacific salmon; sclerochronology

Statements and Declarations

Funding from the State of Alaska Legislature for the Chinook Salmon Research Initiative was received to assist with the preparation of this manuscript. The authors have no relevant financial or non-financial interests to disclose. No approval of research ethics committees was required to accomplish the goals of this study because the work was conducted using tissue samples (scales) from the State of Alaska Department of Fish and Game archives.

Acknowledgements

Thank you to anonymous reviewers whose thoughtful questions led to an improved understanding of the variation in growth over the life of the fish. Thanks to the numerous technicians and biologists at the Alaska Department of Fish and Game who counted, sampled, and estimated the age of Chinook salmon over the years. Thanks to J. Baker, J. Siegel, J. Chahanovich, C. Finch, C. McConnell, S. Hinton, D. DeSloover, J. Leon, S. Berkman, B. Rosky, W. Whelan, A. Norman, and M. Lovejoy who measured Chinook salmon scales analyzed in this paper. Thank you to T. Frawley and B. Rosky whose programming expertise allowed for importing and organizing the measurement data into an Oracle database.

Data availability: Data are provided at the following link: https://github.com/commfish/Female-Chinook-salmon-growth-analyses. No novel code was used for this manuscript.

INTRODUCTION

Chinook salmon (*O. tshawytscha*) are distinguished among *Oncorhynchus* species by larger size and older maturation age (Healey 1991). Due in part to their large size, Chinook salmon are highly valued in Alaska for food security (Loring and Gerlach 2010; Brown and Godduhn 2015), cultural significance (Carothers et al. 2021), and commercial and recreational fisheries (Lew and Larson 2012; Seung 2017). However, during recent decades, Chinook salmon populations from around Alaska have exhibited troubling declines in abundance, size, and age at maturity (Lewis et al. 2015; Ohlberger et al. 2018; Munro 2023). It would be simplistic to assume that all Alaska Chinook salmon populations, which range from southern Southeast Alaska to Kotzebue Sound (Healey 1991), share the same suite of causes for these declines or that they have the same responses to climate. A critical foundation for understanding how Alaska's Chinook salmon will respond to environmental change is understanding regional and population specific patterns in growth and life history.

Growth is coupled with many of the hypothesized causes for declines in abundance, size, and age of Alaska Chinook salmon populations. Growing to a minimum size during the first summer at sea is critical for survival in Yukon River salmon (Howard et al. 2016). In Southeast Alaska populations, survival has been attributed to greater growth during their first year at sea (Graham et al. 2019). Increased growth during their second year at sea was correlated with increasing SST and younger maturation in two western Alaska rivers (Siegel et al. 2017). Across salmon species in Alaska (Chinook, chum, coho *O. kisutch*, and sockeye *O. nerka* salmon), younger maturation age explained 88% of size declines, which the authors associated with changing climate and increased competition at sea (Oke et al. 2020). The broad range of these hypotheses and links to growth suggests that a better understanding of growth and linkages to maturation may shed light on observed demographic changes for Chinook salmon populations.

Most salmon growth occurs at sea, where there is high food availability but also high predation risk compared to initial growth in fresh water (Quinn 2005). After emergence from the gravel and before going to sea, stream-type Chinook salmon, the dominant life history in Alaska (Healey 1991), spend a year in fresh water where they have limited growth (Quinn 2005). Fish growth at sea is generally assumed to be rapid in the first ocean year and then decrease in each subsequent year (Chen et al. 1992; Williams and Shertzer 2005; Katsanevakis and Maravelias 2008). Growth rate variation over the life of the fish, both among and within years, can be assessed from their scales (Fisher and Pearcy 2005). Scale radius has a linear relationship with fish length (Bilton 1985; Fukuwaka and Kaeriyama 1995); thus, measurements of scale increment growth from the end of one winter to the end of the next represent increases in fish length among years of life. During late-marine residency, maturing salmon allocate energy to gonad production (Myers et al. 2010), which entails decreased somatic growth (Roff 1984). Faster growing Chinook salmon mature at a younger age (Healey 1991), which has been demonstrated in Alaska (McPhee et al. 2016; Siegel et al. 2017) and elsewhere (Vøllestad et al. 2004; Wells et al. 2007).

Growth history is strongly correlated with maturation age in salmonids. For example, in three Chinook salmon populations introduced to New Zealand with disparate maturation patterns, common-garden rearing experiments revealed no divergence among populations in females' age at maturity after accounting for individual growth history (Kinnison et al. 2011). Maturation is thought to be triggered by an individual attaining a threshold body size or growth rate at a particular age (Heino et al. 2002), which may be early in life (Morita and Fukuwaka 2006; Siegel et al. 2018). In western Alaska, maturation in two populations was most influenced by growth during their second year at sea, and the maturation threshold was at larger size and later in life for females than for males (Siegel et al. 2018). Thus, environmental conditions that affect salmon growth in early life, such as during the second year at sea, can result in plastic changes in maturation age (Morita and Fukuwaka 2006; Siegel et al. 2018). In the North Pacific, some variation in growth and maturation may be coupled with population spatial distribution, as age and length tend to vary with latitude for females, and the apparent proportion of fish maturing after their third year at sea follows a positive latitudinal cline (Healey 1991; Roni and Quinn 1995; Ohlberger et al. 2018).

Differences among areas and populations are important to consider when examining demographic trends such as changing maturation age and size. These trends have been spatially inconsistent in Alaska: between 1975–1993, ages were stable in western Alaska, declining in southeast Alaska, and increasing in central Alaska (Bigler et al. 1996). More recently (1985–2015), nearly all populations were declining in age, with the greatest declines occurring in central Alaska (Lewis et al. 2015). The complicated spatial and temporal patterns in maturation may be partially explained by direct effects of environmental changes that vary spatially. For example, Chinook salmon show stock-specific differences in their distribution in the western Gulf of Alaska (GOA) and the Bering Sea (Tucker et al. 2012; Larson et al. 2013). SSTs were warmer and increasing faster in the western GOA than in the central and eastern Bering Sea (Kalnay et al. 1996), which impacts prey abundance and distribution (Kaeriyama et al. 2004; Mueter and Litzow 2008) and has varying influences on growth (Wells et al. 2016; Yasumiishi et al. 2020). Populations might also show adaptive variation in maturation probabilities (Taylor 1991; Baum et al. 2004; Quinn

2005), which would result in apparent differences in growth and its relationship with maturation among populations in a common rearing environment. Additionally, there may be differences in age-dependent plasticity in growth and maturation among populations because of the variety of environments at different life stages (*e.g.*, Baum et al. 2004; Nilsson-Örtman et al. 2015). Comparing phenotypic differences in growth and maturation thresholds among populations over the life of the fish, within and among geographic areas, would advance our understanding of the causes of trends in size and age of Chinook salmon.

The causes of Chinook salmon size declines have been obscured, in part, due to limited sampling in the ocean where salmon rear for most of their lives. Because fish scales recapitulate freshwater and saltwater growth histories, our goal was to examine scales to better understand the growth and maturation age of female Chinook salmon from populations from across Alaska. We focused on two types of growth: increment growth (fresh water, FW; 1st through 4th year in salt water, SW1–SW4), and "maturation-related growth", defined as the difference in growth increments between fish that matured at age 5 and those that matured at age 6 by increment in a population. Our specific objectives were to (1) identify patterns in increment growth (state-wide, regional, and population-specific); (2) identify patterns in maturation-related growth (typical values, regional, and population-specific differences by increment).

METHODS

OVERVIEW

Annual growth of female Chinook Salmon was estimated from measurements of scale increments, in fresh water and for each year at sea, from 14 populations in Alaska. Each increment represents the period of growth from the end of winter in one year to the end winter of the following year starting in fresh water and four years at sea. We fit a multivariate random-effects model to scale measurements and estimated the variation in increment and maturation-related growth among populations. "Population increment growth" was a population's deviation from the increment average of a population and increment random effect. "Population maturation-related growth" was the difference in growth between fish that matured at age 5 and those that matured at age 6 by increment in a population-, increment- and maturation age-specific random effect. To meet both of our objectives, we identified patterns in growth, examined correlations in population growth among increments, described regional patterns in growth among populations, and examined correlations between growth and population ranking when ordered from southeast to northwest (alongshore coastal order).

SCALE SAMPLING

Field sampling of Chinook salmon scales was performed by the Alaska Department of Fish and Game (ADF&G) following standard procedures (*e.g.*, Molyneaux et al. 2008) for the purpose of population assessment and fisheries management. At the time of scale sampling, fish length (mid-eye to fork of tail, MEF), sex (visual inspection), and sample day were recorded for each fish. Three to four scales were taken from the preferred area on the body of the fish (Scarnecchia 1979) and placed on gummed cards. Gummed cards were pressed against a plastic acetate to make an impression of the scales that were viewed with a microfiche reader to estimate age (Clutter and Whitesel 1956).

We analyzed 14 Chinook salmon populations sampled at 13 rivers: the Unuk, Stikine, Taku, Chilkat, Copper, Deshka, Kenai, Nushagak, Kuskokwim, Yukon, Kogrukluk (a tributary to the Kuskokwim), East Fork Andreafsky ("Andreafsky," a tributary to the Yukon), and Unalakleet rivers (Fig. 1). In the Kenai River, early- and late runs were sampled at the same location, but the sample was divided into two temporally distinct populations, with 'early' defined as those captured from earliest sample day to day of year 180 (June 30 in most years) and 'late' as those sampled from day of year 181 to the last day of sampling, typically around August 5 (Reimer 2013). In the Copper and Unalakleet river systems, fish were sampled in nearshore locations just outside of the river mouth (Supplemental Table 1). Most populations had scales sampled in years 1980–2013, with an overall range from 1966 for the Yukon River through 2015 for the Copper and Stikine rivers.

The populations we focused on were largely the indicator populations chosen by a team of Chinook salmon experts to represent a diversity of watershed types and sizes, a wide range of ecological and genetic attributes, and geographic range spanning from the eastern Gulf of Alaska to northern Bering Sea (ADF&G 2013). We did not include two indicator populations, the Karluk and Chignik rivers, because they had limited numbers of years of sampling or few fish sampled per year.

Only mature female Chinook salmon of the main ages at which females matured, 5 and 6 years, were included in this study (percent of main ages in the return are provided in Supplemental Table 2). These fish spent one winter as an embryo developing in the gravel, generally one year rearing in the river, and three or four years at sea before returning to their natal river to spawn (Healey 1991). This study synthesized data used in previous studies (Ruggerone et al. 2009; Howard et al. 2016; Berkman 2017; Siegel et al. 2018; Graham et al. 2019), as well as new data from Copper, Deshka, Kenai early and late runs, and Nushagak river populations.

Growth measurement

Scale imaging and measurement procedures were based on methods established by Hagen et al. (2001). Scale measurement started with scanning 30–35 images of female Chinook salmon scales sampled from each return year and age. Scanned scales met legibility criteria and appeared to be from the preferred area on the body of the fish (Scarnecchia 1979; Hagen et al. 2001). Legibility criteria included that resorption of scale material along the margin, which is erosion of growth patterns due to salmon using scale material as energy reserves as they return to spawn (e.g., Mosher 1968), should not affect measurement transect length. Scale images were scanned using an Indus 4601-11 Screen Scan and 22 mm lens. Images were high-resolution, 584 pixels per mm and 400 dpi. Scales were measured using the software Image Pro Premier 9.2 and the Otolith and Fish Scale Analysis macro, version 2.17 (Cybernetics 2015), in millimeters, to the nearest 0.1 micrometer. Up to 25 of the most legible scales were measured for each year and age. Increment growth, starting with the center of scale growth (the focus) to the end of the first winter's growth and each subsequent period of growth from the end of winter to the end of the next winter, was measured along the longest transect from the focus to the scale margin. Measured increments were the increment growth in the river (FW), and at sea (SW1, SW2, SW3, and SW4).

Independent readers re-measured 45 randomly selected scales per population to test for an effect of reader on scale increment measurements using multiple analysis of variance (MANOVA). If a reader effect was found, increment placements on scales were reviewed, and the measurements (test or original) that better reflected increment growth patterns were identified (scale growth pattern descriptions in Fukuwaka 1998; Fisher and Pearcy 2005). When the test measurements better reflected growth patterns, original measurements were reviewed, and those that did not reflect increment growth patterns were re-measured. When original measurements better reflected growth patterns, scale measurement methods were reviewed with the independent reader. After scales were re-measured or methods were reviewed with the independent reader, a new set of scales were randomly selected and measured for a comparison. This process occurred for each population until there was no effect of reader on scale increment measurements (MANOVA $P > 0.05$ for each population). At least one reader was shared among all populations, assuring measurements were comparable among populations.

ANALYTICAL METHODS

Chinook salmon growth is affected by processes that occur at many levels, including over the life of the fish, among years, populations, and areas. Growth measurements within these levels are correlated, and analyses should account for this non-independence. We used a random-effects model, where random effects are parameters that represent shared processes and model non-independence in the response variable (Thorson and Minto 2015). All analyses were performed in R version 4.0.5 (R Core Team 2021).

Our modeling approach was shaped by the scale measurement dataset's unique qualities. Models were deliberately formulated to enable partitioning of variance in observed growth into explanatory variables (Weisberg et al. 2010), in our case, increment and maturation-related growth. Although measurements were taken from individual fish, we did not include a random effect for individual fish because, from preliminary analysis (descriptive models are provided in Supplemental Table 3), growth did not consistently vary among individuals after accounting for common growth year, maturation age, and increment effects by population and increment. Also in preliminary analysis, growth was not independent between increments, so we examined growth for correlations between increments within populations, brood years, and ages at maturity. Any dependence of growth between increments would not affect estimates of variation by increment (*i.e.*, one year of life; the random effects in the model below). We did not include a factor for water environment (fresh or salt) or a factor for life stage (fry, juvenile, immature, maturing) because we have only one measurement from fresh water and to avoid parameter redundancy. Where shown, the coefficient of variation (CV) of random effects by increment was the standard error (SE) of the effect divided by the mean increment measurement, because the mean of random effects is zero. Some effects were not normally distributed, so we examined Pearson correlations (r) for normally distributed data, or Kendall's Tau (r_T) correlations for non-normally distributed data, unless specified otherwise. We tested for normality using the Durbin Watson test (function durbinWatsonTest() in the package car; Fox and Weisberg 2018) and correlations were calculated using cor() in base R.

While growth is typically modeled as a function of previous growth (Chen et al. 1992; Katsanevakis 2006), we found that a multivariate random-effects model adequately described growth variation over the life of the fish.

We had initially considered using the nonlinear Ludwig Von Bertalanffy (LVB; Von Bertalanffy 1938) growth model for growth rate and other comparisons among populations (*e.g.*, Wang and Thomas 1995; Robards et al. 2002; Martin et al. 2010). However, in preliminary analysis of saltwater increment measurements (SW1–SW4), a model with typical LVB model parameters performed poorly compared to a fixed effects-only model including only an increment effect (-53,117 ΔAIC_C).

Random effects model

A multivariate random-effects model (MREM) was fit to scale measurements to estimate variation in increment and maturation-related growth. From preliminary analyses (not shown), we knew there was variability in growth over calendar years (i.e., shared environmental conditions affecting growth irrespective of fish age), so we included a population, increment, and calendar year random effect. The MREM had the form:

$y_{imykg} \sim N\left(\mu + \gamma_{k,g} + \delta_{m,k,g} + \varphi_{y,k,g}\ , \sigma^2\right)$, for $i = 1, \ldots, n$ (Equation 1)

$\gamma_{k,g} = N\left(0, \sigma_\gamma^2\right)$, for populations $k = 1, \ldots, K$ and increments $g = 1, \ldots, G$

$\delta_{m,k,g} = N(0, \sigma_\delta^2)$, for maturation age m = 5 or 6, populations 1, …, K, and increments 1, … G.

$\varphi_{y,k,g} = N\left(0, \sigma_\varphi^2\right)$, for years y, … Y , populations 1, …, K, and increments 1, … G

Where y_{imykg} was growth measurement on a scale from fish i with maturation age m from calendar year y in population k from increment g, and μ was an overall intercept. The parameter $\gamma_{k,g}$ was a random effect for population k and increment g. The parameter $\delta_{m,k,g}$ was a random effect for maturation age m, population k, and increment g. Including both increment ($\gamma_{k,g}$) and maturation age-specific ($\delta_{m,k,g}$) growth in the same model meant that the latter solely represented the effects of the two maturation ages by population. The parameter $\varphi_{y,k,g}$ was a nuisance random effect for calendar year y, population k, and increment g to account for variation within calendar years by population and increment. All random effects were intercepts.

The MREM was fit using the lmer() function in the lme4 package (Bates et al. 2015). The SE of random effects was the square root of the conditional variance-covariance matrix of the random effect generated by lmer() function (Bates et al. 2015). Parameter confidence intervals were provided by likelihood profiling using the function confint() in the package lme4 (Bates et al. 2015). We made standard assumptions for the distributions of the model errors, including homoscedasticity and normality. We visually examined a plot of model residuals for patterns and a qqplot, generated using the function 'qqnorm()' in base R for deviations from normality. We fit model residuals to an auto-regressive integrated moving average (ARIMA) model to test for the presence of time-series differencing, auto-regression, and a moving average. We fit the residuals to an ARIMA model using the function 'auto.arima()' in the package 'forecast' (Hyndman and Khandakar 2008). We calculated the adjusted intraclass-correlation coefficient (icc_{ajd}), the proportion of the variance explained by the grouping structure in the population related to the random effects, using the function 'icc()' in the package 'performance' (Lüdecke et al. 2021). Model degrees of freedom (df) were approximated using Satterthwaite's approach using the package 'lmerTest' (Kuznetsova et al. 2017). We evaluated goodness of fit by computing the conditional r-squared values for mixed effects models (Nakagawa et al. 2017) using the function 'r2_nakagawa()' in the package 'performance' (Lüdecke et al. 2021).

Population increment growth

Population increment growth was a population's deviation from the mean by increment of an increment- and population-specific random effect ($\gamma_{g,k}$) estimated in a MREM (Equation 1). We calculated the sum of increment growth (Sum_{inc}), which represented the population's deviation from the mean. Population increment growth was examined for spatial patterns and for correlations among increments, with alongshore coastal order from southeast to northwest, and with Sum_{inc}.

Growth among increments

Using the raw scale measurements, we used Pearson's correlations to examine the relationship between growth of increment pairs (*e.g.*, FW and SW1; SW1 and SW2), within populations, brood years, and ages at maturity. We expected positive correlations between consecutive increment pairs (*e.g.,* FW and SW1; SW1 and SW2) because large size is an advantage for growth in following years. We expected negative correlations between consecutive increment pairs when depressed growth was followed by accelerated growth (*i.e.*, compensatory growth; Ali et al. 2003). We also examined correlations between non-adjacent increment pairs (*e.g.*, FW and SW2, SW1 and SW3) in case of ontogenetic interdependence of growth among juvenile (FW and SW1), immature (SW2 and SW3 for fish that mature at age 6), maturing fish (i.e., growth during their final year at sea, SW3 for age 5 fish and SW4 for age 6 fish). We excluded brood year, population, and age at maturity combinations with <10 scale measurements. For each increment pair we then calculated the average of the correlations among brood years for each population and age at maturity.

Population maturation-related growth (MRG)

Population maturation-related growth (MRG) was a population's difference in increment growth between fish that matured at age 5 and those that matured at age 6, estimated from an increment-, population-, and maturation age-specific random effect ($\delta_{m,k,g}$) in a MREM (Equation 1). The mean growth for fish that matured at age 6 was subtracted from the mean growth for fish that matured at age 5 for each population *k* and increment *g*:

$$\mathrm{MRG} = \delta_{5,k,g} - \delta_{6,k,g} \qquad \text{(Equation 2).}$$

The standard deviation of MRG was:

$$\mathrm{SD(MRG)} = \sqrt{var(\delta_{5,k,g}) + var(\delta_{6,k,g}) + 2 \cdot \mathrm{cov}(\delta_{5,k,g}, \delta_{6,k,g})} \qquad \text{(Equation 3).}$$

To determine if MRG was similar among increments, we examined correlations among all MRG_g. We calculated the sum of MRG of all increments (MRG_{total} = sum of MRG_{FW} and MRG_{SW1} through MRG_{SW4}), which was the population's mean MRG. Maturation-related growth by increment (MRG_g) was examined for spatial patterns, in particular correlation with population alongshore coastal order, and also for correlation with MRG_{total}.

RESULTS

Growth measurements

Scales from a total of 17,137 female Chinook salmon yielded 78,722 increment measurements (Table 1). There was an average of 20 scales measured for each maturation age and year per population. The mean of measurements by increment were: FW = 0.33 mm (CV = 19%), SW1 = 1.32 mm (CV = 14%), SW2 = 1.14 mm (CV = 18%), SW3 = 1.15 mm (CV = 22%), and SW4 = 0.94 mm (CV = 24%). Measurements by population and increment are shown in Figs. 2 and 3. Cumulative measurements are shown by population, increment, and maturation age in Supplemental Fig. 1 and by increment, population, maturation age, and calendar year in Supplemental Fig. 2.

Random effects model

The multivariate random-effects model for increment, maturation-related, and calendar year growth explained much of the variability in measurements ($R^2_{\text{conditional}} = 0.83$; $\text{icc}_{\text{adj}} = 0.83$; Table 2). Increment effects by population ($\gamma_{k,g}$; Supplemental Fig. 3) accounted for most of the variation explained by random effects (92.5%), followed by maturation age effects by increment and population (5.4%; Supplemental Fig. 4). The population, increment, and calendar year effect accounted for the least variation explained by random effects (2.2%).

Calendar-year variation by population and increment was the greatest in SW4 (CV = 5.2%), followed by FW, SW2, and SW3 (CV = 4.7%, 4.6% and 4.5%, respectively), and was the least in SW1 (CV = 3.7%).

Patterns in population increment growth

Increment growth was greater in salt water than in fresh water and declined with each year in salt water, except that in some populations SW3 growth was larger than SW2 or SW1 growth. The means by increment of the population and increment random effect ($\gamma_{k,g}$, equation 1) were: FW = -0.63 (CV = 6%), SW1 = 0.32 (CV = 7%), SW2 = 0.17 (CV = 4%), SW3 = 0.19 (CV = 9%), and SW4 = -0.05 (CV = 11%). Although freshwater growth was approximately 3x less than marine growth, the estimated standard errors were similar between fresh and saltwater growth because of not including a factor for water environment (fresh or salt).

Regional patterns in increment growth were evident among populations for all increments but SW2, which instead showed an alongshore coastal cline (Fig. 4). Southeast populations (Unuk, Stikine, Taku, and Chilkat) had average to below-average growth in most increments, especially in SW3 and SW4, and above-average growth in SW2. Central GOA populations (Copper in Prince William Sound (PWS); and Kenai early, Kenai late, and Deshka in Cook Inlet) had below average FW and SW1 growth, average SW2 growth, and above-average SW3 growth. Bering Sea populations had above average FW and SW1 growth and average to below average SW2 and SW3 growth. SW4 growth patterns were generally consistent with SW3 growth but less geographically clustered and shifted north: the four Southeast and two Bering Sea populations, Andreafsky and Kogrukluk, had below average SW3 and SW4 growth. While the four central GOA populations had the largest SW3 growth, only two central GOA populations, Kenai early and Kenai late, and two Bering Sea populations, Nushagak and Kuskokwim, had above average SW4 growth. The two remaining central GOA populations, Copper and Deshka, and two Bering Sea populations, Yukon and Unalakleet, had close to average SW4 growth.

Regional patterns in increment growth differed between those formed before and after SW2. For SW1, GOA stocks (Southeast, PWS, and Cook Inlet) had below average growth, growth of Cook Inlet stocks was particularly low, while Bering Sea stocks had above average growth (*i.e.*, Bering Sea > Southeast and PWS > Cook Inlet). For SW3 and SW4 growth (SW4 patterns mirrored SW3 but shifted north, described above), Cook Inlet and PWS > Bering Sea > Southeast. SW2 growth was strongly negatively correlated with alongshore coastal order (r = -0.9; $P = 1 \times 10^{-5}$; Supplemental Fig. 5). Growth in FW and SW1 were positively correlated with alongshore coastal order (FW, r = 0.6; $P = 0.02$; SW1, r = 0.55; $P = 0.04$; Supplemental Fig. 5).

Variation among populations in increment growth was greatest for SW4 (CV = 11.4%), followed by SW3 (CV = 8.9%), SW1 (CV = 7.1%), FW (CV = 6.4%) and least for SW2 (CV = 4.3%). We found both positive and negative correlations in increment growth between increment pairs, with an apparent transition at SW2 (Fig. 4; correlations, Supplemental Fig. 5). FW and SW1, and SW3 and SW4, were positively correlated (FW and SW1 r = 0.6, $P = 0.02$; SW3 and SW4 $r_T = 0.63$, $P = 0.002$). SW2 was negatively correlated with SW4 (r = -0.59, $P = 0.03$) and was not correlated with FW, SW1, or SW3.

Kenai late had the highest overall mean increment growth (Sum_{inc}) and Stikine and Taku had the lowest overall Sum_{inc} (Table 3). Population variation in Sum_{inc} was correlated with SW3 ($r_T = 0.75$, $P = 2.7 \times 10^{-4}$) and SW4 (r = 0.92, $P = 2.6 \times 10^{-6}$) but not with FW, SW1, or SW2 (Supplemental Fig. 5).

Correlations in growth among increments

Within populations and brood years, the relationship of growth of an increment with the growth of other increments varied among increment pairs (Fig. 5), with non-consecutive increment pairs (i.e., FW and SW2, FW and SW3, SW1 and SW3, SW2 and SW4) having stronger (double the magnitude; excluding pairs with SW4 that are only present in age 6 fish) and, more consistently the same sign (positive or negative) than consecutive increment pairs. FW growth consistently increased with SW2 growth for both ages at maturity in all populations. For fish that matured at age 6, increased FW and SW1 growth meant increased SW3 growth in most populations (13 out of 14). On the other hand, for fish that matured at age 6, increased SW1, SW2, and SW3 growth meant decreased SW4 growth in most or all populations (11, 14, and 10 populations, respectively). Fish that matured at age 6 from Cook Inlet populations had the strongest correlations (absolute value > 0.25) in consecutive increment pairs: increased FW growth meant decreased SW1 growth (Kenai early and Kenai late), increased FW growth meant increased SW3 growth (Kenai Early), and increased SW3 growth meant reduced SW4 growth (Deshka). Plots of correlations between increment pairs within populations, brood years, and ages at maturity are in supplementary material (Supplementary Figs. 6–14).

Patterns in population maturation-related growth

Increment maturation-related growth (MRG_g) generally increased with increment, especially at the transition to saltwater growth and at SW2 (Fig. 6). MRG_g was greatest in SW2 for about half of the populations (Unuk, Stikine, Taku, Chilkat, Andreafsky, and Kogrukluk) and greatest in SW3 for the remaining populations except Kenai late, where the largest MRG occurred in SW1.

Patterns in MRG_g corresponded to increment growth but regional groupings were less clear than for increment growth. MRG_{SW2} variation corresponded to SW1 regional groups ($r_T = 0.73$, $P = 0.003$). For example, Deshka and Kenai early had the lowest MRG_{SW2} and the smallest SW1 growth, and most Bering Sea populations had high MRG_{SW2} and large SW1 growth. MRG_{SW3} variation corresponded to SW4 regional groups ($r = 0.54$, $P = 0.008$). For example, four Southeast populations and two Bering Sea populations, Andreafsky and Kogrukluk, had below-average SW4 growth and low MRG_{SW3}, while Kenai early and two southern Bering Sea populations, Nushagak and Kuskokwim, had above average SW4 growth and high MRG_{SW3}. Kuskokwim stood out among populations with high MRG_{SW2} and MRG_{SW3}. MRG_{FW} and MRG_{SW2} had similar patterns among populations ($r = 0.55$; $P = 0.04$; Supplemental Fig. 15). MRG_{SW1} had no spatial pattern and was not correlated with any other growth measurement. MRG_g were not correlated with alongshore coastal order (Supplemental Fig. 15).

Kuskokwim had the highest overall mean MRG_{total}, and Unuk and Chilkat had the lowest overall mean MRG_{total} (Table 3). Population variation in mean MRG (MRG_{total}) was correlated with MRG_{SW3} ($r_T = 0.72$, $P = 4.1 \times 10^{-4}$) and not with MRG_{FW}, MRG_{SW1}, or MRG_{SW2} (Supplemental Fig. 15).

DISCUSSION

Our analysis of 17,137 scales from female Chinook salmon from 14 populations across Alaska yielded state-wide, regional, and population-specific patterns in growth. SW2 growth was the least variable among populations but showed a clinal pattern, with highest growth in the southeast and lowest growth in the northwest. Geographic area (Southeast, PWS, Cook Inlet, and Bering Sea) contributed to increment growth patterns, which we suggest are related to nearshore productivity and differences in age and size at maturity (described below). We found that faster growing Chinook salmon matured at a younger age, a typical pattern for Chinook salmon (Healey 1991; McPhee et al. 2016; Siegel et al. 2017). Divergence in growth between maturation ages (MRG) was evident in SW1 but was greater in SW2 and SW3. Among-population variation in MRG by increment more closely corresponded with growth of adjacent increments than with geographic patterns, suggesting maturation and increment growth are linked between years of life. These growth patterns allow for a better understanding of the potential life history tradeoffs among growth, maturation, and survival.

Spatial patterns in SW1 growth corresponded to regional groups, *i.e.*, Bering Sea > Southeast and PWS > Cook Inlet. The Bering Sea ecosystem has greater linkage complexity among species groups, higher biomass of total producers and consumers including phytoplankton and demersal fish (Gaichas et al. 2009), and thus may be a better Chinook salmon rearing area than the Gulf of Alaska ecosystem (Aydin et al. 2007). The Cook Inlet estuary is highly turbid from glacial sediments, which reduces primary productivity (Speckman et al. 2005) and limits visual feeding and the prey field for juvenile salmon (Moulton 1997). At-sea surveys indicated that after their first summer at sea, Bering Sea Chinook salmon were smaller than those from Southeast (Trudel et al. 2007); however, Bering Sea fish were observed to have higher fall growth rates and energy stores ($kJ \cdot g^{-1}$) than fish in Southeast (Trudel et al. 2007; Moss et al. 2016). This suggests that fall and winter growth must be greater for Bering Sea fish than for Southeast fish to arrive at the SW1 growth patterns we observed. Chinook salmon in the Bering Sea likely grow more than Southeast Chinook salmon over the first fall and winter due to the higher productivity and availability of herring and capelin observed in late summer (Yasumiishi et al. 2020). Chinook salmon in the Bering Sea grow and maintain their somatic tissue energetic density through the winter by rearing in deeper and warmer water, and feeding on prey such as squid *Berryteuthis magister* (Davis et al. 2009; Myers et al. 2010).

Spatial variation in SW2 growth may reflect region-specific responses to tradeoffs among survival, growth, and maturation. By the second year at sea, Chinook salmon from various natal stocks are converging toward similar rearing areas and conditions (Myers and Rogers 1988; Larson et al. 2013), which could explain SW2 growth patterns being more consistent among populations than SW1 growth patterns. However, it does not explain the clinal variation in SW2 growth we observed. At-sea surveys provide evidence that for Alaska Chinook salmon, macroscopic ovarian development occurs during SW2, 1–2 years before spawning (Myers et al. 2010), connecting SW2 growth to oocyte production. Older age and larger size at maturity are favored at high latitudes where it is colder (Arendt 2011) and there are shorter growing seasons (Alm 1959; Roff 1983, 1992). Given the correlation between fast SW2 growth and early maturation (*e.g.*, Siegel et al. 2018), the environment and associated life histories of populations at higher latitudes might favor reduced foraging activity to prioritize survival over growth during SW2. The prioritization of survival over SW2 growth with increasing latitude may result in larger, older, higher fecundity individuals with increasing latitude that allocate energetic resources to gonadal production later in life. Supporting these patterns, fecundity standardized to fish length increased with latitude for 44 populations (Beacham and Murray 1993) and age at maturity tends to increase with latitude (Lewis et al. 2015; Ohlberger et al. 2018). Fecundity and egg size are further affected by selection pressures during their final year(s) at sea and at the spawning grounds. Growth and maturity patterns over the life of the fish would be further illuminated with more at-sea observations.

The differences in MRG among increments and populations may reflect different allocations of energy by population among somatic growth (with growth in length reflected in scale growth), energy stores, and gonads. The low magnitude and low among-population variation in MRG_{SW1} may indicate that somatic growth is prioritized during the 1st year at sea among all populations, which makes sense given size-selective mortality during the first summer at sea (Farley et al. 2007; Howard et al. 2016). MRG_{SW2} was smallest in Cook Inlet populations, which had the lowest SW1 growth, suggesting that populations that typically do not grow as much during their first year at sea continue to prioritize somatic growth during the second year regardless of maturation age. Populations with the smallest MRG_{SW3} (Southeast and the Kogrukluk and Andreafsky populations from the Bering Sea region) had the lowest SW3 and SW4 growth and tended to have the lowest total increment growth (*i.e.*, overall body length). These populations might experience less selection for large length at maturity and therefore less reason for age-6 females to continue to invest in somatic growth in later ocean years. Also, these populations might experience greater selection to divert energy to energy stores or gonads and therefore age-6 females are constrained from investing more in somatic growth. Given the large geographic distances between the Bering Sea (Kogrukluk and Andreafsky) and Southeast, different mechanisms may be responsible for the differences in maturation growth observed across the populations.

Correlations between growth increments within populations (calculated within brood years within populations to produce population-specific means) yielded complex patterns that were not consistent entirely with compensatory growth (negative correlations between adjacent increments) or an advantage of size for future growth (positive correlations). SW1 and SW2 tended to be positively correlated, albeit weakly, providing some support for the idea that fish that achieve larger size after their first year at sea also grow better during their second year at sea. The strongest signals of compensatory growth (negative correlations) were between FW and SW1 and between SW3 and SW4 in Cook Inlet populations. The typically low SW1 growth of these populations suggests limited opportunity for catch-up growth during the first year at sea, but it could also imply a greater need for the smallest fish to grow as fast as possible during SW1. Moreover, given compensatory growth, we may expect to see less FW growth combined with greater SW1 growth, and less SW3 growth combined with greater SW4 growth. However, a post-hoc review of scale measurements yields results that contrast with expectations from compensatory growth. For scale measurements from age-6 Kenai late fish, the population and age at maturity with the strongest negative correlations between FW and SW1, the five brood years with the strongest negative correlations had close to average FW and SW1 growth (mean of years with the strongest negative correlations: FW, 0.34 mm vs. average 0.33 mm, and SW1, 1.12 mm versus average, 1.14 mm). For scale measurements from age-6 Deshka fish, the population and age at maturity with the strongest negative correlations between SW3 and SW4 growth, SW3 growth was greater than average during the five brood years with the strongest negative correlations (mean of years with the strongest negative correlations, 1.28 mm vs. average, 1.20 mm) and SW4 growth was less than average (mean of years with the strongest negative correlations, 0.54 mm vs. average, 0.91 mm).

Alternatively, within brood-year patterns of reduced SW1 growth after greater FW growth, and reduced SW4 after greater SW3 growth, may be plastic responses to warming. Increased growth and energy stores during the fall and winter of freshwater residency are associated with earlier maturation and reduced marine survival (Spangenberg et al. 2014; Beckman et al. 2017; Harstad et al. 2018). Cook Inlet populations had the strongest correlations between FW and SW1 and are in a warmer environment than other areas of Alaska. Alaska is warming the fastest in the winter and spring (Markon et al. 2012), possibly increasing FW growth and affecting life history, including SW1 growth. Across Alaska, faster growing juvenile and immature fish may be able to grow less and shift more energy to gonads in their maturation year. For age 6 females, faster SW1, SW2, and SW3 growth was associated with slower SW4 growth. For age 5 females from GOA populations, faster SW2 growth meant slower SW3 growth. For age 5 females from Bering Sea populations, which typically grow less during SW2 than GOA populations, SW2 growth was positively correlated with SW3 growth, which may indicate the need to achieve large size at maturity and allocation of energy to gonadal production later in life. The trend towards greater growth of juvenile and immature fish and lower growth of maturing fish (the final year at sea) is consistent with smaller size at maturity in a warming environment, a phenomenon observed in fish species in other areas of the world (van Rijn et al. 2017; Hattab et al. 2021; Ikpewe et al. 2021) and for other species in the Bering Sea (Oke et al. 2022). Given the strength and persistence of the negative correlations among populations and the unusual growth patterns of Cook Inlet Chinook salmon more generally, these topics are worthy of further investigation.

The increment growth patterns we found suggests growth over the life of female Chinook salmon does not conform to the typical assumptions of fish growth, contributing to their characteristic large body size. Fundamental assumptions of growth are that it declines over the life of the fish (*e.g.*, Hamre et al. 2014) and fish that mature at large size have the greatest juvenile growth rate (*e.g.*, Groot and Margolis 1991; Sibly et al. 2015). Faster FW growth was consistently associated with faster SW2 growth for both ages at maturity, suggesting early-life growth patterns can modify later-life energetic allocations and tradeoffs between feeding and survival (*e.g.* Sigourney et al. 2008; Higgins et al. 2015). Regardless of SW1 growth, SW2 growth followed an alongshore-order cline (described previously), while SW3 growth could be consistently greater than SW1 or SW2 growth, such as in Cook Inlet populations. In addition, growth during SW3 and SW4 was positively correlated with total increment growth, while SW1 growth was not. The unusual growth pattern of Cook Inlet populations might be due to inhospitable nearshore environments during their first year at sea, coupled with the need to attain large adult body size. Although selection on size at maturity has not been studied in these populations, Cook Inlet populations include some of the largest-bodied populations of Chinook salmon in the North Pacific (e.g., Kenai Late; Roni and Quinn 1995).

While scale measurements supply known population, maturation age, and increment width estimates, there are uncertainties introduced by using scale measurements to represent growth. Scale radius and fish length are linearly related (Bilton 1985; Fukuwaka and Kaeriyama 1995; Fisher and Pearcy 2005) but there are differences in this relationship between the stream- and ocean type life histories (Hyun et al. 1998), among seasons (Fisher and Pearcy 2005), ages (Bilton and Ludwig 1966), and possibly among populations and years, as found for Chum salmon (Martinson and Helle 2000). Differences in fish length-scale measurement relationships may impact population increment growth estimates because increment growth measured the magnitude of growth at age among populations. We suggest that the variation in the scale radius to fish length relationship is small enough (Supplemental Fig. 16) that it would not meaningfully impact estimated growth patterns (mean slope = 176, CV of slopes = 3.0%). Differences in the fish length-scale measurement relationship would have minimal impact on MRG_g because that metric reflects the within-population differences in growth between maturation ages.

Measuring growth from fish that survived to sexual maturity adds uncertainty to the interpretation of our results because we do not know how well measured growth represents growth of the whole population during the period when the growth occurred. Salmon survival is thought to be size selective early in marine life (Beamish and Mahnken 2001; Murphy et al. 2013; Howard et al. 2016). Sampling growth from surviving adults could have preferentially captured the growth patterns of faster growing fish that matured earlier and may have been less susceptible to predation, whereas sampling fish at sea could over-represent slower-growing fish that have not matured and may be susceptible to predation in later years (Healey 1991). Alternatively, the fastest growing individuals may not be represented in our samples because of increased feeding bouts, reduced vigilance, and increased exposure to predators increasing their mortality, and the slower-growing individuals may be over-represented in our samples because of reduced exposure to predators. While scale measurements supply information at lower cost than at-sea surveys and provide age at maturity, they are not a perfect representation of age-specific population growth. More surveys are needed of stock-specific body size, age, and energetic and maturity status to better understand mortality at sea.

Scale measurements from individual fish revealed spatial and age-specific patterns in growth that may have multifarious implications for Chinook salmon populations in a rapidly changing environment. To date, hypotheses to explain changing Chinook salmon population demography have focused on extrinsic effects: fisheries-induced evolution (Ricker 1980), river discharge (Neuswanger et al. 2015), timing of ice leaving the river in the spring (Cunningham et al. 2018), estuarine or early-life survival (Howard et al. 2016; Murphy et al. 2017), size-selective predation of the largest fish (Ohlberger et al. 2018; Manishin et al. 2021), competition at sea (Cunningham et al. 2018; Oke et al. 2020), and climate (Lewis et al. 2015; Cunningham et al. 2018; McPhee et al. 2019; Oke et al. 2020). Our study suggests that population-specific variation in increment and maturation-related growth patterns correspond with life history tradeoffs among growth, maturation, and survival that are mediated by the freshwater and marine environment. Correlations between growth patterns and demographic changes would help to disentangle intrinsic effects, such as life stage-specific growth response to environmental change, from hypothesized extrinsic effects on temporal variation in maturation age, productivity, and length at age. Testing these hypotheses is beyond the scope of this study but is the subject of a second analysis (Wilson et al. in prep.). Better understanding among-population variation in growth at age would improve population dynamics models, return forecasts, and fisheries management during a time of rapid environmental change.

Author contributions

All authors contributed to the study conception and design. Funding acquisition was performed by Milo Adkison and Megan McPhee. Material preparation, data collection, and analysis were performed by Lorna Wilson, Milo Adkison, and Megan McPhee. The first draft of the manuscript was written by Lorna Wilson and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

References

ADF&G Chinook Salmon Research Team (2013) Chinook salmon stock assessment and research plan, 2013. Alaska Department of Fish and Game, Special Publication No. 13-01, pp 1–62 (Available at http://www.adfg.alaska.gov/FedAidPDFs/SP13-01.pdf)

Ali M, Nicieza A, Wootton RJ (2003) Compensatory growth in fishes: a response to growth depression. Fish Fish 4(2):147-190. https://doi.org/10.1046/j.1467-2979.2003.00120.x

Alm G (1959) Connection between maturity, size, and age in fishes. Inst Freshwat Res Rep 40:4-145.

Arendt JD (2011) Size-fecundity relationships, growth trajectories, and the temperature-size rule for ectotherms. Evol 65(1):43-51. https://doi.org/10.1111/j.1558-5646.2010.01112.x

Aydin KY, Gaichas SK, Ortiz I, Kinzey DH, Friday N (2007) A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. U.S. Dep Commer, NOAA tech memo NMFS-AFSC-178, 298 p.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1406.5823. https://doi.org/10.48550/arXiv.1406.5823

Baum D, Laughton R, Armstrong JD, Metcalfe NB (2004) Altitudinal variation in the relationship between growth and maturation rate in salmon parr. J Anim Ecol 73(2):253-260. https://doi.org/10.1111/j.0021-8790.2004.00803.x

Beacham T, Murray C (1993) Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). J Fish Biol 42(4):485-508. https://doi.org/10.1111/j.1095-8649.1993.tb00354.x

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49:423-437. https://doi.org/10.1016/S0079-6611(01)00034-9

Beckman BR, Harstad DL, Spangenberg DK, Gerstenberger RS, Brun CV, Larsen DA (2017) The impact of different hatchery rearing environments on smolt-to-adult survival of spring Chinook salmon. Trans Am Fish Soc 146(3):539-555. https://doi.org/10.1080/00028487.2017.1281168

Berkman S (2017) Evaluation of growth and migration trends on the survival and recruitment of Chinook Salmon in Southeastern Alaska rivers. Thesis, University of Alaska

Bigler BS, Welch DW, Helle JH (1996) A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Can J Fish Aquat Sci 53:455-465. https://doi.org/10.1139/f95-181

Bilton H (1985) The body-scale relationship for adult sockeye (*Oncorhynchus nerka*), pink (*O. gorbuscha*), chum salmon (*O. keta*), and Chinook salmon (*O. tshawytscha*). Can Tech Rep Fish Aquat Sci 1353, pp 1–26

Bilton HT, Ludwig SAM (1966) Times of annulus formation on scales of sockeye, pink, and chum salmon in the Gulf of Alaska. J Fish Res Board Can 23:1403-1410. https://doi.org/10.1139/f66-127

Brown CL, Godduhn AR (2015) Socioeconomic effects of declining salmon runs on the Yukon River. Alaska Department of Fish and Game Technical Paper No. 398, pp 1–182 (Available at https://www.adfg.alaska.gov/techpap/TP398.pdf)

Carothers C, Black J, Langdon SJ, Donkersloot R, Ringer D, Coleman J, Gavenus ER, Justin W, Williams M, Christiansen F (2021) Indigenous peoples and salmon stewardship: a critical relationship. Ecol Soc 23(1):16. https://doi.org/10.5751/ES-11972-260116

Chen Y, Jackson D, Harvey H (1992) A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. Can J Fish Aquat Sci 49(6):1228-1235. https://doi.org/10.1139/f92-138

Clutter R, Whitesel L (1956) Collection and interpretation of sockeye salmon scales. International Pacific Salmon Fisheries Commission, New Westminster, Canada. pp 1–159

Cunningham CJ, Westley PAH, Adkison MD (2018) Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model. Global Change Biol 24(9):4399-4416. https://doi.org/10.1111/gcb.14315

Cybernetics M (2015) Otolith App for Image-Pro Premier. Media Cybernetics, Inc., Rockville, MD

Davis ND, Myers KW, Fournier WJ (2009) Winter food habits of Chinook salmon in the Eastern Bering Sea. N Pac Anadromous Fish Comm Bull 5:243-253.

Farley EV, Moss JH, Beamish RJ (2007) A review of the critical size, critical period hypothesis for juvenile Pacific salmon. N Pac Anadromous Fish Comm Bull 4:311-317.

Fisher JP, Pearcy WG (2005) Seasonal changes in growth of coho salmon *(Oncorhynchus kisutch)* off Oregon and Washington and concurrent changes in the spacing of scale circuli. Fish Bull 103:34-51.

Fox J, Weisberg S (2018) An R companion to applied regression

Fukuwaka M (1998) Scale and otolith patterns prove growth history of Pacific salmon. N Pac Anadromous Fish Comm Bull 1:190-198.

Fukuwaka M, Kaeriyama M (1995) Relationship between scale growth and somatic growth in sockeye salmon, *Oncorhynchus nerka*. N Pac Anadromous Fish Comm Bull 148:1-11.

Gaichas S, Skaret G, Falk-Petersen J, Link JS, Overholtz W, Megrey BA, Gjøsæter H, Stockhausen WT, Dommasnes A, Friedland KD (2009) A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. Prog Oceanogr 81(1-4):47-62. https://doi.org/10.1016/j.pocean.2009.04.005

Graham CJ, Sutton TM, Adkison MD, McPhee MV, Richards PJ (2019) Evaluation of growth, survival, and recruitment of Chinook salmon in southeast Alaska rivers. Trans Am Fish Soc 148(2):243-259. https://doi.org/10.1002/tafs.10148

Groot C, Margolis L (1991) Pacific Salmon Life Histories. Vancouver, BC, pp 1–564

Hagen PT, Oxman DS, Agler BA (2001) Developing and deploying a high resolution imaging approach for scale analysis. N Pac Anadromous Fish Comm Doc 567:1-11.

Hamre J, Johnsen E, Hamre K (2014) A new model for simulating growth in fish. Peerj 2:16. https://doi.org/10.7717/peerj.244

Harstad DL, Larsen DA, Miller J, Adams I, Spangenberg DK, Nance S, Rohrbach L, Murauskas JG, Beckman BR (2018) Winter-rearing temperature affects growth profiles, age of maturation, and smolt-to-adult returns for yearling summer Chinook Salmon in the upper Columbia River basin. N Am J Fish Manag 38(4):867-885. https://doi.org/10.1002/nafm.10186

Hattab T, Gucu A, Ventero A, De Felice A, Machias A, Saraux C, Gasparevic D, Basilone G, Costantini I, Leonori I, Bourdeix JH, Iglesias M, Barra M, Giannoulaki M, Ferreri R, El Ayoubi S, Malavolti S, Genovese S, Somarakis S, Juretic T, Ticina V, Certain G (2021) Temperature strongly correlates with regional patterns of body size variation in Mediterranean small pelagic fish species. Mediterr Mar Sci 22(4):800-811. https://dx.doi.org/10.12681/mms.26525

Healey M (1991) Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In: C Groot, L Margolis, (ed) Pacific salmon life histories. UBC Press., Vancouver, BC, pp 311–394

Heino M, Dieckmann U, Godø OR (2002) Measuring probabilistic reaction norms for age and size at maturation. Evol 56(4):669-678. https://doi.org/10.1111/j.0014-3820.2002.tb01378.x

Higgins RM, Diogo H, Isidro EJ (2015) Modelling growth in fish with complex life histories. Rev Fish Biol Fish 25(3):449-462. https://doi.org/10.1007/s11160-015-9388-8

Howard KG, Murphy JM, Wilson L, Moss JH, Farley Jr EV (2016) Size-selective mortality of Chinook salmon in relation to body energy after the first summer in nearshore marine habitats. N Pac Anadromous Fish Comm Bull 6:1-11.

Hyndman RJ, Khandakar Y (2008) Automatic time series forecasting: the forecast package for R. J Stat Softw 26(3):1-22. https://doi.org/10.18637/jss.v027.i03

Hyun S-Y, Myers KW, Sneva J (1998) The time of annulus formation in Chinook salmon caught in Washington coastal waters. N Pac Anadromous Fish Comm Doc 352:1-30.

Ikpewe IE, Baudron AR, Ponchon A, Fernandes PG (2021) Bigger juveniles and smaller adults: Changes in fish size correlate with warming seas. J Appl Ecol 58(4):847-856. https://doi.org/10.1111/1365-2664.13807

Kaeriyama M, Nakamura M, Edpalina RR, Bower JR, Yamaguchi H, Walker RV, Myers KW (2004) Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. Fish Oceanogr 13(3):197-207. https://doi.org/10.1111/j.1365-2419.2004.00286.x

Kalnay E, Kanamitsu M, Kistler R, Collins W, Deaven D, Gandin L, Iredell M, Saha S, White G, Woollen J (1996) The NCEP/NCAR 40-year reanalysis project. Bull Am Meteorol Soc 77(3):437-472.

Katsanevakis S (2006) Modelling fish growth: model selection, multi-model inference and model selection uncertainty. Fish Res 81(2-3):229-235. https://doi.org/10.1016/j.fishres.2006.07.002

Katsanevakis S, Maravelias CD (2008) Modelling fish growth: Multi-model inference as a better alternative to a priori using von Bertalanffy equation. Fish Fish 9(2):178-187. https://doi.org/10.1111/j.1467-2979.2008.00279.x

Kinnison M, Quinn T, Unwin M (2011) Correlated contemporary evolution of life history traits in New Zealand Chinook salmon, *Oncorhynchus tshawytscha*. Hered 106(3):448-459. https://doi.org/10.1038/hdy.2010.162

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: Tests in Linear Mixed Effects Models. J Stat Softw 82(13):1-26. https://doi.org/10.18637/jss.v082.i13

Larson WA, Utter FM, Myers KW, Templin WD, Seeb JE, Guthrie III CM, Bugaev AV, Seeb LW (2013) Single-nucleotide polymorphisms reveal distribution and migration of Chinook salmon (*Oncorhynchus tshawytscha*) in the Bering Sea and North Pacific Ocean. Can J Fish Aquat Sci 70(1):128-141. https://doi.org/10.1139/cjfas-2012-0233

Lew DK, Larson DM (2012) Economic values for saltwater sport fishing in Alaska: A stated preference analysis. N Am J Fish Manag 32(4):745-759. https://doi.org/10.1080/02755947.2012.681012

Lewis B, Grant WS, Brenner RE, Hamazaki T (2015) Changes in size and age of Chinook Salmon *Oncorhynchus tshawytscha* returning to Alaska. Plos One 10(6):e0130184. https://doi.org/10.1371/journal.pone.0132872

Loring PA, Gerlach C (2010) Food security and conservation of Yukon River salmon: Are we asking too much of the Yukon River? Sustainability 2(9):2965-2987. https://doi.org/10.3390/su2092965

Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D (2021) {performance}: An {R} package for assessment, comparison and testing of statistical models. J Open Source Softw 6(60):3139. https://doi.org/10.21105/joss.03139

Manishin KA, Cunningham CJ, Westley PA, Seitz AC (2021) Can late stage marine mortality explain observed shifts in age structure of Chinook salmon? Plos One 16(2):e0247370. https://doi.org/10.1371/journal.pone.0247370

Markon CJ, Trainor SF, Chapin III FS (2012) The United States national climate assessment-Alaska technical regional report. US Geological Survey, 2330-5703

Martin KE, Steele CA, Brunelli JP, Thorgaard GH (2010) Mitochondrial variation and biogeographic history of Chinook salmon. Trans Am Fish Soc 139(3):792-802. https://doi.org/10.1577/T09-080.1

Martinson EC, Helle JH (2000) Time of annulus formation on scales of chum salmon in the North Pacific Ocean in 1998 and 1999 N Pac Anadromous Fish Comm Bull 2:137-143.

McPhee MV, Leon JM, Wilson LI, Siegel JE, Agler BA (2016) Changing growth and maturity in Western Alaskan Chinook salmon, *Oncorhynchus tshawytscha*, brood years 1975–2005. N Pac Anadromous Fish Comm Bull 3:307-327.

McPhee MV, Siegel JE, Adkison MD (2019) Is a warming Bering Sea leading to smaller Chinook salmon? N Pac Anadromous Fish Comm Tech Rep 15:117-119.

Molyneaux DB, Folletti DL, Brodersen AR (2008) Salmon age, sex, and length catalog for the Kuskokwim Area, 2007. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A08-05, pp 1–82 (Available at http://www.adfg.alaska.gov/FedAidPDFs/RIR.3A.2008.05.pdf.)

Morita K, Fukuwaka Ma (2006) Does size matter most? The effect of growth history on probabilistic reaction norm for salmon maturation. Evol 60(7):1516-1521. https://doi.org/10.1111/j.0014-3820.2006.tb01230.x

Mosher KH (1968) Photographic atlas of sockeye salmon scales. Fish Bull 67(2):243-280.

Moss JH, Murphy JM, Fergusson EA, Heintz RA (2016) Allometric relationships between body size and energy density of juvenile Chinook (*Oncorhynchus tshawytscha*) and chum (*O. keta*) salmon across a latitudinal gradient. N Pac Anadromous Fish Comm Bull 6:161-168.

Moulton LL (1997) Early marine residence, growth, and feeding by juvenile salmon in northern Cook Inlet, Alaska. Alaska Fish Res Bull 4(2):154-177.

Mueter FJ, Litzow MA (2008) Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol Appl 18(2):309-320. https://doi.org/10.1890/07-0564.1

Munro AR (2023) Summary of Pacific Salmon Escapement Goals in Alaska with a Review of Escapements from 2014 to 2022. Alaska Department of Fish and Game, Fishery Manuscript Series No. 23-01, pp 1–84 (Available at https://www.adfg.alaska.gov/FedAidPDFs/FMS23-01.pdf)

Murphy J, Howard K, Eisner L, Andrews A, Templin W, Guthrie C, Cox K, Farley E (2013) Linking abundance, distribution, and size of juvenile Yukon River Chinook salmon to survival in the northern Bering Sea. N Pac Anadromous Fish Comm Tech Rep (9):25-30.

Murphy JM, Howard KG, Gann JC, Cieciel KC, Templin WD, Guthrie CM (2017) Juvenile Chinook salmon abundance in the northern Bering Sea: Implications for future returns and fisheries in the Yukon River. Deep Sea Res II Top Stud Oceanogr 135:156-167. https://doi.org/10.1016/j.dsr2.2016.06.002

Myers K, Walker R, Davis N, Armstrong J, Fournier W, Mantua N, Raymond-Yakoubian J (2010) Climate-ocean effects on AYK Chinook salmon. Arctic Yukon Kuskokwim Sustainable Salmon Initiative, Project Final Product. SAFS-UW-1003., Seattle, WA.

Myers KW, Rogers DE (1988) Stock origins of Chinook salmon in incidental catches by groundfish fisheries in the eastern Bering Sea. N Am J Fish Manag 8(2):162-171. https://doi.org/10.1577/1548-8675(1988)008<0162:SOOCSI>2.3.CO;2

Nakagawa S, Johnson P, Schielzeth H (2017) The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J R Soc Interface 14(134):20170213. https://doi.org/10.1098/rsif.2017.0213

Neuswanger JR, Wipfli MS, Evenson MJ, Hughes NF, Rosenberger AE (2015) Low productivity of Chinook salmon strongly correlates with high summer stream discharge in two Alaskan rivers in the Yukon drainage. Can J Fish Aquat Sci 72(8):1125-1137. https://doi.org/10.1139/cjfas-2014-0498

Nilsson-Örtman V, Rogell B, Stoks R, Johansson F (2015) Ontogenetic changes in genetic variances of age-dependent plasticity along a latitudinal gradient. Hered 115(4):366-378. https://doi.org/10.1038/hdy.2014.126

Ohlberger J, Ward EJ, Schindler DE, Lewis B (2018) Demographic changes in Chinook salmon across the Northeast Pacific Ocean. Fish Fish 19(3):533-546. https://doi.org/10.1111/faf.12272

Oke K, Cunningham C, Westley P, Baskett M, Carlson S, Clark J, Hendry A, Karatayev V, Kendall N, Kibele J (2020) Recent declines in salmon body size impact ecosystems and fisheries. Nat Commun 11:4155. https://doi.org/10.1038/s41467-020-17726-z

Oke KB, Mueter FJ, Litzow MA (2022) Warming leads to opposite patterns in weight-at-age for young versus old age classes of Bering Sea walleye pollock. Can J Fish Aquat Sci 79(10):1655-1666. https://doi.org/10.1139/cjfas-2021-0315

Quinn TP (2005) The behavior and ecology of Pacific salmon and trout. Bethesda, MD

R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reimer AM (2013) Migratory timing and distribution of Kenai River Chinook salmon, 2010–2013, a report to the Alaska Board of Fisheries, 2014. Alaska Department of Fish and Game, Division of Sport Fish, Regional

Information Report 2A13-06, pp 1–76 (Available at https://www.adfg.alaska.gov/FedAidPDFs/RIR.2A.2013.06.pdf)

Ricker WE (1980) Causes of the decrease in age and size of chinook salmon *(Oncorhynchus tshawytscha)*. Can Tech Rep Fish Aquat Sci No. 944:1-30.

Robards MD, Rose GA, Piatt JF (2002) Growth and abundance of Pacific sand lance, *Ammodytes hexapterus*, under differing oceanographic regimes. Environ Biol Fishes 64:429-441. https://doi.org/10.1023/A:1016151224357

Roff DA (1983) An allocation model of growth and reproduction in fish. Can J Fish Aquat Sci 40(9):1395-1404. https://doi.org/10.1139/f83-161

Roff DA (1984) The evolution of life history parameters in teleosts. Can J Fish Aquat Sci 41(6):989-1000.

Roff DA (1992) The Evolution of life histories: theory and analysis. New York, NY

Roni P, Quinn TP (1995) Geographic variation in size and age of North American Chinook salmon. N Am J Fish Manag 15(2):325-345. https://doi.org/10.1577/1548-8675(1995)015<0325:GVISAA>2.3.CO;2

Ruggerone GT, Nielsen JL, Agler BA (2009) Linking marine and freshwater growth in western Alaska Chinook salmon *Oncorhynchus tshawytscha*. J Fish Biol 75(6):1287-1301. https://doi.org/10.1111/j.1095-8649.2009.02364.x

Scarnecchia DL (1979) Variation of scale characteristics of coho salmon with sampling location on the body. Prog Fish Cult 41(3):132-135. https://doi.org/10.1577/1548-8659(1979)41[132:VOSCOC]2.0.CO;2

Seung CK (2017) A multi-regional economic impact analysis of Alaska salmon fishery failures. Ecol Econ 138:22-30. https://doi.org/10.1016/j.ecolecon.2017.03.020

Sibly RM, Baker J, Grady JM, Luna SM, Kodric-Brown A, Venditti C, Brown JH (2015) Fundamental insights into ontogenetic growth from theory and fish. Proc Natl Acad Sci USA 112(45):13934-13939. https://doi.org/10.1073/pnas.1518823112

Siegel JE, Adkison MD, McPhee MV (2018) Changing maturation reaction norms and the effects of growth history in Alaskan Chinook salmon. Mar Ecol Prog Ser 595:187-202. https://doi.org/10.3354/meps12564

Siegel JE, McPhee MV, Adkison MD (2017) Evidence that marine temperatures influence growth and maturation of western Alaskan Chinook salmon. Mar Coast Fish 9(1):441-456. https://doi.org/10.1080/19425120.2017.1353563

Sigourney DB, Letcher BH, Obedzinski M, Cunjak RA (2008) Size-independent growth in fishes: patterns, models and metrics. J Fish Biol 72(10):2435-2455. https://doi.org/10.1111/j.1095-8649.2008.01830.x

Spangenberg D, Larsen DA, Gerstenberger R, Brun C, Beckman BR (2014) The effects of variation in rearing conditions on growth, smolt development, and minijack rate in yearling Chinook Salmon: a hatchery scale experiment. Trans Am Fish Soc 143(5):1220-1230. https://doi.org/10.1080/00028487.2014.931304

Speckman SG, Piatt JF, Minte-Vera CV, Parrish JK (2005) Parallel structure among environmental gradients and three trophic levels in a subarctic estuary. Prog Oceanogr 66(1):25-65. https://doi.org/10.1016/j.pocean.2005.04.001

Taylor EB (1991) A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquac 98(1-3):185-207. https://doi.org/10.1016/0044-8486(91)90383-I

Thorson JT, Minto C (2015) Mixed effects: a unifying framework for statistical modelling in fisheries biology. ICES J Mar Sci 72(5):1245-1256. https://doi.org/10.1093/icesjms/fsu213

Trudel M, Thiess ME, Bucher C, Farley E, MacFarlane RB, Casillas E, Fisher J, Morris JF, Murphy JM, Welch DW (2007) Regional variation in the marine growth and energy accumulation of juvenile Chinook salmon and coho salmon along the west coast of North America. In: CB Grimes, RD Brodeur, LJ Haldorson, SM McKinnell, (ed) Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. American Fisheries Society, New York, NY, pp 205–232 https://doi.org/10.47886/9781888569957

Tucker S, Trudel M, Welch DW, Candy JR, Morris JFT, Thiess ME, Wallace C, Beacham TD (2012) Annual coastal migration of juvenile Chinook salmon: static stock-specific patterns in a highly dynamic ocean. Mar Ecol Prog Ser 449:245-262. https://doi.org/10.3354/meps09528

van Rijn I, Buba Y, DeLong J, Kiflawi M, Belmaker J (2017) Large but uneven reduction in fish size across species in relation to changing sea temperatures. Global Change Biol 23(9):3667-3674. https://doi.org/10.1111/gcb.13688

Vøllestad LA, Peterson J, Quinn TP (2004) Effects of freshwater and marine growth rates on early maturity in male coho and Chinook salmon. Trans Am Fish Soc 133(3):495-503. https://doi.org/10.1577/T03-033.1

Von Bertalanffy L (1938) A quantitative theory of organic growth (inquiries on growth laws. II). Hum Biol 10(2):181-213.

Wang YG, Thomas MR (1995) Accounting for individual variability in the von Bertalanffy growth model. Can J Fish Aquat Sci 52(7):1368-1375. https://doi.org/10.1139/f95-132

Weisberg S, Spangler G, Richmond LS (2010) Mixed effects models for fish growth. Can J Fish Aquat Sci 67(2):269-277. https://doi.org/10.1139/F09-181

Wells BK, Grimes CB, Waldvogel JB (2007) Quantifying the effects of wind, upwelling, curl, sea surface temperature and sea level height on growth and maturation of a California Chinook salmon (*Oncorhynchus tshawytscha*) population. Fish Oceanogr 16(4):363-382. https://doi.org/10.1111/j.1365-2419.2007.00437.x

Wells BK, Santora JA, Schroeder ID, Mantua N, Sydeman WJ, Huff DD, Field JC (2016) Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Mar Ecol Prog Ser 552:271-284. https://doi.org/10.3354/meps11757

Williams EH, Shertzer KW (2005) Effects of fishing on growth traits: a simulation analysis. Fish Bull 103(2):392-403.

Yasumiishi EM, Farley Jr EV, Maselko J, Aydin KY, Kearney KA, Hermann AJ, Ruggerone GT, Howard KG, Strasburger WW (2020) Differential north–south response of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) marine growth to ecosystem change in the eastern Bering Sea, 1974–2010. ICES J Mar Sci 77(1):216-229. https://doi.org/10.1093/icesjms/fsz166

Tables

Table 1 Number of female Chinook salmon scales measured by population showing total by maturation age, and the count, number of missing years, oldest, and newest sampled return year

	Number of scales			Years sampled (age-5 fish)				Years sampled (age-6 fish)			
Population	Age 5	Age 6	Total	Count	Missing	Oldest	Newest	Count	Missing	Oldest	Newest
Unuk	491	492	983	23	6	1984	2012	26	5	1982	2012
Stikine	550	611	1,161	27	8	1981	2015	27	8	1981	2015
Taku	665	651	1,316	30	3	1981	2013	30	3	1981	2013
Chilkat	554	618	1,172	30	1	1983	2013	29	1	1984	2013
Copper	959	927	1,886	41	7	1968	2015	41	7	1968	2015
Deshka	413	310	723	19	0	1995	2013	19	0	1995	2013
Kenai, early	302	390	692	28	1	1986	2014	28	1	1986	2014
Kenai, late	251	443	694	28	1	1986	2014	28	1	1986	2014
Nushagak	498	1,331	1,829	26	4	1984	2013	34	2	1979	2014
Kuskokwim	410	837	1,247	37	3	1975	2014	38	2	1975	2014
Kogrukluk	384	757	1,141	32	4	1978	2013	34	2	1978	2013
Yukon	762	1,397	2,159	48	0	1966	2014	49	0	1966	2014
Andreafsky	441	767	1,208	33	0	1980	2012	33	0	1980	2012
Unalakleet	283	643	926	29	4	1981	2013	31	2	1981	2013
Total	6,963	10,174	17,137	431	42	1966	2015	447	34	1966	2015
Average	497	727	1,224	31	3	1981	2013	32	2	1980	2014

Table 2 Variance explained by parameters in a multivariate random-effects model (Equation 1) fit to age 5 and 6 female Chinook salmon scale increment growth measurements (freshwater and four years at sea) from 14 populations in Alaska, 1966–2015

Random effect	**SD**	**2.5% CI**	**97.5% CI**	**Number of Obs.**
Population, Increment	0.354	0.298	0.420	70
Population, Increment, Maturation age	0.085	0.071	0.104	126
Population, Increment, Calendar year	0.054	0.052	0.056	2,347
Residual	0.165	0.164	0.166	78717 (df)
Fixed effect	**Estimate**	**2.5% CI**	**97.5% CI**	**df**
Intercept	0.981	0.896	1.065	69.7

Abbreviations: SD = Standard deviation, CI = confidence interval, Obs. = observations, df = degrees of freedom.

Table 3 Population variation in increment growth and maturation-related growth (how much more fish that matured at age 5 grew than matured at age 6) estimated from a random-effects model fit to scale measurements from female Chinook salmon sampled from 14 populations in Alaska, 1966–2014

Population	Sum(Inc.)	Sum(MRG_g)
Unuk	-0.13	0.26
Stikine	-0.26	0.35
Taku	-0.26	0.30
Chilkat	-0.18	0.28
Copper	0.18	0.45
Deshka	-0.10	0.31
Kenai early	0.16	0.33
Kenai late	0.21	0.33
Nushagak	0.12	0.46
Kuskokwim	0.17	0.57
Kogrukluk	-0.03	0.33
Yukon	0.10	0.51
Andreafsky	-0.05	0.28
Unalakleet	0.08	0.44
Average	0	0.37

Figure captions

Fig. 1 Map of the 14 Chinook salmon populations in Alaska included in this study

Fig. 2 Measurements of individual freshwater increments on scales sampled from female Chinook salmon from 14 Alaska populations, 1966–2015. Fill colors are populations, ordered left to right from southeast to northwest alongshore coastal order. Filled areas represent 25th and 75th data percentiles (inter-quartile range, IQR), horizontal lines are medians, vertical whiskers represent 1.5x the IQR or data extent, and points are measurements outside of the whiskers (here and Fig. 3)

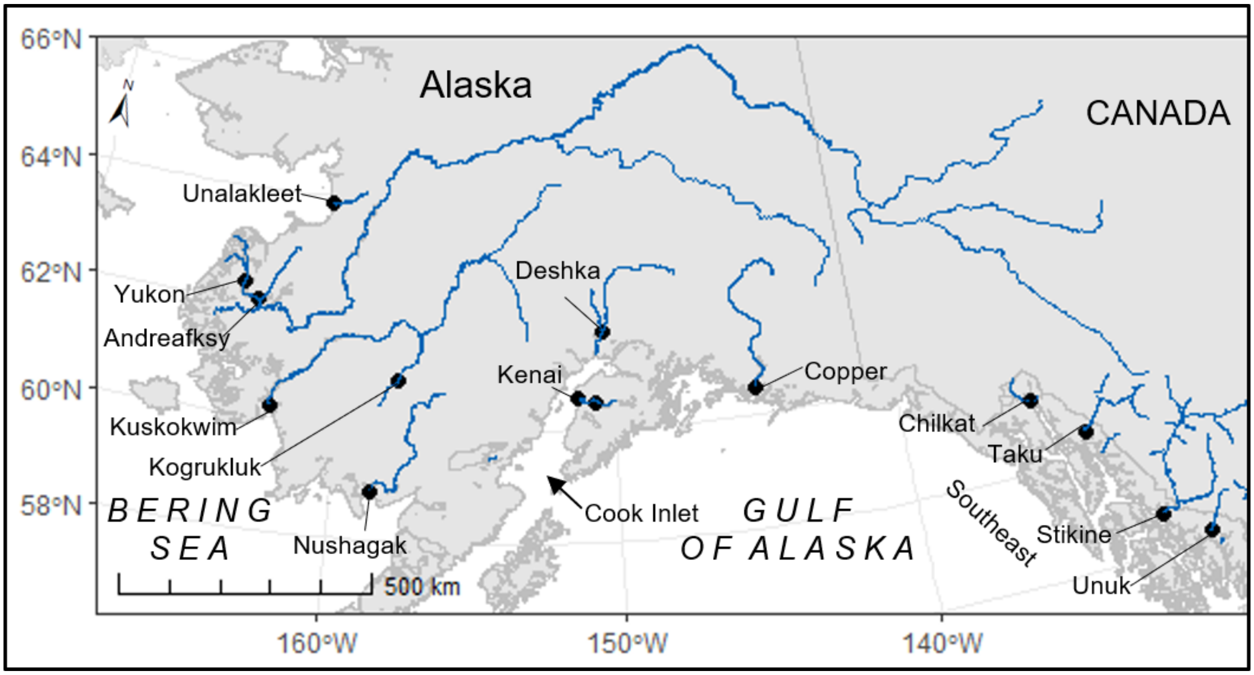
Fig. 3 Measurements of individual increments on scales for the first (SW1), second (SW2), third (SW4), and fourth (SW4) year at sea (groups, left to right) sampled from female Chinook salmon from 14 Alaska populations, 1966–2015. Fill colors are populations, ordered left to right from southeast to northwest alongshore coastal order

Fig. 4 Increment growth variation by population, estimated from a multivariate random-effects model of Chinook salmon scale measurements during fresh water and each year at sea (top to bottom, fresh water = FW, first (SW1), second (SW2), third (SW3), and fourth years at sea (SW4), from 14 populations (bar = 1 population, error bars = 1 standard error), 1966–2015. Values represent a population’s deviation from among-population average growth

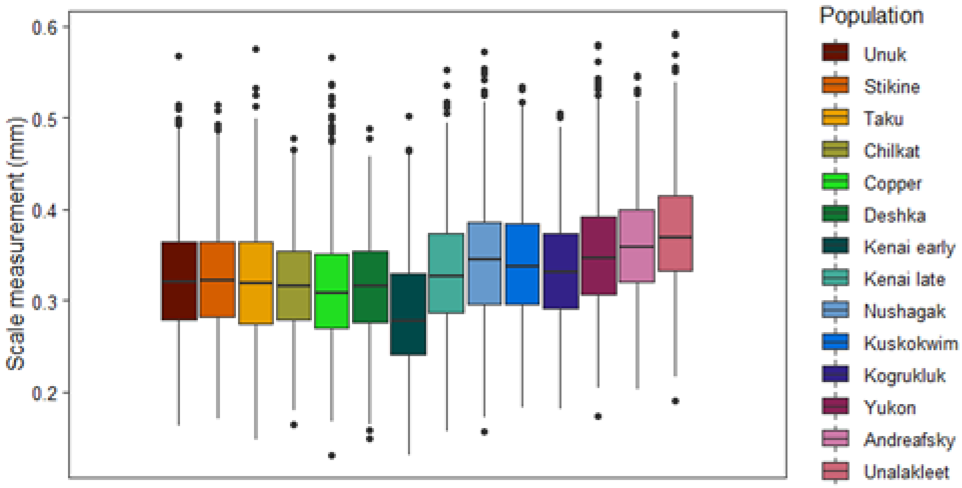
Fig. 5 Mean correlation in growth among brood years between growth increment pairs (right-hand labels, descriptions in manuscript) by age at maturity (columns), and population (bars). Whiskers are 25th and 75th percentiles

Fig. 6 Maturation-related growth by increment (fresh water = FW, first through third years at sea = SW1, SW2, and SW3, left to right) and population (color and order as in Fig. 3) estimated from a multivariate random-effects model for female Chinook salmon growth fit to scale measurements of 14 Alaska populations, 1966–2014. Positive values indicate that fish maturing at age 5 grew more during at a given increment than fish maturing at age 6. Error bar = 1 standard deviation

Fig. 1.

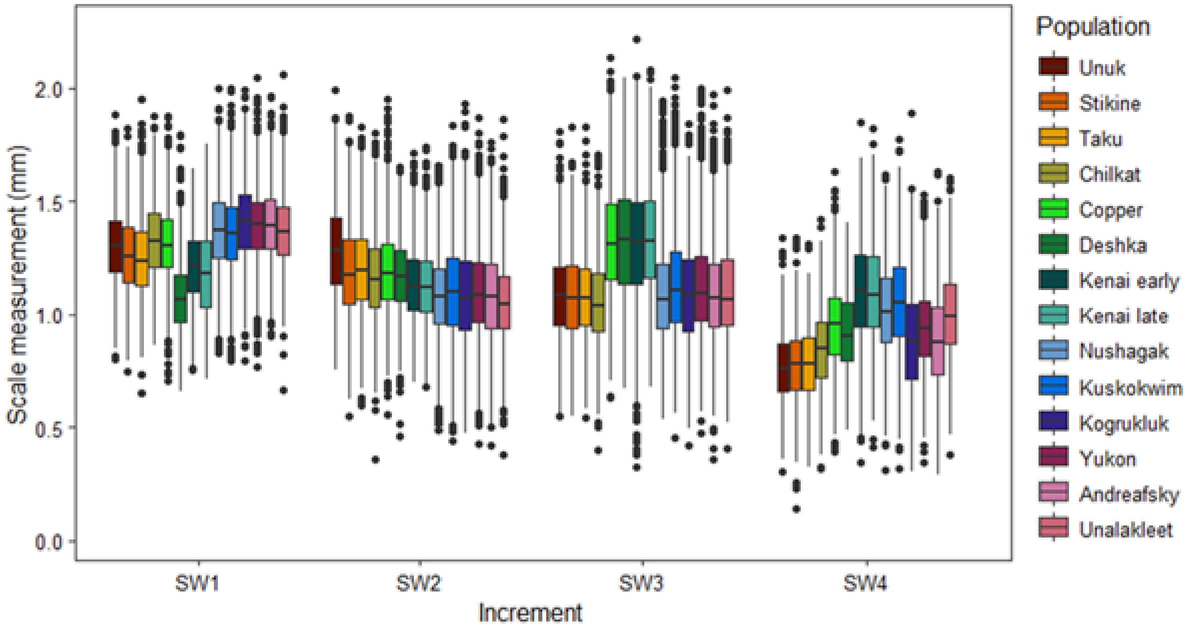

66°N
64°N
62°N
60°N
58°N
160°W
150°W
140°W
N
Alaska
CANADA
Unalakleet
Yukon
Andreafksy
Kuskokwim
Kogrukluk
Nushagak
Deshka
Kenai
Copper
Cook Inlet
Chilkat
Taku
Stikine
Unuk
Southeast
BERING SEA
GULF OF ALASKA
500 km

811 **Fig. 2**.

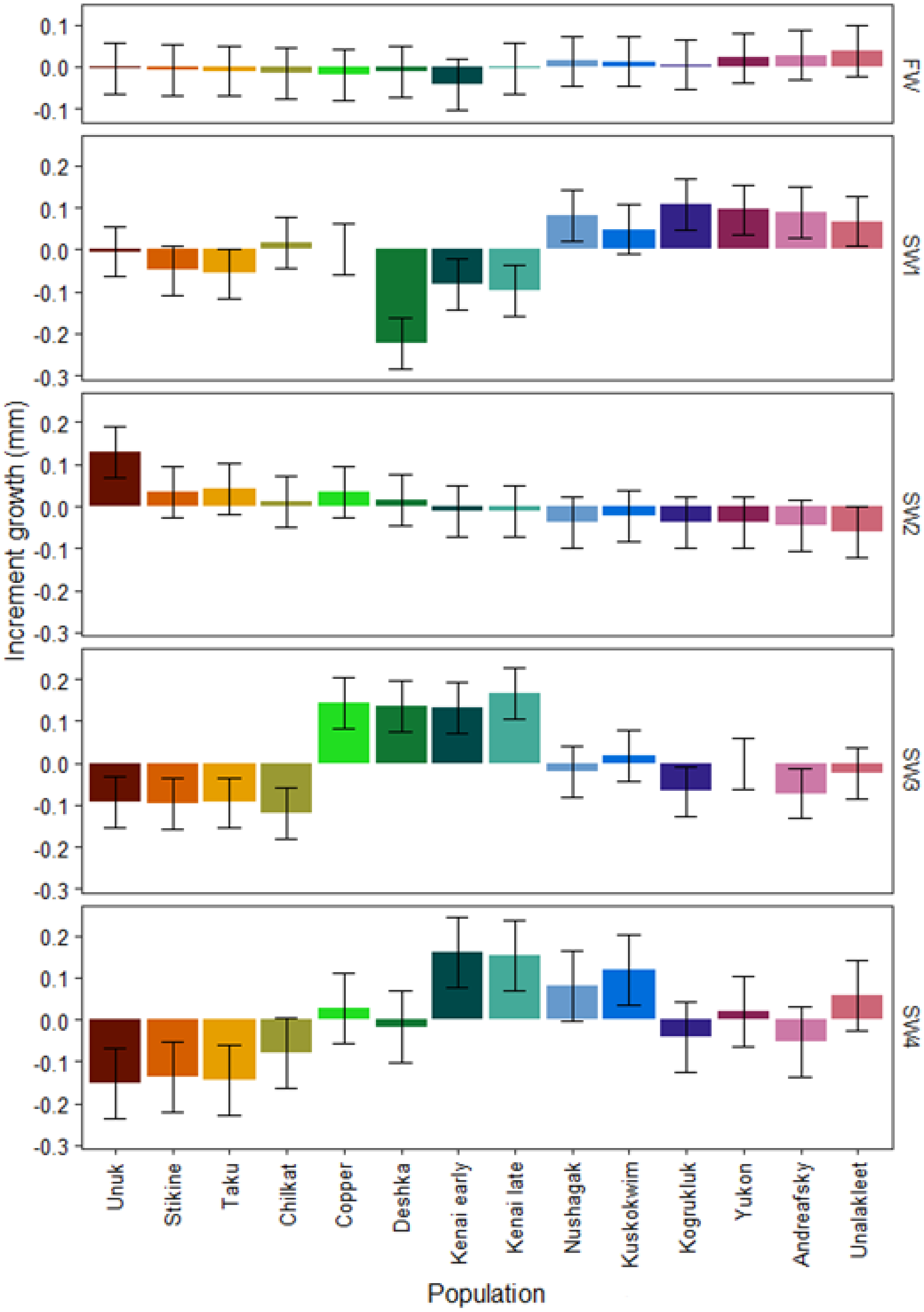

Scale measurement (mm)
0.6
0.5
0.4
0.3
0.2
Population
Unuk
Stikine
Taku
Chilkat
Copper
Deshka
Kenai early
Kenai late
Nushagak
Kuskokwim
Kogrukluk
Yukon
Andreafsky
Unalakleet

812

Fig. 3.


Scale measurement (mm)
2.0
1.5
1.0
0.5
0.0
SW1
SW2
SW3
SW4
Increment
Population
Unuk
Stikine
Taku
Chilkat
Copper
Deshka
Kenai early
Kenai late
Nushagak
Kuskokwim
Kogrukluk
Yukon
Andreafsky
Unalakleet

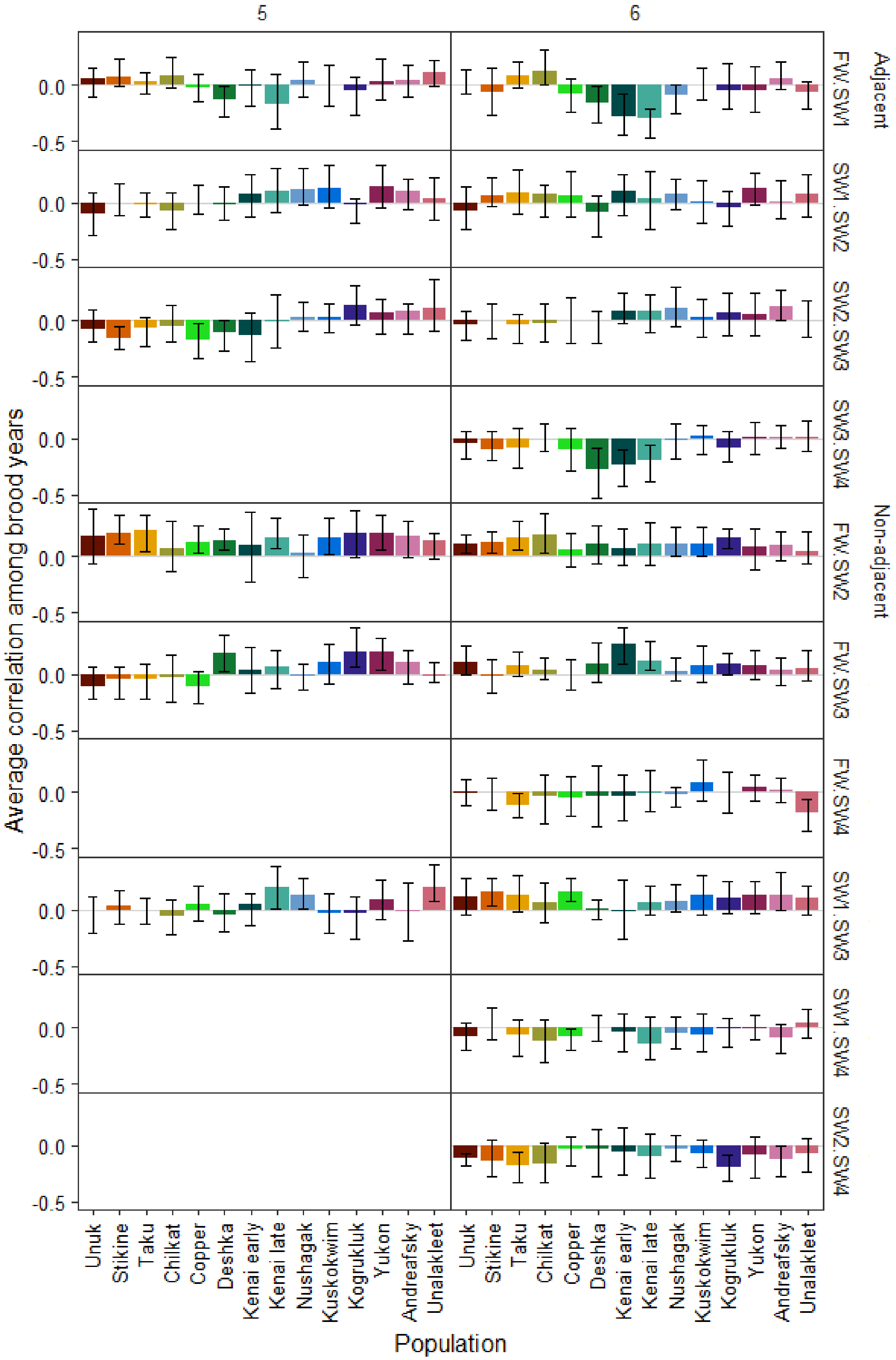
815 **Fig. 4**.



816

817

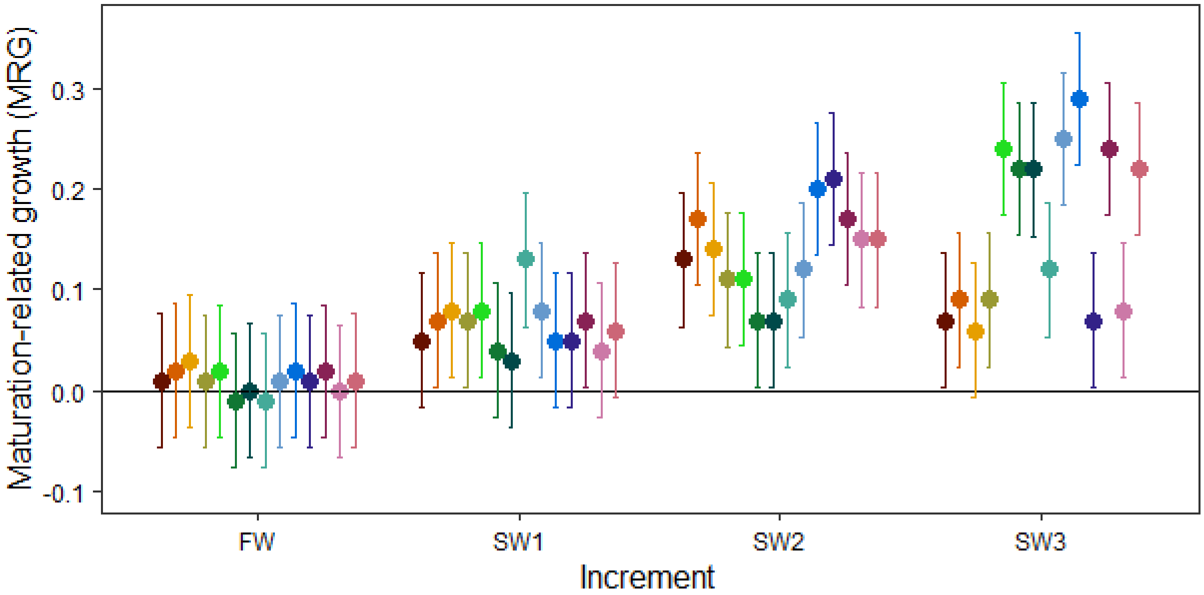
818 **Fig. 5.**



5
6
Adjacent
Non-adjacent
FW.SW1
SW1.SW2
SW2.SW3
SW3.SW4
FW.SW2
FW.SW3
FW.SW4
SW1.SW3
SW1.SW4
SW2.SW4
0.0
-0.5
Average correlation among brood years
Unuk
Stikine
Taku
Chilkat
Copper
Deshka
Kenai early
Kenai late
Nushagak
Kuskokwim
Kogrukluk
Yukon
Andreafsky
Unalakleet
Population

819

820 **Fig. 6**.

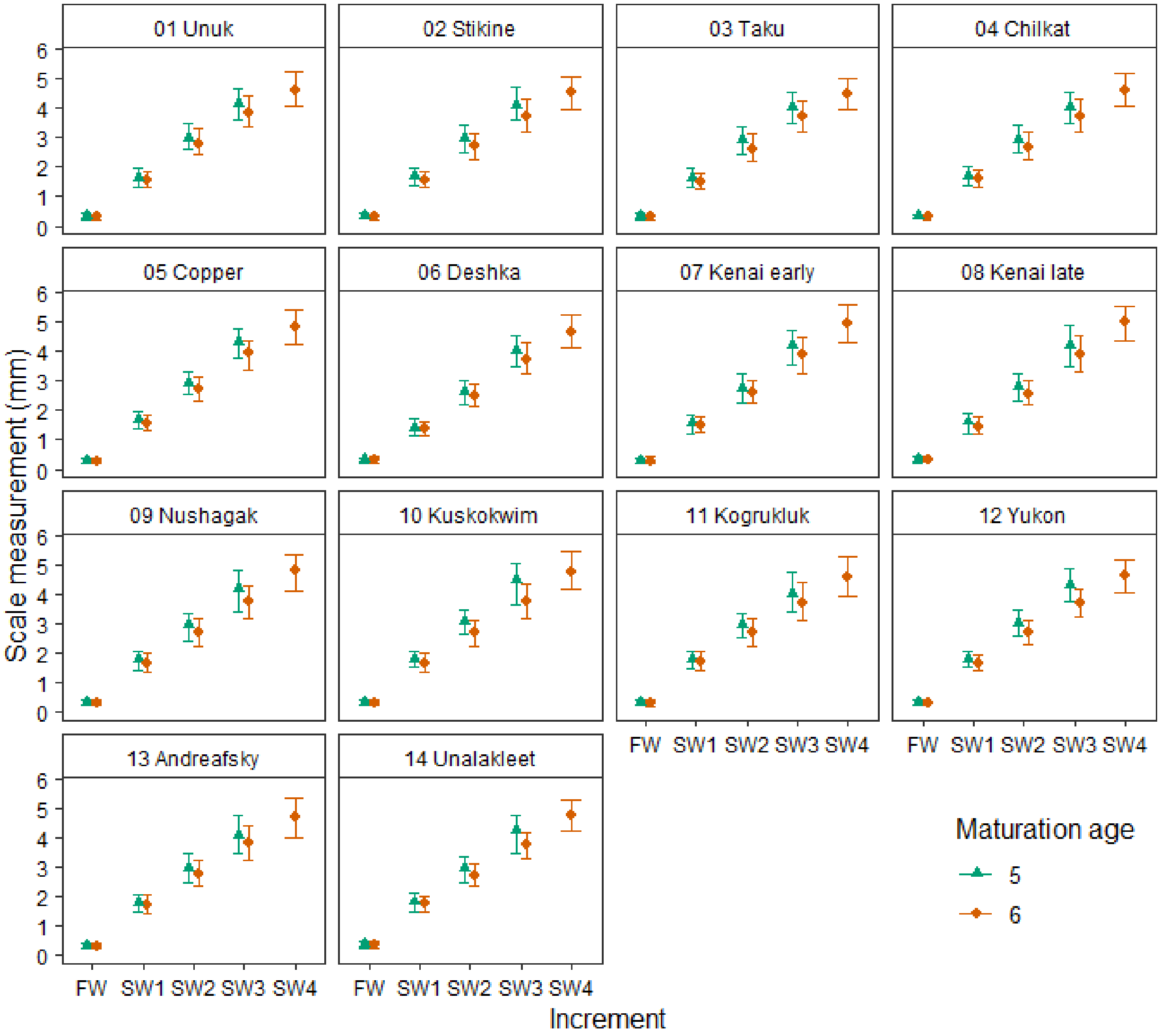


Maturation-related growth (MRG)
0.3
0.2
0.1
0.0
-0.1
FW
SW1
SW2
SW3
Increment

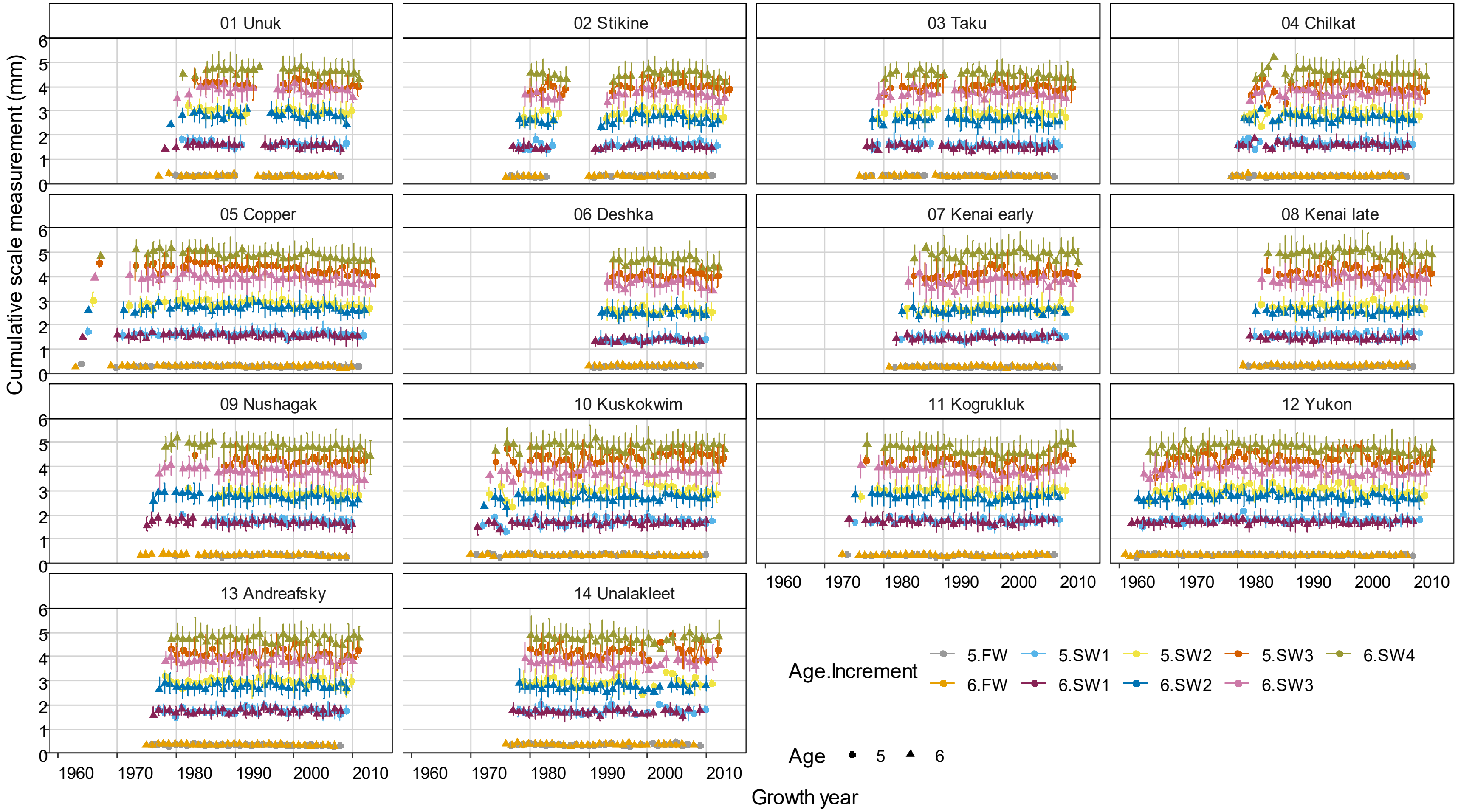
821

Supplementary Material for Wilson et al. - Spatial variation in age-specific growth of female Chinook salmon

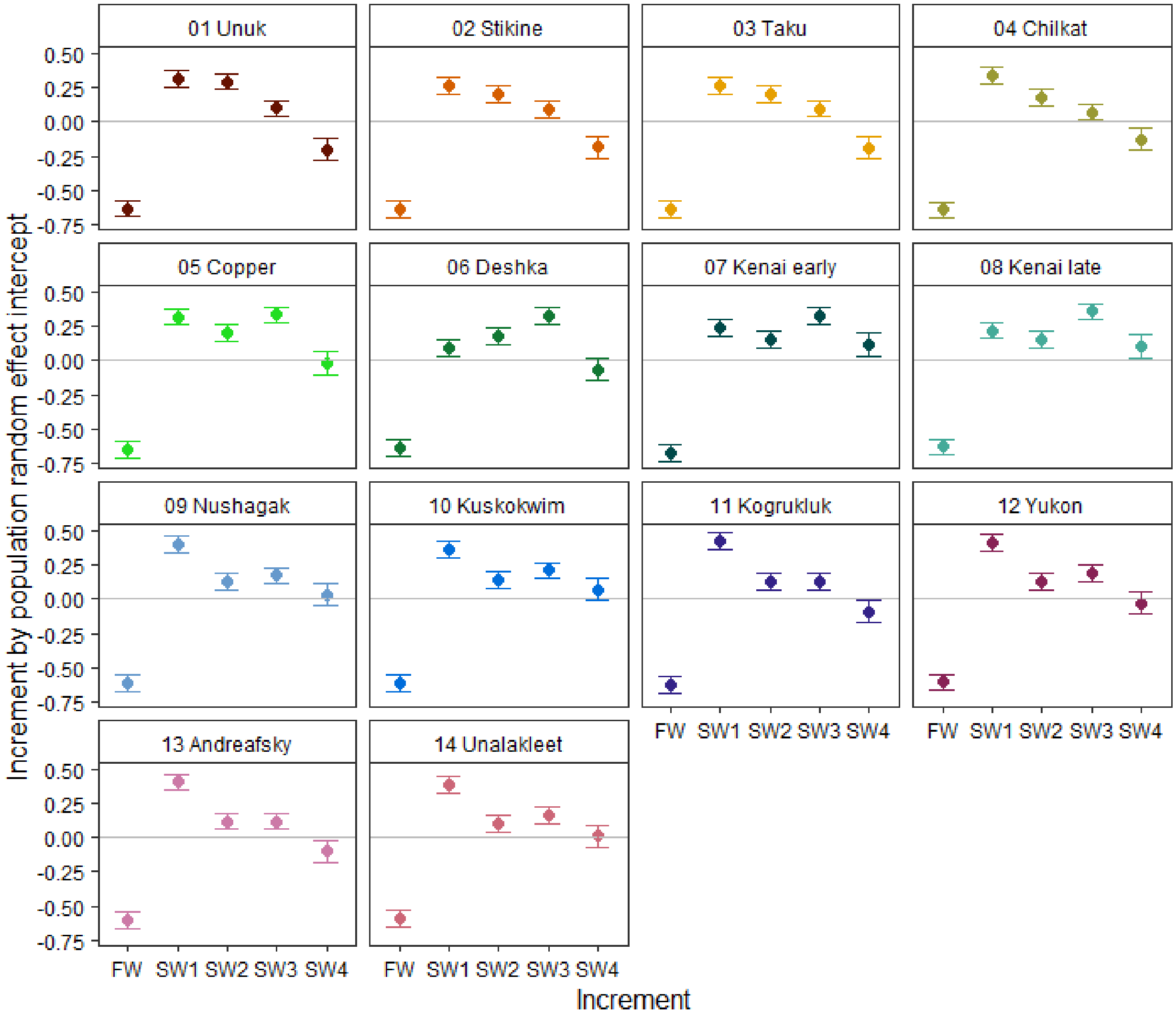
Supplemental Figure 1: Scale measurements by increment (FW, SW1, …, SW4) and maturation age (green = age 5, orange = age 6) for female Chinook salmon from 14 Alaska populations. Scale measurements for each increment are sum of growth for that increment and prior increments. Points are median and error bars indicate 90% quantiles of measurements by population from growth years 1993–2010.



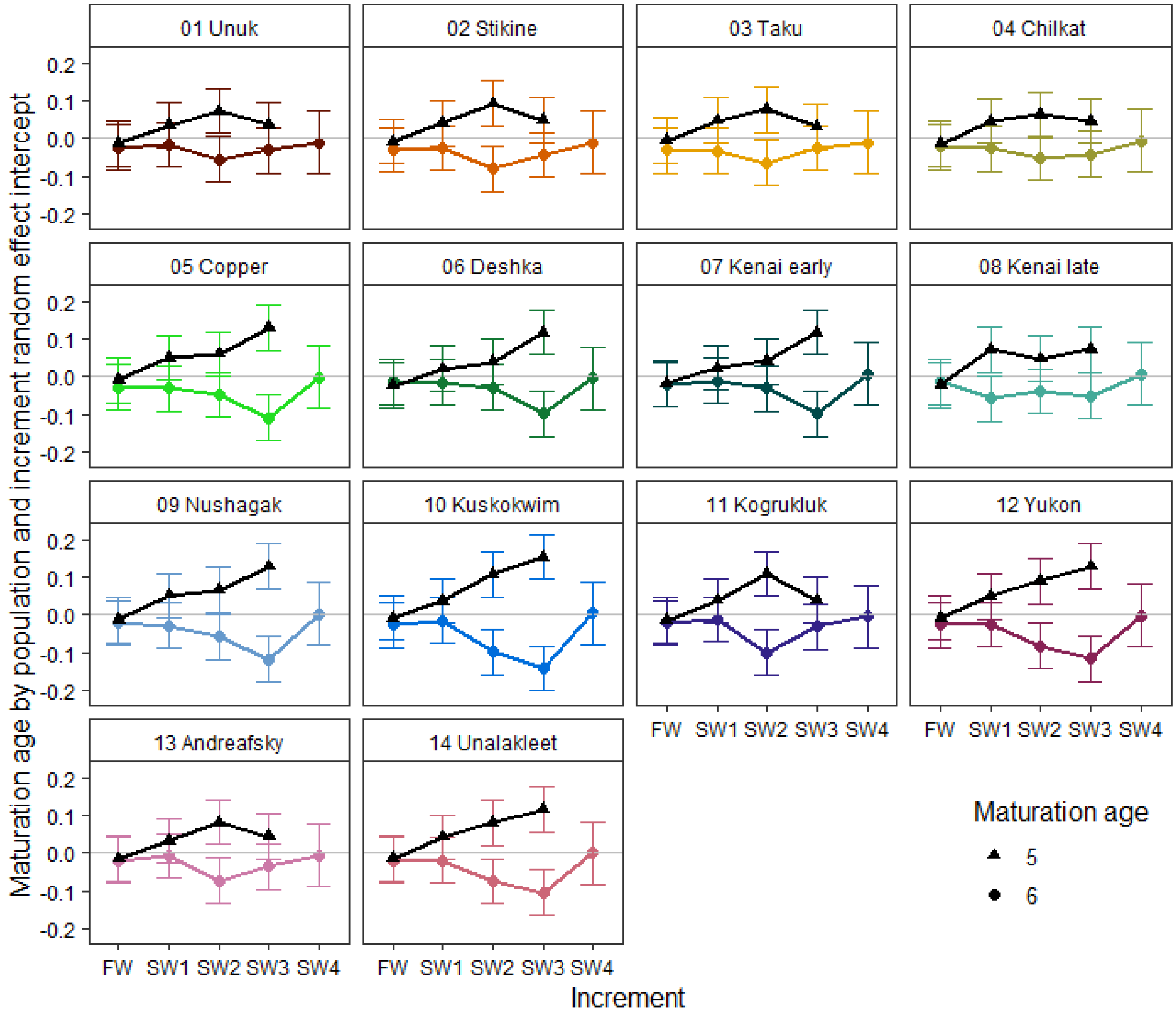
Supplemental Figure 2: Female Chinook salmon scale size during the year in fresh water (FW) and from the first (SW1) through fourth (SW4) years at sea for fish that matured at age 5 (circle) and 6 (triangle), growth years 1961–2014. Size is estimated from scale measurements shown in terms of fish length. Shaded bands are 90% quantiles.

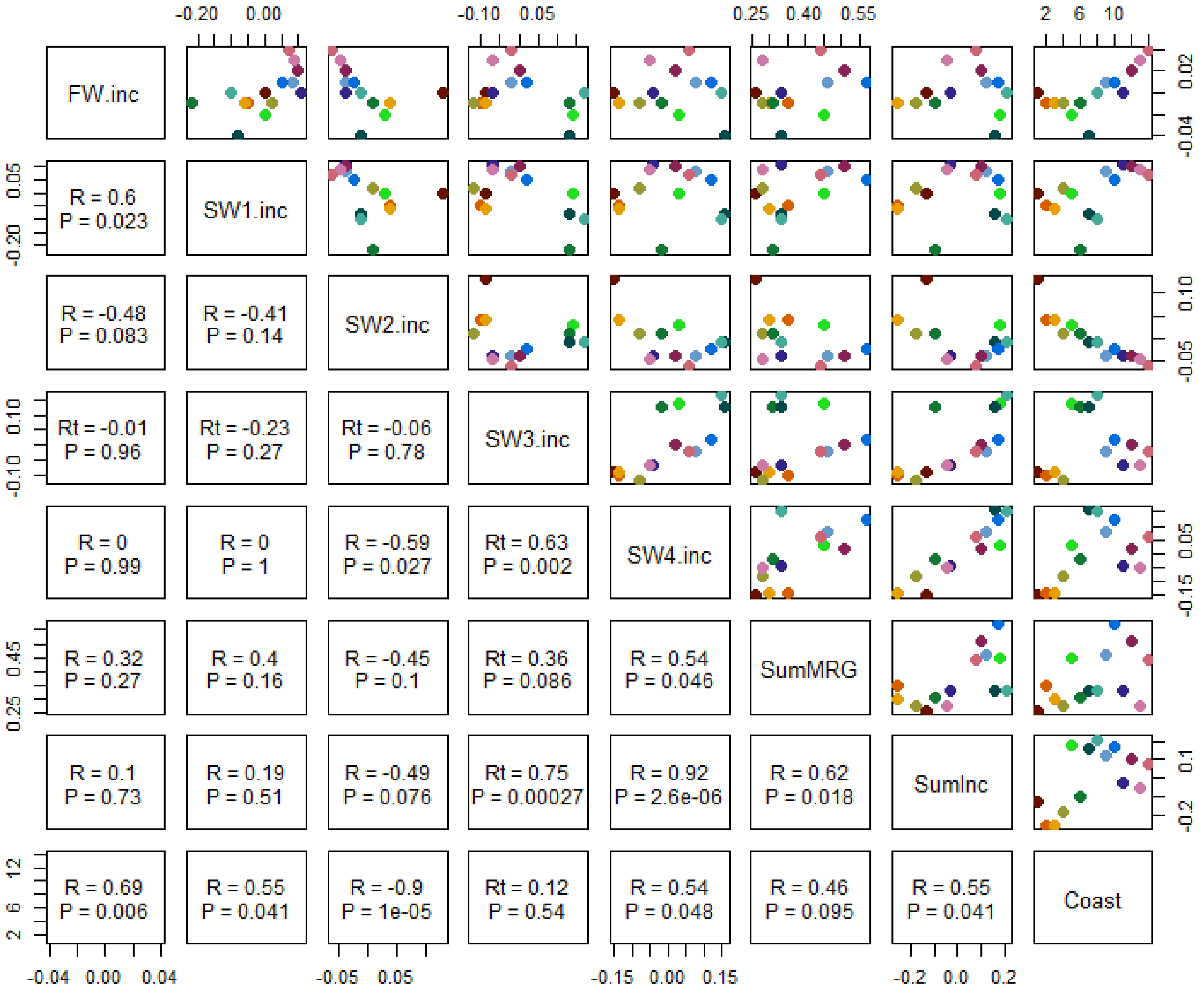


Supplemental Figure 3: Increment by population random effect intercepts, in a model for scale measurements from female Chinook salmon from 14 populations, 1965–2014. The mean among populations of increment effects were, FW = -0.63, SW1 = 0.32, SW2 = 0.17, SW3 = 0.19, and SW4 = -0.05. Other random effects included in the model were maturation age effects by population and calendar year effects by increment and population.



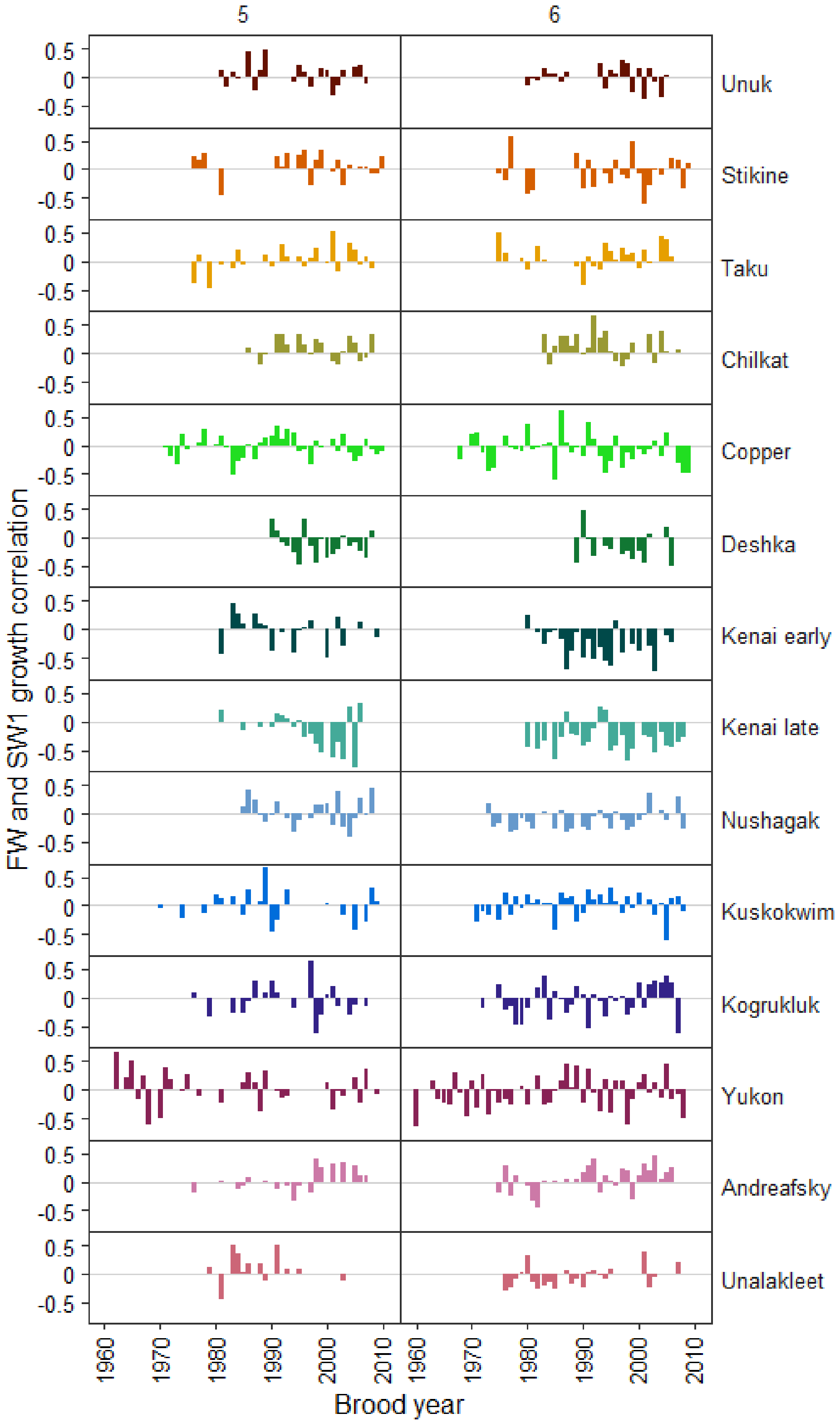
Supplemental Figure 4: Maturation age by increment and population random effect intercepts in a model for scale measurements from female Chinook salmon from 14 populations, 1965–2014. Other random effects included in the model were maturation age by population and calendar year by increment and population.



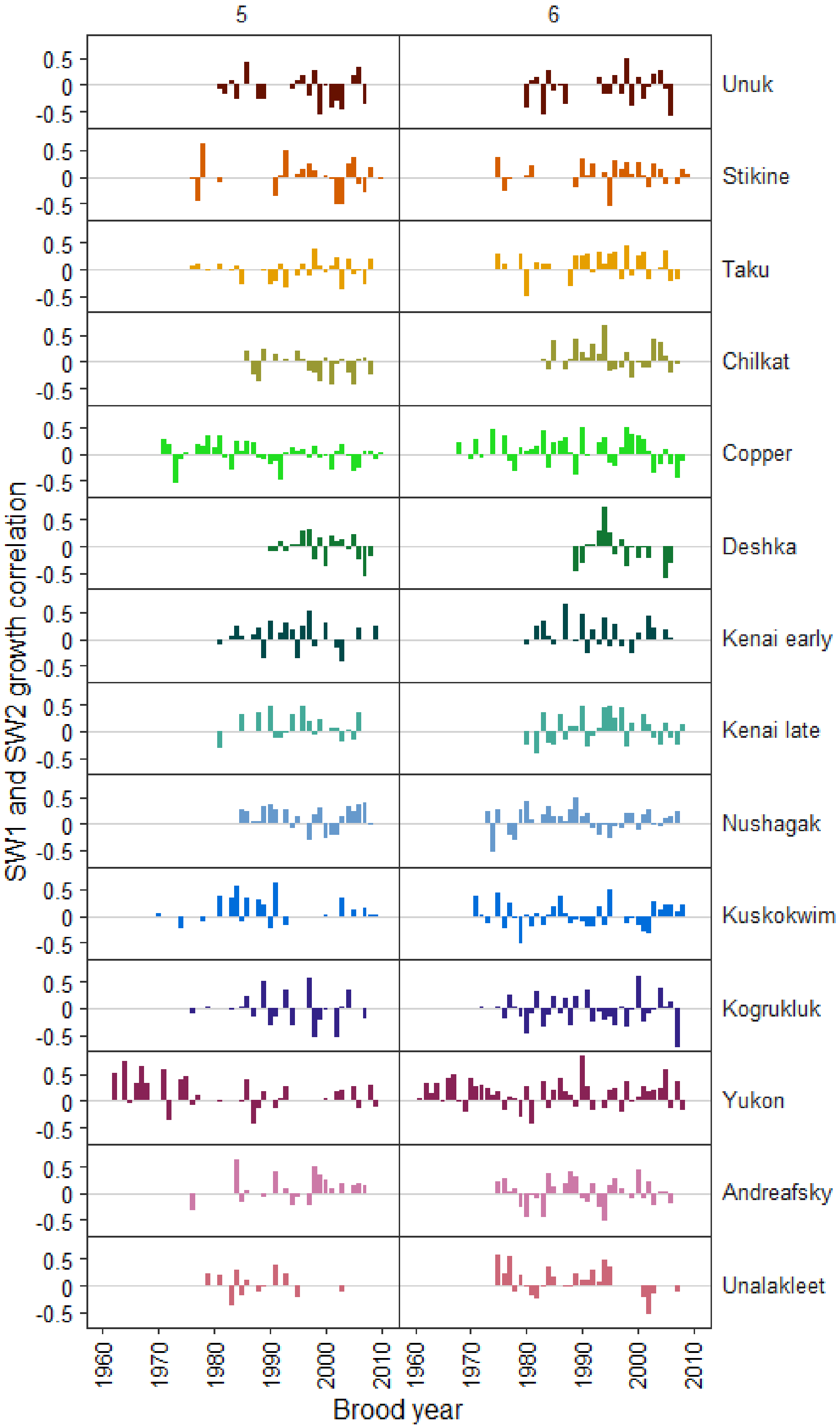


Supplemental Figure 5: Correlation matrix of increment growth, sum of maturation-related growth (SumMRG), sum of increment growth (SumInc), and river mouth alongshore coastal order from southeast to northwest (Coast) for female Chinook salmon from 14 populations in Alaska, 1965–2014 (populations listed in Supplemental Figure 1). Maturation-related growth were the incremental differences in growth of fish that matured at age 5 vs. age 6. Increment growth was a population's deviation from the mean increment growth among populations and included FW.inc, SW1.inc through SW4.inc. Maturation-related and increment growth were estimated in a random-effects model that also included a random effect for calendar year by increment and population. Correlation coefficients (R = Pearson, Rt = Kendall's tau) and *P* values are shown below the diagonal, and plotted values above the diagonal.

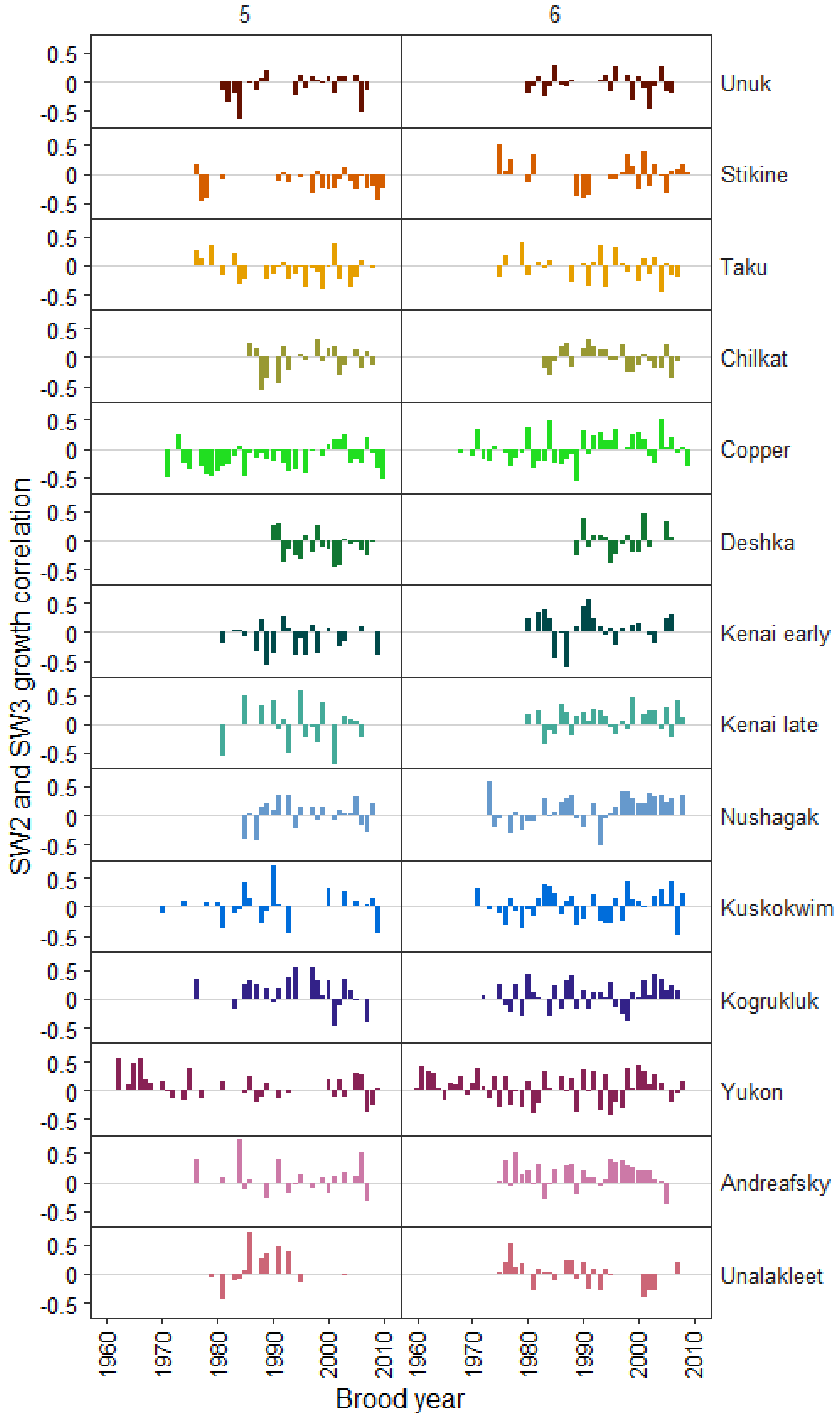
Supplemental Figure 6: Correlation between FW and SW1 growth of female Chinook salmon by age at maturity (age 5, left column; age 6, right column), population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



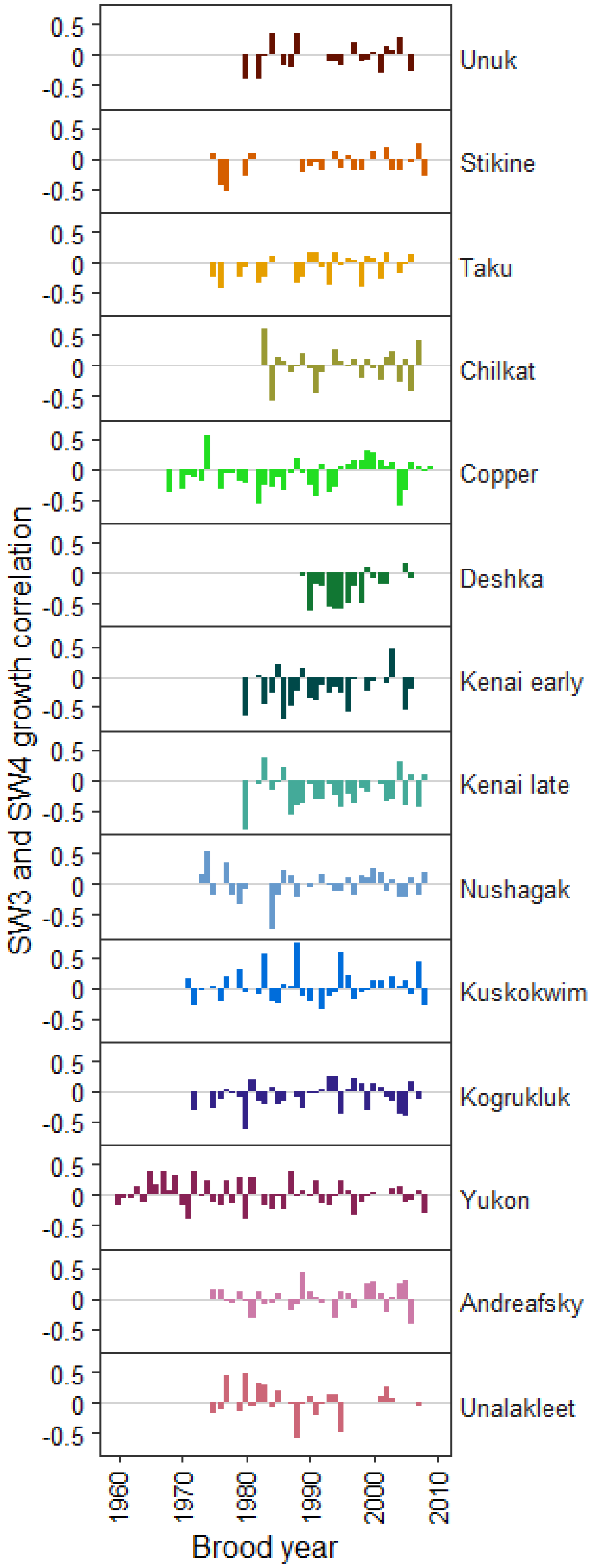
Supplemental Figure 7: Correlation between SW1 and SW2 growth of female Chinook salmon by age at maturity (age 5, left column; age 6, right column), population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



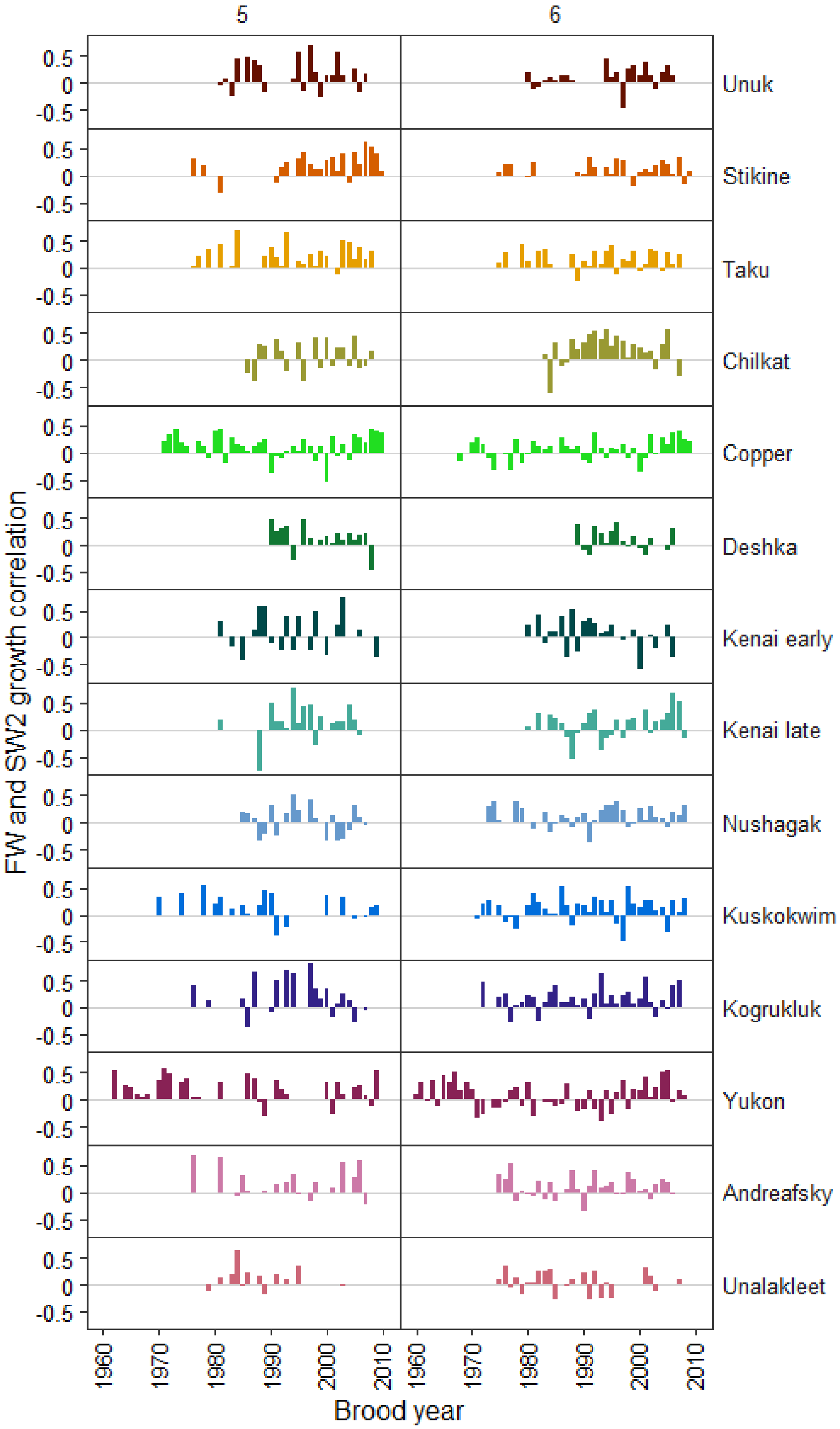
Supplemental Figure 8: Correlation between SW2 and SW3 growth of female Chinook salmon by age at maturity (age 5, left column; age 6, right column), population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



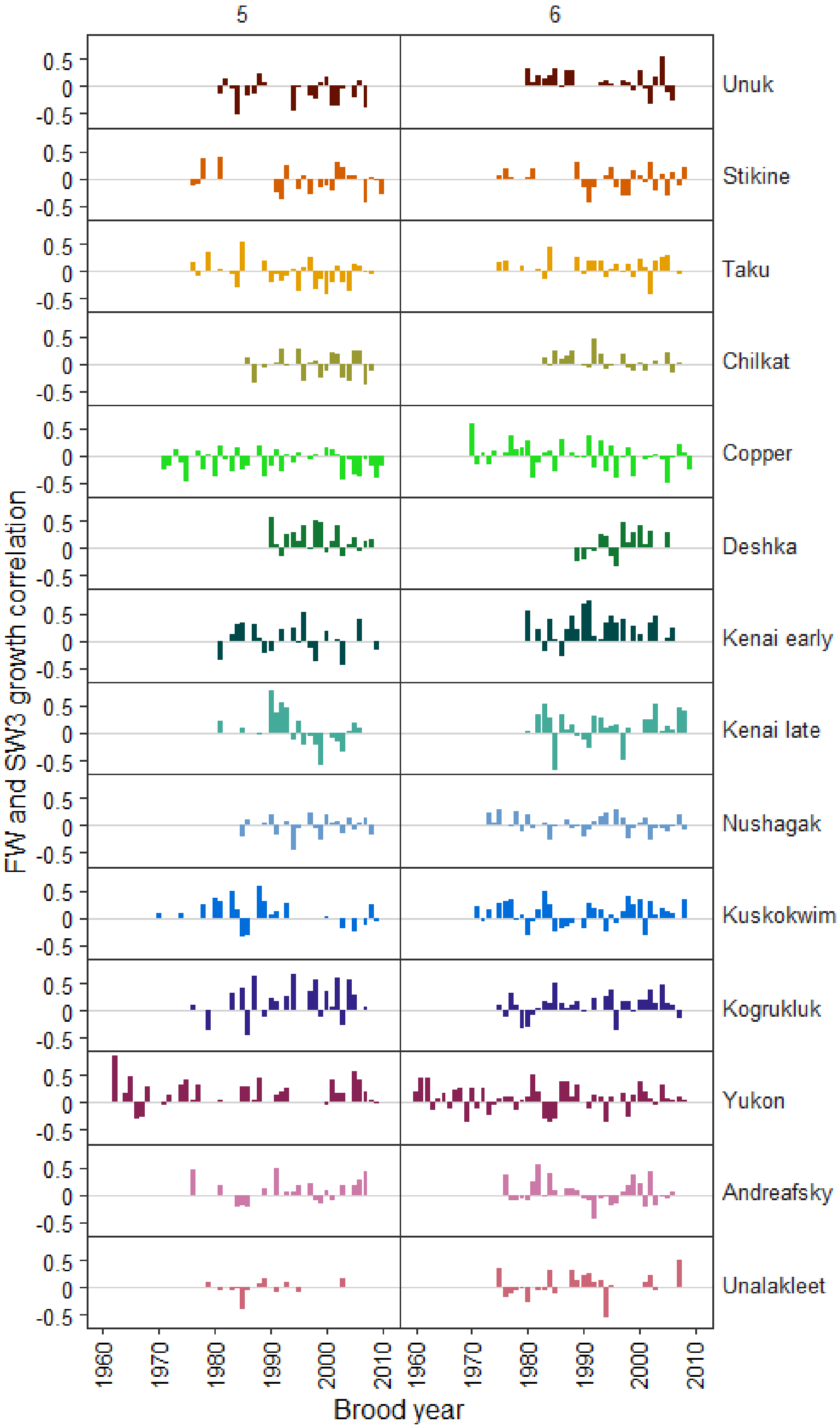
Supplemental Figure 9: Correlation between SW3 and SW4 growth for female Chinook salmon that matured at age 6, by population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



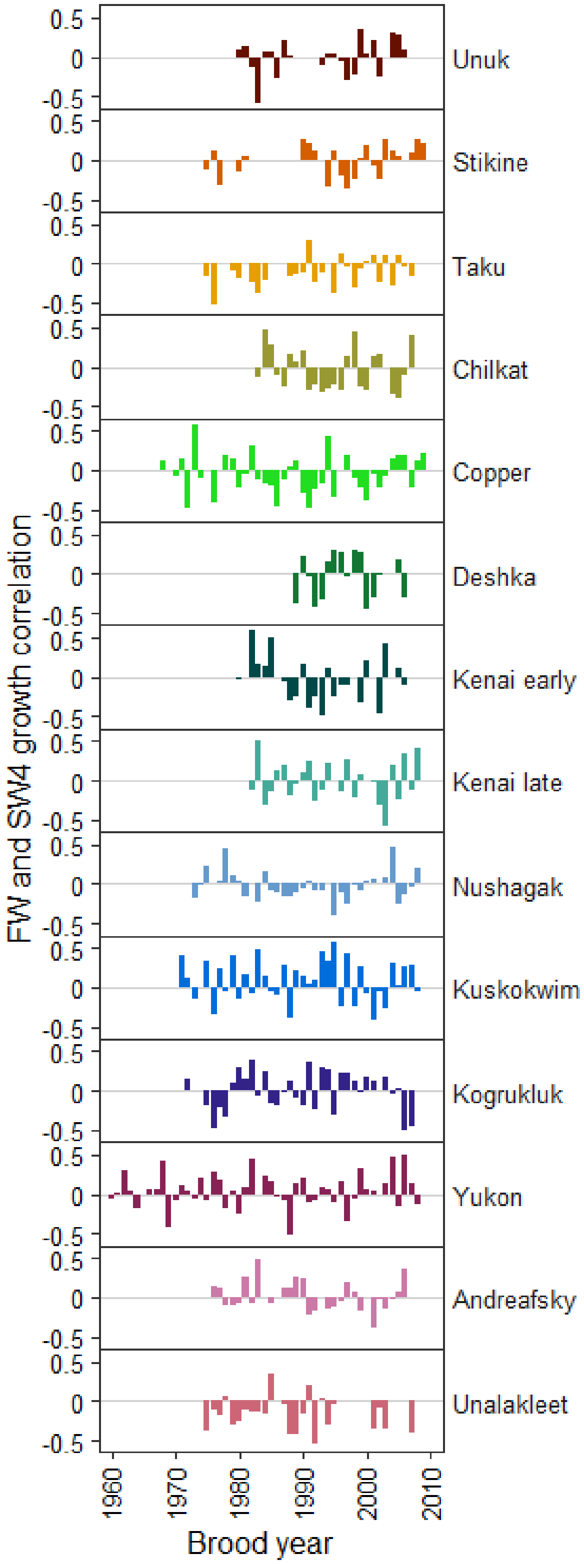
Supplemental Figure 10: Correlation between FW and SW2 growth of female Chinook salmon by age at maturity (age 5, left column; age 6, right column), population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



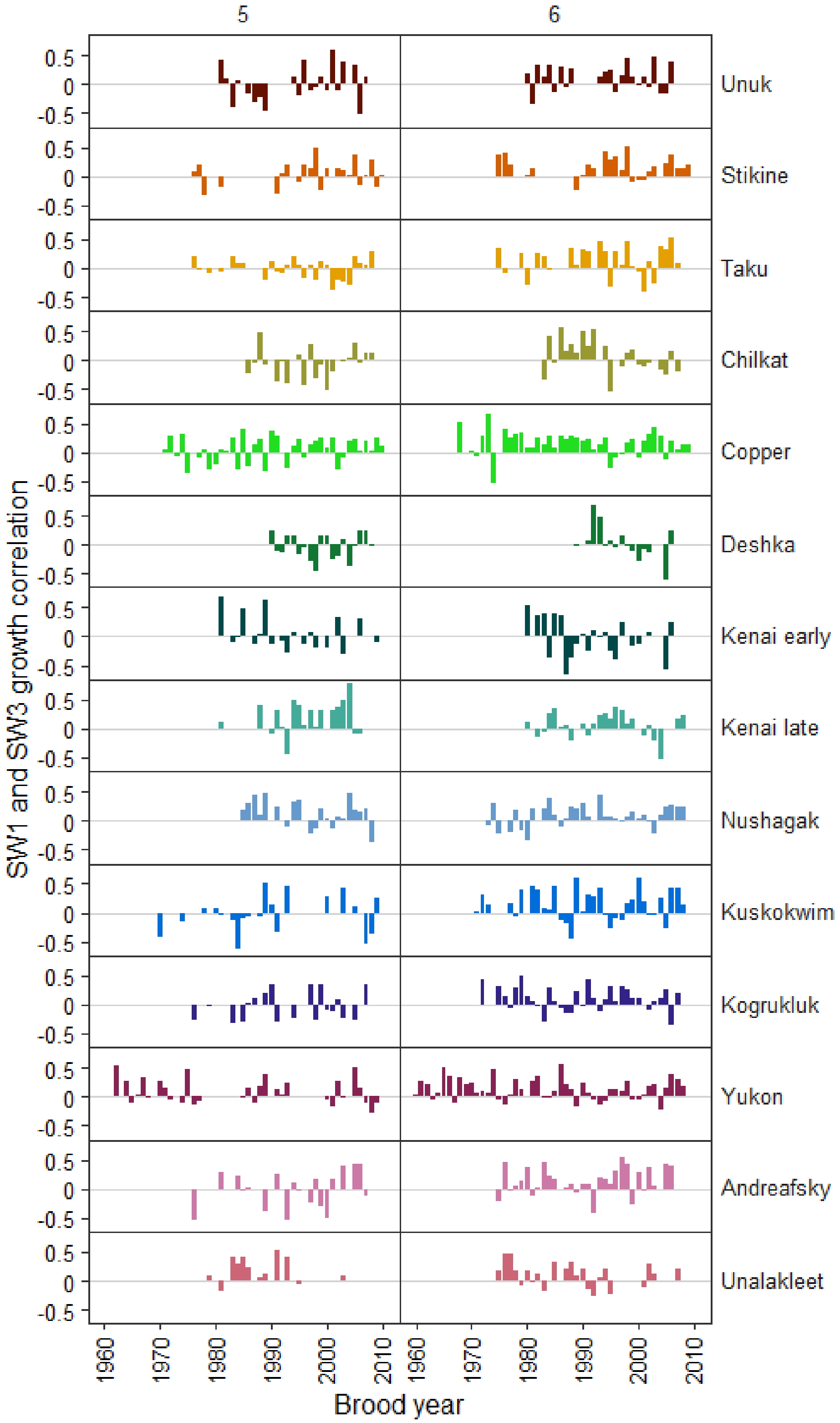
Supplemental Figure 11: Correlation between FW and SW3 growth of female Chinook salmon by age at maturity (age 5, left column; age 6, right column), population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



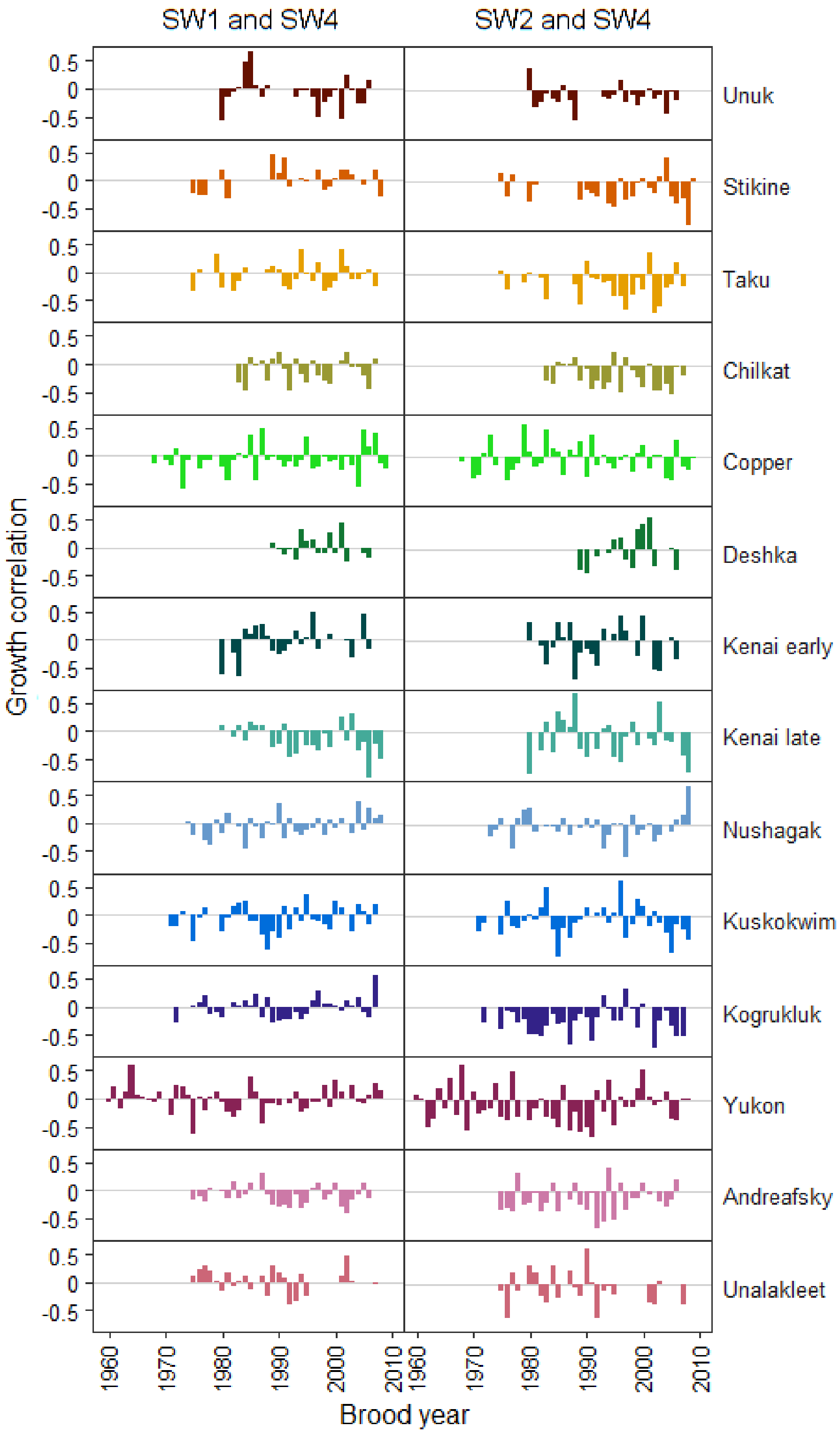
Supplemental Figure 12: Correlation between FW and SW4 growth for female Chinook salmon that matured at age 6, by population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



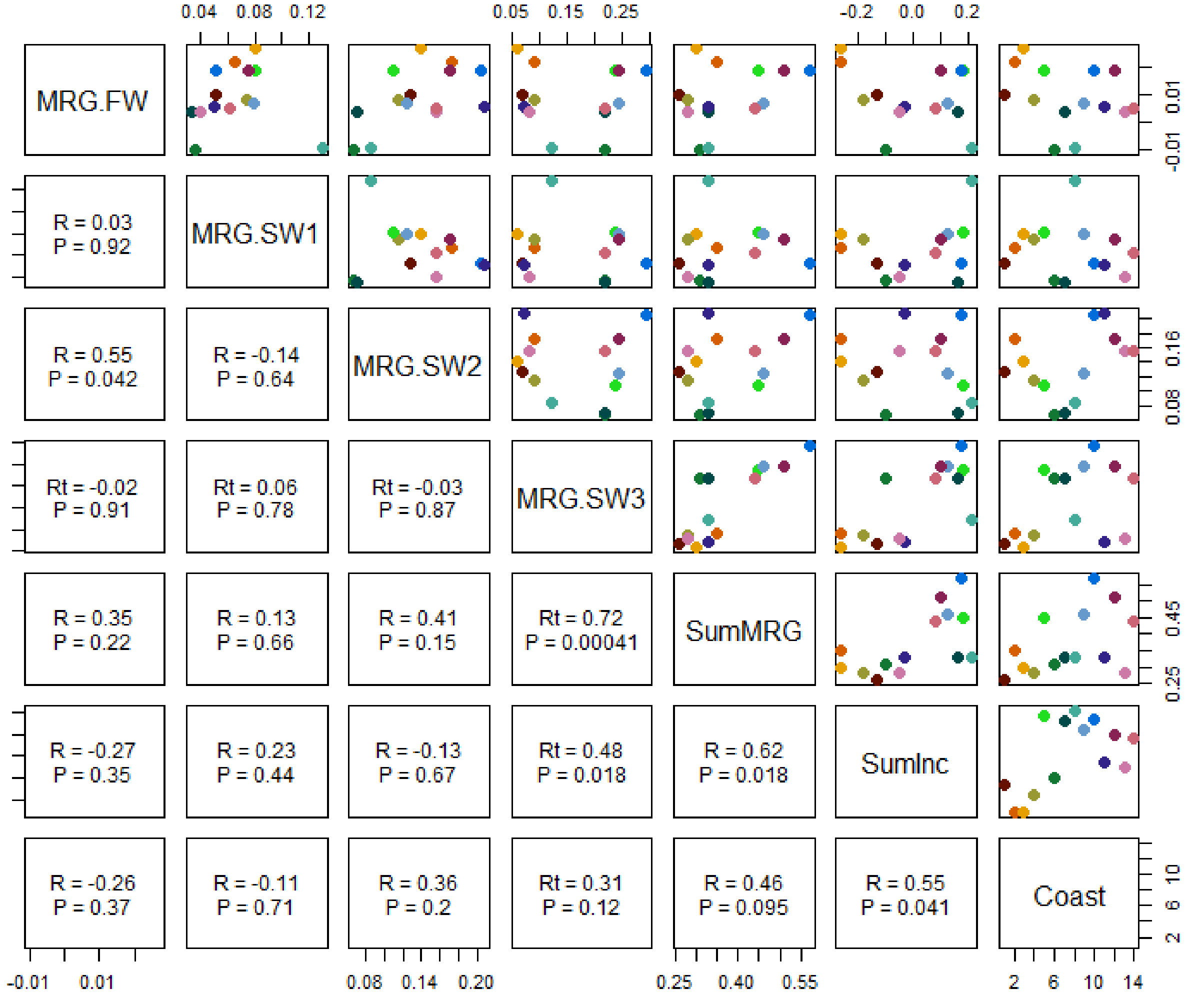
Supplemental Figure 13: Correlation between SW1 and SW3 growth of female Chinook salmon by age at maturity (age 5, left column; age 6, right column), population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



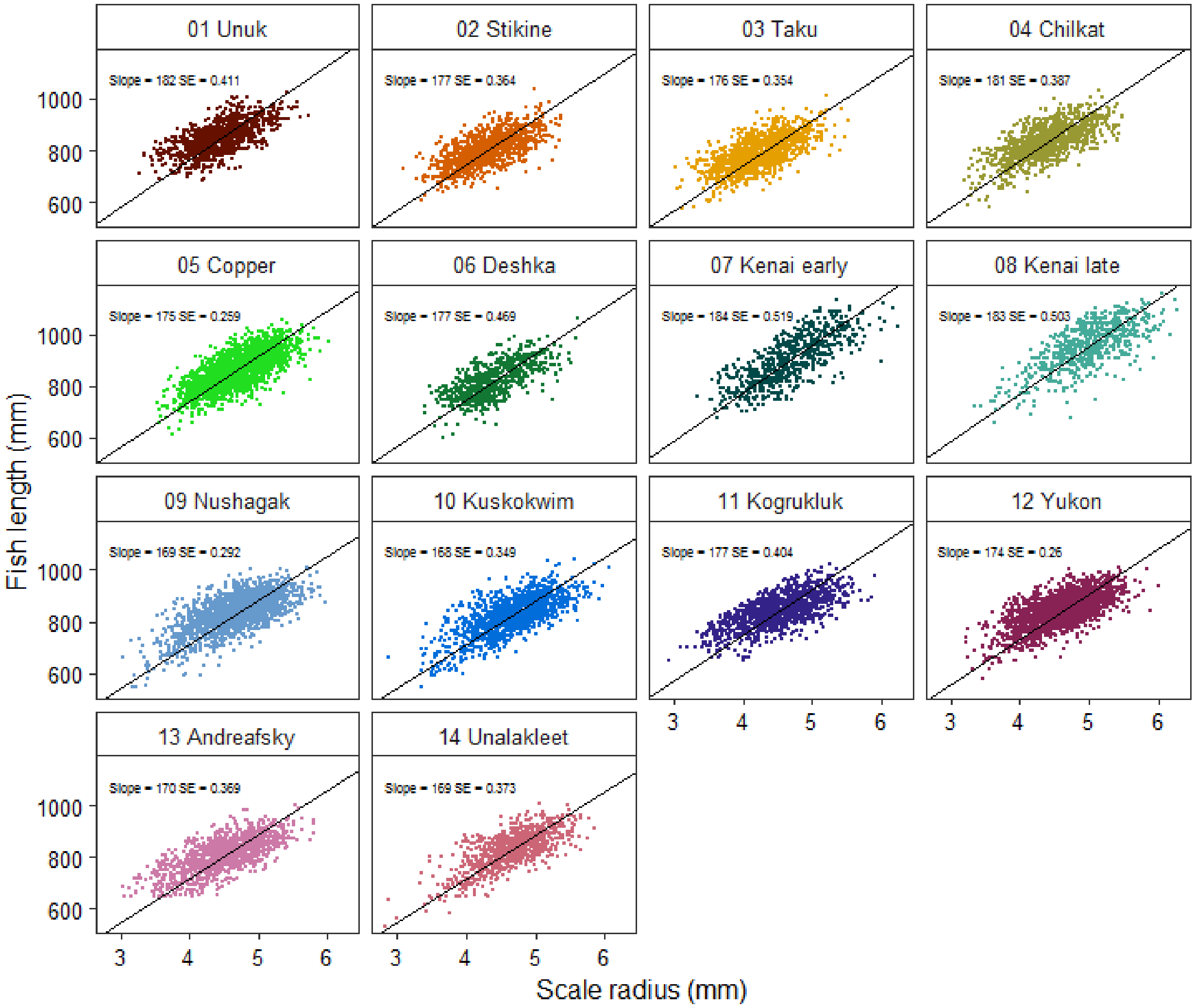
Supplemental Figure 14: Correlation between SW1 and SW4 growth (left column) and between SW2 and SW4 growth (right column) for female Chinook salmon that matured at age 6, by population (rows), and brood year (x-axis) for 14 populations in Alaska, sampled 1965–2014.



Supplemental Figure 15: Correlation matrix of maturation-related growth, sum of maturation-related growth (SumMRG), sum of increment growth (SumInc), and river mouth alongshore coastal order from southeast to northwest (Coast) for female Chinook salmon from 14 populations in Alaska, 1965–2014 (populations listed in Supplemental Figure 1). Maturation-related growth were the incremental (FW, SW1–SW3) differences in growth of fish that matured at age 5 vs. age 6 (MRG.FW, MRG.SW1, MRG.SW2, and MRG.SW3). Increment growth was a population's deviation from the mean increment growth among populations. Maturation-related and increment growth were estimated in a random-effects model that also included a random effect for calendar year by increment and population. Correlation coefficients (R = Pearson, Rt = Kendall's tau) and *P* values are shown below the diagonal, and plotted values above the diagonal.



Supplemental Figure 16: Slope estimated from a linear regression between scale radius (longest axis, mm) and fish length (mid-eye to fork of tail, mm) and the standard error of the slope (SE) from female Chinook salmon sampled from 14 populations in Alaska.



Supplemental Table 1: Salmon scale sampling project description and gear type used to sample Chinook salmon scales from 14 study populations in Alaska. For the project description, Com. = Commercial and Esc. = Escapement. Study populations are Unuk (UU), Stikine, (SK), Taku (TC), Chilkat (CT), Copper (CP), Deshka (DC), Kenai early (KE), Kenai late (KL), Nushagak (NC), Kuskokwim (BC), Kogrukluk (KO), Yukon (FY), Andreafsky (AY), and Unalakleet (UK).

		Population														
Project, Gear		UU	SK	TC	CT	CP	DC	KE[a]	KL[a]	NC	BC	KO	FY	AY	UK	Total
Com.	Drift gillnet			24		1,886				647	812		13			3,382
	Set gillnet			13						33	59		454		554	1,113
	Not recorded									5						5
Test	Drift gillnet			16							254		50			320
	Set gillnet												1,647		282	1,929
	Hand troll														1	1
Subsistence Harvest															8	8
Esc.	Beach seine									33				9	43	85
	Drift gillnet		900	3	656					1,049						2,608
	Set Gillnet	553	9	165	70											797
	Fish wheel			757	266											1,023
	Sport hook and line	62														62
	Handpicked	225	147	18	67					15				423		895
	Dip net	35			62											97
	Weir	108	56	109	21		383				122	1,141		767	37	2,744
	Snag				30											30
	Not recorded		49	67			340			47				9		512
	Set gillnet							665	583							1,248
	Handpicked														1	1
	Spawning grounds			144												144
Sport	Set gillnet (marine)												1			1
Sport	Hook and line (fresh water)							41	97							138
Population total		983	1,161	1,316	1,172	1,886	723	706	680	1,829	1,247	1,141	2,165	1,208	926	17,143

[a] Most years were >80% escapement samples. Exceptions in the early run were 85% sport-sampled in 1986, 45% in 2004, 23% in 2006, and 40% in 2010. Exceptions in the late run were 100% sport in 1986, 27% in 1990, 33% in 1993, 100% in 2004, and 27% in 2009. Length distributions of fish with scales sampled in 1986 and 2004 were not different when compared to previous and next year (KS test P > 0.05) or with sport-sampled scales were compared to escapement-sampled scales within the same year in all years (KS test P > 0.05).

Supplemental Table 2: Average percent of females by age class sampled in the return for 14 Chinook salmon populations in Alaska. Years sampled are in manuscript Table 1. Sampling projects are described in Supplemental Table 1.

	Percent of female return		
Population	Age 4	Ages 5 and 6	Age 7
Unuk	6.9%	91.7%	1.1%
Stikine	2.5%	96.4%	0.9%
Taku	8.9%	90.2%	0.7%
Chilkat	1.4%	97.0%	1.6%
Copper	7.5%	90.8%	1.6%
Deshka	10.5%	89.3%	0.2%
Kenai early	3.6%	93.7%	2.7%
Kenai late	4.2%	91.4%	4.4%
Nushagak	10.7%	86.2%	3.1%
Kuskokwim	2.7%	89.7%	7.5%
Kogrukluk	0.1%	93.5%	6.4%
Yukon	0.7%	90.0%	9.2%
Andreafsky	7.4%	87.4%	5.2%
Unalakleet	7.4%	82.7%	5.7%
Average	5.3%	90.7%	3.6%

Supplemental Table 3: Random effect models showing the difference in AIC_C (ΔAIC_C) relative to the model with the lowest AIC_C. Header rows are: random effects (RE, intercepts) included in each model, variance explained by the random effect (Var) and the standard deviation (SD) of the RE variance. Also shown is the percent of variation explained by fish. Models are sorted top to bottom from lowest to highest ΔAIC_C.

Model	ΔAIC_C	RE	Var	SD	RE	Var	SD	RE	Var	SD	RE	Var	SD	% Fish
1	0	Pop:Inc:Time	0.0029	0.0540	Pop:Inc:Mat	0.0073	0.0852	Inc:Pop	0.1252	0.3539				
2	1.29	Pop:Inc:Time	0.0029	0.0540	Pop:Inc:Mat	0.0073	0.0851	Inc:Pop	0.1252	0.3538	Fish	0.0001	0.0079	0.05%
3	133.35	Pop:Inc:Time	0.0029	0.0540	Pop:Inc:Mat	0.1431	0.3783							
4	134.65	Pop:Inc:Time	0.0029	0.0540	Pop:Inc:Mat	0.1431	0.3783	Fish	0.0001	0.0079				0.04%
5	2323.38	Pop:Time	0.0011	0.0332	Pop:BY	0.0004	0.0188	Pop:Inc:Mat	0.0072	0.0849	Inc:Pop	0.1260	0.3550	
6	3380.15	Pop:Inc:Mat	0.0074	0.0861	Inc:Pop	0.1262	0.3552	Time	0.0005	0.0227				
7	3614.03	Pop:BY	0.0005	0.0225	Pop:Inc:Mat	0.0072	0.0851	Inc:Pop	0.1259	0.3548				
8	4027.08	Pop:Inc:Mat	0.0074	0.0858	Inc:Pop	0.1258	0.3547	BY	0.0002	0.0154				
9	4279.36	Pop:Inc:Mat	0.0072	0.0849	Inc:Pop	0.1259	0.3548							
10	4413.29	Pop:Inc:Mat	0.1439	0.3794										
11	7145.63	Inc:Pop	0.1259	0.3548	Mat	0.0047	0.0688							
12	7258.18	Pop:Inc:Time	0.0032	0.0568	Inc:Pop	0.1255	0.3543	Fish	0.0014	0.0380				1.11%
13	7527.18	Pop:Inc:Time	0.0032	0.0569	Inc:Pop	0.1256	0.3545							
14	11156.72	Inc:Pop	0.1265	0.3557	Time	0.0005	0.0223							
15	11610.29	Inc:Pop	0.1262	0.3553	Fish	0.0015	0.0384							1.15%
16	11640.87	Inc:Pop	0.1263	0.3553	BY	0.0002	0.0158							
17	11847.55	Inc:Pop	0.1263	0.3554										
18	14603.36	Inc:Pop:Time	0.1288	0.3588	Fish	0.0014	0.0379							1.11%
19	14870.56	Pop:Inc:Time	0.1287	0.3588										
20	18169.53	Inc:Time	0.1198	0.3461	Mat	0.0048	0.0691							
21	21296.14	Inc:Time	0.1201	0.3465	Pop	0.0006	0.0239							
22	22308.13	Inc:Time	0.1201	0.3466	Fish	0.0008	0.0288							0.68%
23	22367.85	Inc:BY	0.1201	0.3466										
24	22367.85	Inc:Time	0.1201	0.3466										

-Continued-

Supplemental Table 3.-Continued.

Model	ΔAIC$_C$	RE	Var	SD	RE	Var	SD	RE	Var	SD	RE	Var	SD	% Fish
25	22904.84	Inc	0.1485	0.3854	Time	0.0006	0.0246							
26	23374.46	Inc	0.1480	0.3847	BY	0.0003	0.0182							
27	23591.79	Inc	0.1480	0.3847	Fish	0.0007	0.0266							0.47%
28	23632.11	Inc	0.1480	0.3847										
29	134737.9	Pop:Mat:Time	0.0227	0.1508										
30	136667.15	Pop:Time	0.0136	0.1168										
31	137179.31	Time:Mat	0.0091	0.0954										
32	137847	Mat	0.0048	0.0694										
33	138014.93	BY:Mat	0.0028	0.0527										
34	138346.37	Time	0.0036	0.0601										
35	138497.54	Pop:Mat:BY	0.0022	0.0473										
36	138658.95	Pop	0.0006	0.0237										
37	138820.15	Pop:BY	0.0005	0.0228										
38	138820.15	BY:Pop	0.0005	0.0228										
39	138869.74	BY	0.0001	0.0100										

Note: Pop = population, Inc = increment (fresh water, and first through fourth year at sea; FW, and SW1–SW4), calendar year of growth (Time), brood year (BY), age at maturity (Mat, 5 or 6), and individual fish.

Note: Many models that included Fish as a random effect are not shown because they had a singular fit (meaning one or more variances are zero or very close to zero), including a model with a single random effect for fish and a model with a random effect for population and a random effect for fish.