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Growth, Age & Survival of AYK Chinook Salmon

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ABSTRACT

Abundances of Chinook salmon across the Arctic-Kuskokwim-Yukon (AYK) region, and other regions of Alaska, declined over the past 15 years or more, leading to hardships for people that depend on Chinook salmon for subsistence and income. In an effort to understand factors that have contributed to these declines, we reconstructed indices of Yukon, Kuskokwim, and Nushagak Chinook salmon growth during each life stage in fresh water and the ocean to test leading hypotheses about factors affecting growth as well as hypotheses for how growth and environmental factors affect survival and age at maturation. We were particularly interested in understanding a seemingly paradoxical pattern in Alaskan Chinook salmon stocks. Both the size and age at maturity of adult Chinook salmon declined over the past few decades, a pattern counter to life history theory that predicts age at maturity should be inversely related to growth. We found strong evidence that slower growth (during most life stages, but especially during the second and third years at sea) leads to delayed maturation of individual fish, as expected. However, we also found evidence indicating that lower percentages of older Chinook salmon (age 6+) were associated with reduced growth during the second and third years at sea and/or increased abundance of Russian pink salmon (potential competitors). Because slower growth should lead to a higher percentage of older Chinook salmon, this finding suggests that reduced late marine growth and competition with pink salmon might have contributed to increased mortality during late marine stages. In support of this hypothesis, we found some evidence for a negative relationship between productivity of Yukon and Kuskokwim Chinook salmon and the abundance of Russian pink salmon. Furthermore, both productivity and percentage of older Chinook salmon produced by even-year broods tended to be lower than that produced by odd-year broods, further suggesting a link to the alternating-year pattern of Russian pink salmon abundance. We discuss these findings in light of other potentially influential environmental factors. Of these variables, sea surface temperature during summer and the North Pacific Gyre Oscillation (NPGO) tended to have the greatest influence on growth at sea and the productivity of the Chinook salmon stocks considered. Our findings, which are based on the most comprehensive analysis of life stage specific patterns in Alaskan Chinook growth to date, highlight the potential for increased mortality during late marine life to influence long-term declines in AYK Chinook salmon abundance and productivity.

Key words: Chinook salmon, Yukon, Kuskokwim, Nushagak, Alaska, North Pacific Ocean, scale growth, climate, sea surface temperature, density dependence, pink salmon

INTRODUCTION

Many Pacific salmon populations (*Oncorhynchus* spp.) originating from North America are depressed in abundance and have been identified as stocks of concern or listed for protection under the Endangered Species Act (NWFSC 2015, Shaul et al. 2007, Riddell et al. 2013). Most of these depleted stocks are located along the west coast of North America from California through southern British Columbia. Key factors responsible for depressed and declining stocks include degradation of salmon habitat in fresh water and estuaries, unfavorable ocean conditions, competition for resources and reduced genetic fitness in response to large-scale salmon hatchery production, and fishery harvests (ISAB 2015, NWFSC 2015). In contrast, most habitat in Alaska is relatively pristine and most species of salmon in the region are not of conservation concern (Clark et al. 2006, Blyth-Skyrme et al. 2013), although wild pink salmon (*O. gorbuscha*) in Prince William Sound and chum salmon (*O. keta*) in Southeast Alaska appear to be adversely influenced by large scale hatchery production and associated fishery management issues (Hilborn and Eggers 2001, Brenner et al. 2012, Piston and Heinl 2012, 2014, Blyth-Skyrme et al. 2013). Overall abundances of wild pink, chum, and sockeye (*O. nerka*) salmon in Alaska are 1.3 to 2.8 times higher since the ocean regime shift in the mid-1970s (Ruggerone et al. 2010, Irvine and Ruggerone 2016).

Abundances of Chinook salmon (*O. tshawytscha*) in Alaska, however, have declined over the past three decades (Irvine et al. 2012). Although the decline has occurred throughout Alaska, the decline has been especially pronounced in the Arctic-Yukon-Kuskokwim (AYK) region of western Alaska over the past 15 years. Stocks of concern have been identified and disaster declarations have been issued by state and federal authorities because of the high dependency of people in this large region (Fig. 1) on Chinook salmon for subsistence and for income (Schindler et al. 2013, Munro and Volk 2015, http://www.aykssi.org/background-goals/).

The cause(s) of the Chinook salmon decline are not known but the large-scale nature of it suggests factors at sea, or region-wide climate-related factors during freshwater residence, may be responsible (Schindler et al. 2013). Chinook salmon length at age and age at maturation across 10 Alaskan stocks declined from 1983 to 2012 (Lewis et al. 2015), suggesting that growth-related factors at sea may be a key factor in the decline of abundance. In addition, there is evidence that the productivity of these Chinook salmon stocks is negatively related to the timing of river ice break-up and positively related to the North Pacific Gyre Oscillation (NPGO), a dominant pattern of sea surface height variability, further suggesting that broad scale environmental processes may have contributed to Chinook salmon declines (Ohlberger et al. 2016). Abundances of AYK Chinook salmon seem to respond to large-scale climate shifts: Chinook salmon harvests, which are correlated with abundance, increased immediately following the 1976/77 ocean regime shift, then declined and

remained low after the 1997/98 El Niño (Ruggerone and Agler 2010). Some evidence suggests that the high abundance of pink salmon during the past several decades may reduce growth and survival of Chinook salmon (Ruggerone and Nielsen 2004, Ruggerone et al. 2016).

Growth is a key factor affecting survival and life history of Pacific salmon, including Chinook salmon (e.g., Healey 1986, Henderson and Cass 1991, Sogard 1997, Farley et al. 2007, Ruggerone and Goetz 2004, Ruggerone and Connors 2015). Faster growing salmon are more capable of avoiding predators and surviving winter when prey availability is low (Beamish and Mahnken 2001). For example, relatively rapid early marine growth of Bristol Bay and Chignik sockeye salmon (*O. nerka*) occurred immediately after the mid-1970s ocean regime shift that led to substantially greater abundances of salmon throughout northern areas (Ruggerone et al. 2007a). Analysis of salmon scales indicates higher survival of larger and faster growing Chinook salmon and sockeye salmon in the Bering Sea and other regions (Duffy and Beauchamp 2011, Murphy et al. 2013, Ruggerone et al. 2013). Climate-related factors, such as the NPGO, appear to have also influenced the size of Chinook salmon (Jeffrey et al. 2016).

The goal of our investigation was to test the following hypotheses:

1) Chinook salmon growth in fresh water is influenced by density-dependent processes (e.g., parental generation spawner abundance), and/or abiotic factors, such as water temperature.

2) Chinook salmon growth during each year at sea is influenced by density-dependent processes (e.g., competition with abundant pink salmon) and/or abiotic factors, such as seasonal sea surface temperature (SST), ice cover, wind-related mixing, and climate indices (e.g., PDO, Aleutian Low, Arctic Oscillation; Table 1). A sub-hypothesis is that climate mediates the influence of competition (e.g., competition effects are greater in years of poor ocean conditions).

3) Chinook salmon productivity is influenced by growth in fresh water, growth during each year at sea, abiotic factors, and/or age at maturation.

4) Mean age at maturation of Chinook salmon is influenced by growth in fresh water, and/or the ocean.

5) Female Chinook salmon mature at an older age than male salmon, potentially contributing to fewer female than male salmon returning to the watersheds.

6) Growth of early maturing Chinook salmon (age 1.3) begins to exceed that of late maturing Chinook salmon (age 1.4) during early life stages.

7) Growth of female Chinook salmon exceeds that of male Chinook salmon beginning at an early life stage, thereby highlighting the importance of growth to female Chinook salmon.

OBJECTIVES

Specific objectives identified in our AYK SSI proposal are provided below along with a brief statement on the outcome of our research relative to each objective. Further details on the data sources and analyses as well as interpretation are provided in the subsequent Methods, Results and Discussion sections.

1. *Extend the existing Chinook salmon scale growth datasets for Yukon, Kuskokwim, and Nushagak stocks through year 2013.*

The ADF&G Mark, Tag, and Age Lab updated the scale measurement database through the 2013 adult return year, corresponding to brood years 2007 and 2008 depending on salmon age. A total of 10,906 scales, including about 1 million circuli, were measured as part of this project (see Table 2). ADF&G edited and re-measured some previously measured scales, as described in Methods. All scales were verified, and tests were conducted to ensure consistency of scale measurements among readers. Scale measurements were archived by ADF&G using an ORACLE database.

2. *Test for biological and physical factors affecting annual Chinook salmon scale growth during freshwater versus ocean life stages.*

Scale growth was strongly influenced by gender and age at maturation. Female Chinook salmon grew faster than males and younger adult Chinook salmon (age 1.3) grew faster than older adult Chinook salmon (age 1.4). Faster growth of age-1.3 Chinook salmon began in fresh water and continued during each year at sea. In fresh water, growth was not associated with spawner abundance - an important finding related to management of spawning escapement - or with environmental variables, although there was very weak evidence that greater growth may be associated with earlier ice break-up and higher river flow. Growth during the first year at sea was primarily influenced by SST during summer and to a lesser extent by date of ice break-up (earlier break-up associated with faster growth at sea perhaps reflecting earlier sea entry). Other environmental and climate variables had little effect on early marine scale growth. Growth during the second through fourth years at sea was primarily correlated with Russian pink salmon abundance (negative: 3rd & 4th years at sea), wind mixing (negative), Chinook salmon abundance (negative), and SST.

3. *Test whether Chinook scale growth during one or more life stages and biological/physical factors affect abundance, productivity and age at maturation of western Alaska Chinook salmon.*

We found some evidence of growth and environmental effects on Chinook salmon productivity; however, evidence varied among stocks. For example, the productivity of Kuskokwim and Nushagak Chinook salmon was positively related to scale growth and the NPGO during the first year at sea (SW1). We also found evidence that the productivity of both Yukon (strong correlation) and Kuskokwim (weak correlation) Chinook salmon declined with increasing abundance of Russian pink salmon during the third and fourth years of Chinook salmon life at sea.

The percentage of age-6 (e.g., age 1.4) and older Chinook salmon returning to the Yukon and Nushagak rivers was strongly correlated with the abundance of Russian pink salmon during later marine life, whereas age of Kuskokwim Chinook salmon was weakly associated with growth during the second and third years at sea.

4. *Test for the effect of growth and gender on age at maturation of Chinook salmon.*

Growth during fresh water and each year at sea was associated with age at maturation. Age-1.3 Chinook salmon grew faster than age-1.4 salmon, especially during the second and third years at sea. Female Chinook salmon grew faster than male salmon during fresh water, and each year at sea except during the first year. Nevertheless, across all three stocks female Chinook salmon (mostly age 1.4) were older on average than male salmon (mostly age 1.3).

METHODS

Our analyses focused on two broad sets of hypotheses, which we tested with data from three large Chinook salmon complexes in Western Alaska (the Kuskokwim, Nushagak and Yukon river basins; referred to as stocks). The first set of hypotheses we considered were related to environmental factors (both abiotic and biotic) that may influence Chinook salmon growth in fresh water and the marine environment (hypotheses 1, 2, and 3; Table 1). To quantify the strength of data support for these hypotheses, we related growth (size) at a given age (e.g., during the first year a suite of environmental covariates in a hierarchical modeling framework and then used multi-model inference and model averaging to quantify the predicted influence of the environmental variables on growth.

The second set of hypotheses we considered involved the influence of life stage specific growth, as well as environmental factors, on the productivity and age at maturity of each of the Chinook salmon stocks (hypotheses 4, 5, 6, and 7). To test these hypotheses, we related productivity from each stock to growth (size) at a given age, along with strong correlates of growth from the previous analyses and factors previously shown to influence Chinook salmon survival. These analyses accounted for process variation in stock productivity, recruitment, and maturation schedules, as well as observation error in run abundance, harvest, and age composition. The analysis of age at maturity involved many of the same covariates as the productivity analyses.

Below we describe the data used and details of these analyses.

Estimates of Chinook salmon growth by life stage

Salmon body length is correlated with radial scale measurements (Fukuwaka and Kaeriyama 1997, Fisher and Pearcy 2005); therefore, scales provide a useful method to reconstruct life stage-specific indices of annual salmon growth (size) in freshwater and marine habitats.

Acetate impressions of adult Chinook salmon scales from the Yukon, Kuskokwim, and Nushagak rivers were obtained from the Alaska Department of Fish and Game (ADF&G) archive in Anchorage, Alaska. These scales were collected annually to quantify age composition since 1966 (Yukon River), 1964 (Kuskokwim River), 1976 (Nushagak River commercial fishery), or 1983 (Nushagak River escapement). In the Yukon River, scales were selected for measurement only when they were from Chinook salmon captured with 8.5-inch set gillnets (commercial or test fisheries) located in the lower river near Flat Island, Big Eddy, and/or Emmonak. These locations were within a relatively small area of the lower river. Fewer scales were available in the Kuskokwim River, thus we could not be as selective when choosing scales for measurement. In most years, Kuskokwim Chinook salmon scales were selected from salmon captured in commercial and/or test fisheries near Bethel, Alaska. Mesh size was either 5.5-6 inch or 8-8.5 inch mesh. In four years (1986, 1993, 1997, and 2001), the Kuskokwim Chinook salmon fishery was very small; therefore, scales were also selected from fish sampled at weirs located on the tributaries; a statistical difference in life stage-specific scale growth was not detected between weir and fishery scales collected in the same year (see Ruggerone et al. 2007b). For Nushagak River, scales were collected and measured from fish sampled in the commercial fishery and the escapement with a drift gillnet or beach seine, but the statistical tests presented in this report were based upon measurements of the fish sampled in the escapement because two rather than one age classes were measured. Additional details about Nushagak Chinook scales are available in Ruggerone et al. (2012) and Appendix A.

Previous scale measurements for Yukon, Kuskokwim, and Nushagak Chinook salmon were extended through the 2013 adult return year (Ruggerone et al. 2007, 2012). These additional measurements added up to nine years to the datasets. The growth indices for the Yukon and Kuskokwim river stocks now span brood years in the late 1950s through 2007 (age 1.4[1] fish) and 2008 (age 1.3 fish). For the Nushagak River escapement scales, we examined fish from brood years 1978-2007 (age 1.4) and 1979-2008 (age 1.3). Up to 200 scales were measured per year per stock (Table 2). The Kuskokwim dataset was missing several years, primarily in the 1960s. A total of 10,906 Chinook salmon scales were measured, including about 1 million circuli measurements.

Scales were selected for measurement when: 1) we agreed with the age determination previously made by ADF&G; 2) the shape indicated that a scale was removed from the "preferred area" (Clutter and Whitesel 1956, Bilton 1975, Koo, 1962); and 3) circuli and annuli were clearly defined and not affected by regeneration or significant resorption along the measurement axis. The "preferred scale area" is the location on fish where scales are first formed and therefore have greatest size. Our goal was to measure 50 scales per year from each of the two dominant age groups (ages 1.3 and 1.4) in the commercial fishery for the Yukon and Kuskokwim stocks or from the escapement for the Nushagak stock. Equal numbers of male and female salmon were sampled when possible. A sample size of 50 fish per age group per year was found to be sufficient to reduce the standard error around the mean; a greater sample size led to relatively little reduction in variability.

Scale measurements were made by the ADF&G Mark, Tag, and Age Laboratory following well-establish scale reading procedures (Davis et al. 1990, Hagen et al. 2001, Ruggerone et al. 2007a). Scales were scanned on a micro-fiche reader and stored as high resolution images (3360 x 4426 pixels). These images allowed the entire scale to be viewed and provided enough pixels between the narrow circuli (growth rings) to ensure accurate measurements of spacing between circuli (resolution ~0.0017 mm/pixel). Image Pro Plus software was used to collect measurement data using a customized interface to measure circulus spacing (mm) by growth zone (Fig. 2). The scale measurement axis was the longest axis extending from the scale focus to the outermost edge. Distance between circuli was measured and summed within each growth zone, i.e., from the scale focus to the outer edge of the first freshwater annulus (FW1), spring plus growth zone (FWPL), each annual ocean growth zone (SW1, SW2, SW3, SW4), and from the last ocean annulus to the edge of the scale (SWPL). Data associated with each scale, such as date of collection, location, sex, fish length, and gear type (large, small or unrestricted mesh), were included in the

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[1] Age-1.4 Chinook salmon refers to salmon that spent 1 winter in fresh water and four winters at sea, leading to a total age of 6 years when including time during egg and embryo incubation. Age 1.4 and age 1.3 are the dominant age groups of Chinook salmon in Alaska.

dataset. Scale data were stored in an Oracle database maintained by ADF&G and exported to Microsoft Excel for additional analyses and data management.

ADF&G discovered that previously-used image processing software (Optimate) caused loss of measurement calibration on some scale measurements. This calibration shift was corrected in all previously measured salmon scales. Scales were thoroughly examined for issues with reader measurement error (e.g., annulus placement, freshwater plus decision-making). Re-measurements of a random subset of previously measured scales indicated no significant difference in growth zone measurements among scale readers examining the same scales ($P > 0.05$; MANOVA tests).

Environmental variables and salmon data

Numerous environmental variables have been hypothesized to influence the growth and survival of Chinook salmon. We reviewed the literature, with a particular focus on Chinook salmon, to identify plausible environmental drivers of variation in Chinook salmon growth for consideration in our analyses (Table 1).

Data on Chinook salmon spawner abundance, harvest and age composition for the Kuskokwim and Yukon rivers were provided by Toshihide Hamazaki (ADF&G) and for the Nushagak River by Chuck Brazil (ADF&G). Russian pink salmon data were used in this investigation because they are the dominant stock of pink salmon in the Bering Sea and central North Pacific Ocean where these Chinook salmon likely forage (Myers et al. 1996, Irvine and Ruggerone 2016).

Examining a large number of environmental covariates increases the probability of identifying spurious correlations. We therefore encourage readers to interpret the results of our analyses with caution. These analyses are intended to evaluate the relative support for competing hypotheses about what drives variation in growth, productivity and age at maturity and should not be interpreted as statistical null hypothesis tests seeking to identify "significant" correlations. We also emphasize that the environmental covariates were restricted to only those that we consider as leading hypotheses and correlated with salmon growth or survival in other studies. Full details of each environmental variable including hypothesized mechanisms, Chinook life stages affected, and relevant literature are provided in Table 1.

Analyses

Environmental influences on growth

To test whether specific environmental processes (Table 1) influenced Chinook salmon growth, we fit a series of hierarchical linear models to the data:

$$y_{i,j,t} = \beta_0 + \beta_E E_{j,t} + \gamma_{i,j} + \gamma_i + \varepsilon_{i,j,t},$$

$$\gamma_{i,j} \sim N(0, \sigma^2_{\gamma_{i,j}}),$$

$$\gamma_i \sim N(0, \sigma^2_{\gamma_i}),$$

$$\varepsilon_{i,j,t} \sim \phi\varepsilon_{t-1} + N(0, \sigma^2_\varepsilon).$$

(1)

where y is growth at a given life stage (e.g., first year at sea, SW1) estimated from individual i in stock j and year t, β_0 is average growth across individuals and stocks (i.e., the intercept) and β_E represents the influence of environmental variable E on growth (including effects of age at maturity and sex). The terms $\gamma_{i,j}$ and γ_i were included to allow growth to vary among stocks and individuals within stocks, respectively (i.e., as nested random effects with means of zero), and to account for the non-independence of observations at both scales (e.g., multiple growth estimates within a stock in a given year are not independent of each other). Residual error was modeled as an autoregressive process with a lag of one year to account for serial non-independence of growth estimates from year to year.

We used Akaike's information criterion adjusted for small sample sizes (AICc) and Maximum Likelihood estimation (in R package nlme; Pinheiro et al. 2016) to quantify the relative importance of candidate models in explaining variation in growth (Burnham and Anderson 1998; Zuur et al. 2009). We considered models with all possible combinations of the independent variables but restricted each model to no more than four variables to avoid over-fitting (Burnham and Anderson 2002). We based our inference on the relative importance of the hypothesized drivers of variation in growth on two lines of evidence: 1) the relative variable importance (RVI) of each hypothesis, which is the sum of the Akaike model weights of all models in which the variable for the hypothesis occurred (Burnham and Anderson 2002), and 2) the sign, magnitude, and uncertainty in the multi-model averaged parameter estimates representing each hypothesis in standard deviation units. Model averaged parameter estimates were derived according to the "zero" method where missing parameters in a particular model were assigned a value of zero and model-averaged parameter estimates were generated across all models (Grueber et al. 2011). The resulting model averaged parameter estimates account for both model and parameter uncertainty.

Given the potential for multicollinearity among many of the environmental variables, we used the variance inflation factor (VIF) to identify and remove highly collinear variables with VIF scores greater than 3 prior to fitting models to the data (Zuur et al. 2010). All independent and dependent variables were normalized by centering (mean subtracted) and scaling (divide by the standard deviation) prior to model fitting.

Influence of growth on stock productivity

<u>*Assessment model*</u>

We quantified the relationship between Chinook salmon recruitment, components of growth and extrinsic environmental factors (e.g., those with some evidence of an effect on growth) using a modified version of an age-structured Ricker stock-recruitment model (Ricker 1973) similar in structure to Hamazaki et al. (2012) and Fleischman et al. (2013). Our model described the recruitment of each brood year (*t*) returning to spawn as a Ricker stock-recruitment model modified to account for three additional components of recruitment variability: (1) recruitment variability due to variation in growth rate at each life stage, (2) recruitment variability due to extrinsic environmental factors, and (3) recruitment variability due to correlation in recruitment through time. The model was specified:

$$R_t = \alpha S_t e^{-\beta S_t + G_t + E_t + \rho v_{t-1} + \varepsilon_t} \tag{2}$$

where the term $\alpha S_t e^{-\beta S_t}$ describes the stock-recruitment relationship, with S_t representing the escapement of spawners at time *t*, *α* is the intrinsic rate of stock growth (i.e., productivity at low spawner abundance) and *β* is density dependence in relation to the carrying capacity of the stock.

The term G_t represents the component of the stock-recruitment residuals that can be explained by variation in different components of the average scale growth experienced by a given cohort. The growth effect G_t can be deconstructed into a linear set of covariates:

$$G_t = \eta_1 FW1_t + \eta_2 SW1_t + \eta_3 SW2_t + \eta_4 SW3_t + \eta_5 SW4_t \tag{3}$$

where η_{1-5} represent the covariate effect parameters of the average growth increment of each brood year (*t*) during its first year in the freshwater environment (i.e. $FW1_t$) and its first through fourth year in the marine environment (i.e. $SW1_t$, $SW2_t$, $SW3_t$, and $SW4_t$, respectively).

The average growth covariates (i.e., *FW1*, *SW1*, *SW2*, *SW3*, and *SW4*) were calculated as weighted averages of the mean growth of males and females for each brood year. Thus, average growth (ω) for a given age class (Q) was calculated:

$$\omega_{Q,t} = \left[\frac{n_{t,M,1.3}(Z_{t,M,1.3}) + n_{t,F,1.3}(Z_{t,F,1.3})}{n_{t,M,1.3} + n_{t,F,1.3}} + \frac{n_{t,M,1.4}(Z_{t,M,1.4}) + n_{t,F,1.4}(Z_{t,F,1.4})}{n_{t,M,1.4} + n_{t,F,1.4}} \right] / 2 \tag{4}$$

where *n* is the number of fish sampled of a given sex (M: male; F: female) and age (1.3 or 1.4) from brood year *t* and *Z* is normalized growth (mean subtracted and divided by the standard deviation). This approach equally weights

differential growth of male versus female and age-1.3 versus age-1.4 salmon, which is important to account for because of unequal sample sizes among groups in some years.

The term E_t in equation (2) represents the component of the stock-recruitment residuals that can be explained by variation in environmental factors. In this case we only considered environmental factors with some statistical support (i.e., RVI > 0.5) from the growth – environmental covariate analyses plus two additional factors, the NPGO and river discharge, because they have been shown to be correlated with Alaska Chinook salmon productivity (NPGO: Ohlberger et al. 2016; discharge: Neuswanger et al. 2015). These covariates were included in this analysis as E_t which can be deconstructed into linear covariates:

$$E_t = \phi_1 ice.breakup_t + \phi_2 temp.sum.SW1_t + \phi_3 temp.win.SW2_t \qquad (5)$$
$$+ \phi_4 wind.SW3_t + \phi_5 pinks.SW4_t + \phi_6 pinks_t$$
$$+ \phi_7 NPGO_t + \phi_8 flow_t$$

where φ_{1-8} represent the covariate effect parameters of each of the variables considered. For the pink salmon covariate, we used the 2-year running average abundance of Russian pink salmon because there was evidence of an influence of pink salmon on Chinook salmon growth in both the 3rd and 4th year of life at sea.

The term ρv_{i-1} of equation (1) describes the component of the residuals that can be described by first order temporal auto-correlation. The parameter ρ represents the time series correlation in stock-recruitment residuals (i.e., log-scale residual deviation between the realized and expected recruitment) to represent unmeasured environmental influences persisting from year to year. The recruitment residual v_t was calculated:

$$v_t = \log(R_t) - \log\left(\alpha S_t e^{-\beta S_t + G_t + E_t}\right) \qquad (6)$$

where the first term $\log(R_t)$ represents the observed recruitment and the second term $\log(\alpha S_t e^{-\beta S_t + G_t + E_t})$ represents the predicted recruitment. The parameter ε_t in equation (2) represents the additional residual variation in recruitment not described by the stock-recruitment relationship, variation in growth or temporal auto-correlation. We assumed that ε_i conformed to a normal distribution on the log scale with a mean equal to zero and an estimated standard deviation.

Because the rate of maturation among individuals is variable, the number of adults returning to spawn each calendar year was composed of a proportion of fish from different brood years (i.e., ages). We accounted for this variation by calculating the number of returns-at-age as:

$$N_{t,k} = P_k R_{t-k} \tag{7}$$

where k denotes the age of returning fish and P_k represents the expected proportion returning to spawn at age k. Thus, $N_t = \sum_k N_{t,k}$ represents the total number of adults returning to the river each calendar year t. Finally, the escapement for each calendar year was calculated:

$$S_t = N_t\left(1 - U_t\right) \tag{8}$$

where the parameter U_t is the annual exploitation rate.

Model likelihood

Our model likelihood was formulated following Bue et al. (2012) and Hamazaki et al. (2012) with some modifications to accommodate our data structure. We fit our assessment model to three data types, including harvest estimates, escapement estimates, and escapement numbers at age. We specified the likelihood of escapement estimates ($Sobs_t$):

$$\log\left(Sobs_t\right) \sim \text{Normal}\left(\log\left(S_t\right), \sigma_{S,t}\right) \tag{9}$$

where $\log(S_t)$ represents the mean of the normal distribution and $\sigma_{s,t}$ is the year-specific standard deviation calculated as $\log\left(S_t\right)cv_s$, where cv_s is the specified coefficient of variation. The likelihood of the annual harvest numbers ($Hobs_t$) was specified:

$$\log\left(Hobs_t\right) \sim \text{Normal}\left(\log\left(N_t U_t\right), \sigma_{H,t}\right) \tag{10}$$

where $\log(N_t U_t)$ is the log predicted annual harvest and the mean of the normal distribution. The parameter $\sigma_{H,t}$ is a specified vector of standard deviations calculated as $\log\left(N_t U_t\right)cv_H$, where cv_H is the specified coefficient of variation.

Observed numbers at age in the escapement was incorporated into the model by first weighting the numbers based on quality of the data (see below) and then specifying the likelihood of the weighted data. Weighted numbers were calculated as the product of observed age proportions and a theoretical sample size. We specified the likelihood of weighted numbers at age ($Nage_{t,k}$) in the escapement with a multinomial probability density function:

$$Nage_{t,k} \sim \text{Multinomial}\left(P_{t,k}, n\right) \qquad \text{(11)}$$

where $P_{t,k}$ is the probability of returning to spawn at age k and n is the specified theoretical sample size (i.e. multinomial trials).

Precision of each data type (i.e. cv_S, cv_H, n) was supplied as a fixed value in the model likelihood. For the Kuskokwim River, we used cv_S and n from Bue et al. (2012). The value of cv_H was specified as 10% (Hamazaki et al. 2012). For the Yukon River, we obtained values of cv_S from Bue and Hamazaki (2014). We approximated cv_H as 10% and n as 25 (Hamazaki et al. 2012). Parameter inputs for the Nushagak River were approximated from the Kuskokwim and Yukon rivers. We set cv_S to 33%, the largest observed value in our data sets. We set n to 25, the lowest value in Bue et al. (2012), and we set cv_H to 10% (Hamazaki et al. 2012). We ran the analyses with precision set to half and twice the values stated above to evaluate the sensitivity of our assumption about data precision (Appendix C).

Variable selection

We use a Bayesian mixture-model approach (Royle and Dorazio 2008) to quantify the importance of covariates of recruitment variation. By multiplying each covariate parameter by an "inclusion parameter" (Royle and Dorazio 2008, page 72-73), this procedure models the probability that each parameter is included in the best model as a measure of support for the associated hypotheses.

The inclusion parameters (w_v for all v variables in the model) were latent binary variables distributed as Bernoulli trials with an uninformative prior probability of 0.5 (i.e., equal probability that the variable is included or excluded from the model). The mean of the posterior samples of the inclusion parameters corresponds to the probability that the variable is included in the "best" model and indicates the support for the associated hypothesis. Inclusion probabilities ≥ 0.5 indicate that including the parameter in the model results in optimal predictive properties (Barbieri and Berger 2004). Furthermore, the product of the posterior sample of the inclusion parameters (w_v) and the posterior sample of the associated effect parameter (η_{1-5}, φ_{1-8}, and ρ) represents the model averaged posterior distribution of the covariate effects, accounting for both model and parameter uncertainty (Burnham and Anderson 1998). Model probabilities for each of the competing models were then derived from the posterior samples of the inclusion parameters by calculating the proportion of instances of different combinations of parameters of w_v in the posterior sample.

Posterior probability distributions of the model parameters were estimated using a Markov chain-Monte Carlo (MCMC) algorithm implemented in JAGS (Plummer 2003). The model code is provided in Appendix D. We called JAGS from R with library RJAGS (http://mcmc-jags.sourceforge.net). All prior distributions of effect

parameters (η_{1-5} and φ_{1-8}) were specified as uniform distributions with equal probability between -1 and 1, and were verified to have no influence on the posterior probability distributions. We modeled prior distributions of the standard deviation parameters (σ_ε and $\beta_{0,\sigma}$) as uninformative Gamma distributions with a value of 0.1 specified for each shape parameter. Inference was drawn from 4,000 posterior samples taken from four chains of 100,000 samples thinned to every 100. We allowed a burn in of 50,000 samples per chain to remove the effects of initial values. Convergence cannot be diagnosed when modeling inclusion parameters, so we diagnosed convergence for the full model with inclusion parameters fixed at a value of one (prior probability of inclusion = 1) by visual inspection of the MCMC chains for adequate mixing and stationarity and by using the Gelman-Rubin statistic (with values < 1.1 indicating convergence; Gelmin et al. 2004, Kery 2010).

Influence of growth on age at maturity

To test the hypothesis that components of growth and/or extrinsic environmental factors influenced Chinook salmon age at maturity, we fit general linear models to the data from each Chinook salmon stock:

$$\frac{\sum_{x=6}^{7} R_{x,t}}{\sum_{x=1}^{7} R_{x,t}} = \beta_0 + G_t + E_t + \varepsilon_t,$$

$$\varepsilon_t \sim \phi\varepsilon_{t-1} + N(0,\sigma^2).$$

(12)

where $\sum_{x=6}^{7} R_{x,t}$ is the number of recruits that matured at age 6 or older (e.g., ≥ age 1.4) from brood year t, $\sum_{x=1}^{7} R_{x,t}$ is the total recruits from brood year t (i.e., the sum of Chinook that matured after 3 to 7 years of age), β_0 is the average proportion of 6 plus year old recruits (the intercept) and the remaining terms describe the influence of components of growth and extrinsic environmental factors (equations 2-4) on age at maturity.

We modeled the data using a linear equation (in the R package gls; Pinheiro et al. 2016), instead of a logistic one per Hellevik (2009), because it allowed us to account for serially-correlated error (e.g., ϕ = 0.76 for the Kuskokwim). Failure to account for this strong temporal correlation leads to under-dispersion (less variation in data than predicted) when fitting a generalized linear model with a binomial distribution (i.e., logistic regression) and an increased false negative

rate. We verified that modeling the proportion data with a linear model did not violate model assumptions by plotting residuals versus fitted values, each covariate in the model, and each covariate not in the model. In addition, we assessed the residuals for temporal and spatial dependency.

We used AICc and maximum likelihood estimation to quantify the relative importance of candidate models in explaining variation in age at maturity for each Chinook salmon stock independently. We considered models with all possible combinations of the independent variables but restricted each model to no more than four variables. We based our inference on relative importance of hypothesized drivers of variation in age at maturity on the relative variable importance of each hypothesis and the sign, magnitude, and uncertainty in the multimodel averaged parameter estimates representing each hypothesis in standard deviation units.

RESULTS

Trends in scale growth, age, and productivity

Within each stock (Yukon, Kuskokwim, and Nushagak), annual growth of age-1.3 and age-1.4 Chinook salmon was correlated during fresh water (avg. r = 0.40), SW1 (r = 0.66), and SW2 (r = 0.71) (Figs. 3 - 6). Correlation in growth between age-1.3 and age-1.4 salmon was relatively low during SW3 (r = 0.21), likely reflecting differential growth associated with age at maturation (see below).

Scale growth of Chinook salmon during each life stage in fresh water and at sea showed some trends over time (Figs. 3 - 6). Growth of Yukon Chinook salmon declined over time in fresh water where growth was typically below average since the mid-1980s (Fig. 3). Growth of Yukon Chinook salmon also declined over time during the third (SW3) and fourth (SW4) years at sea. Cumulative scale growth of Yukon Chinook salmon (all life stages) was below average since the mid-1980s. Growth of both ages of Kuskokwim Chinook salmon declined over time in fresh water and during the third year at sea for age-1.4 salmon; however, these trends were more distinct in Yukon Chinook salmon. Nushagak Chinook salmon also exhibited reduced growth in fresh water and during the second year at sea, primarily after brood year 2002.

Overall productivity of Yukon and Nushagak Chinook salmon, based on residuals from the Ricker stock recruitment relationships, declined since the mid-1980s (Yukon) or late 1970s (Nushagak; Fig. 7). In contrast, productivity of Kuskokwim Chinook salmon did not exhibit a clear trend over time, a pattern that may reflect strong apparent overcompensation shown in the Ricker recruitment relationship. Productivity of all three stocks was 22% lower, on average, among even-year broods compared with odd-year broods (two-factor ANOVA--stock, odd even year: df = 1, 93; F = 8.52; P < 0.005). Return per spawner of even-year broods

averaged less than one, whereas R/S of odd-year broods averaged greater than one, indicating production from odd-year broods was sustainable but production from even-year broods was not. An interaction between stock and the odd-even year factor was non-significant (P > 0.05), indicating the odd-even year pattern was consistent among the stocks.

The percentage of Chinook salmon maturing at age 6+ (e.g., age 1.4 and older) in each stock declined steadily over the past 25 to 40 years (Fig. 8). The decline was relatively pronounced for Yukon and Nushagak Chinook salmon where the percentage of 6+ year old recruits dropped by half since the early 1980s and less pronounced for Kuskokwim Chinook salmon where 6+ year old recruits declined approximately 25% over the same time period. The decline in the percentage of older Chinook salmon tended to be greater for even versus odd brood years (two-factor ANOVA--stock, odd even year: df = 1, 91; F = 2.82; P < 0.10). An interaction between stock and the odd-even year factor was non-significant (P > 0.10).

In summary, growth in freshwater and at sea, productivity (Yukon and Nushagak stocks), and the percentage of older Chinook salmon have tended to decline over time in Chinook salmon from western Alaska. Additionally, reduced productivity from even-year broods tended to be associated with fewer returns of relatively old Chinook salmon. This trend was unexpected because brood years with earlier than average age at maturity were expected to have higher than average productivity (due to reduced mortality associated with additional years at sea), unless unusually high mortality occurred during late marine life of even-year broods.

Age and gender influences on growth

Scale growth of Chinook salmon by life stage was strongly associated with both age at maturation and gender. Across all life stages, Chinook salmon that matured at age 1.4 grew more slowly than those that matured at age 1.3 and these differences were most pronounced after Chinook salmon spent multiple years at sea (Fig. 9). For example, differences in growth between Chinook salmon that matured at age 1.4 versus age 1.3 were over 3 times greater in the third year of marine life (SW3) than in the first year of life in freshwater (Fig. 9).

At all life stages, females grew faster on average than males, except during the first year of marine life (Fig. 9). These sex specific differences in growth were most pronounced in the third and fourth years of marine life (SW3 and SW4; Fig. 9).

Environmental influences on growth

Although we found some evidence for correlation among environmental variables and growth, most variables evaluated had weak and highly uncertain

relationships with growth. This was illustrated by both low RVI (often less than 0.5) and small model averaged standardized effects with confidence intervals that included zero (Figs. 10-14).

On the other hand, two variables showed strong statistical support: first year growth (SW1) was positively correlated with SST (Fig. 11; RVI = 0.94); and third year growth (SW3) was inversely correlated with the abundance of pink salmon from Russia (Fig. 13; RVI = 1.0). In addition, there was weak evidence (RVI > 0.5 but confidence intervals overlapped zero) indicating that ice breakup was negatively correlated with growth in the first year at sea (SW1), temperature was correlated with growth in the second (SW2) and fourth (SW4) years at sea (Figs. 10-15). We also found that high wind was negatively correlated with growth in the third at sea (SW3). Intraspecific competition (i.e., Chinook salmon abundance) was indicated by growth in the fourth year at sea and interspecific competition (pink abundance) was indicated by growth in the third and fourth years at sea (Figs. 13-15). We found no support for an interaction among pink salmon and environmental variables on growth during the third and fourth years at sea (SW3 and SW4).

Influence of growth on stock productivity

We found some evidence for a potential influence of growth on productivity of Kuskokwim and Nushagak Chinook salmon. In both stocks, growth during the first year of marine life (SW1) was positively correlated with productivity (Figs. 16, 17, 19); however, growth during the fourth year of marine life (SW4) of Nushagak Chinook salmon was negatively correlated with productivity (Figs. 17, 19). We found no evidence the potential influence of growth on productivity of Yukon Chinook salmon (Figs. 18, 19).

We also found strong support for the influence of NPGO on productivity during the first year at sea (SW1) for Kuskokwim and Nushagak Chinook salmon (Figs. 16, 17, 19), and moderate support for the influence of SST during early marine life (SW1) on the productivity of Nushagak Chinook salmon (Figs. 17, 19). There was also support for a negative influence of Russian pink salmon abundance on Yukon and Kuskokwim Chinook salmon productivity (Figs. 16, 18). Productivity of Yukon Chinook salmon was strongly correlated with the percentage of age-6+ Chinook salmon. In other words, productivity was high when older Chinook were abundant relative to younger fish.

In general, the relationships between growth, extrinsic environmental processes and Chinook salmon productivity were robust to uncertainty in estimates of escapement, harvest and age composition (Appendix D). In other words, parameter estimates and their respective inclusion probabilities were relatively insensitive to alternative assumptions about the precision of estimates of escapement, harvest and age composition.

Influence of growth on age at maturity

We found some evidence of an influence of growth on Chinook salmon age at maturity. In the Kuskokwim, age at maturity of Chinook salmon was inversely correlated with growth during the second (SW2) and third (SW3) years of life at sea (Figs. 20, 23), thus slower growing fish matured at an older age. In the Yukon, age at maturity was also inversely correlated with growth during the second year of life at sea (SW2; Figs. 21, 22); however, there was no evidence of a relationship between age at maturity and growth in the Nushagak Chinook salmon (Fig. 21).

Few of the environmental variables that we considered were correlated with age at maturity (Figs. 20, 21, 22). However, we found strong evidence of a negative correlation between Russian pink salmon abundance in the third (SW3) and fourth (SW4) year at sea and age at maturity of Yukon and Nushagak Chinook salmon (Figs. 20, 21, 23). Relatively fewer old Chinook salmon returned during years of high pink salmon abundance. Temperature during the winter in the second year life at sea (SW2) was weakly correlated with age at maturity of Kuskokwim Chinook salmon (Figs. 20).

DISCUSSION

Abundance, harvest, and productivity of Chinook salmon stocks across western Alaska and other regions of Alaska have declined over the past 20-35 years (Irvine et al. 2012, Ohlberger et al. 2016, Ruggerone et al. 2016, this study). Additionally, both adult length at age and the percentage of older Chinook salmon (age 6+) has declined (Lewis et al. 2015, this study). This pattern of decreasing age and reduced adult length at age is paradoxical because reduced growth is typically associated with older not younger salmon (e.g., Healey 1991, Heath et al. 1994, Vøllestad et al. 2004, Quinn 2005, Wells et al. 2007, Ruggerone and Connors 2015). Indeed, our study also has found that growth of late maturing Chinook salmon was less than that of earlier maturing Chinook salmon during each year in fresh water and the ocean, suggesting that the recent decline in adult length at age should have been associated with older not younger Chinook salmon.

Environmental influences on growth

Using historical adult scale collections and measurements, we examined biological and environmental factors affecting Chinook salmon growth during each life stage in fresh water and the ocean. We also explored relationships among Chinook salmon growth during each life stage and key life history characteristics such as life cycle productivity (survival) and age at maturation. In fresh water, we did not find clear evidence that environmental variables, such as river flow, date of ice breakup, or temperature, were associated with growth of Yukon, Kuskokwim, and Nushagak Chinook salmon. In contrast to Chinook salmon stocks in other regions (ISAB 2015), freshwater growth was not associated with spawner abundance, suggesting that growth was not density dependent, an important finding that has implications for management of spawning escapement in these systems. This finding indicates that the density dependence observed in stock recruitment relationships for these stocks, including the particularly strong appearance of overcompensation in the Kuskokwim River, is not driven by growth in fresh water.

Growth of Yukon, Kuskokwim, and Nushagak Chinook salmon during the first year at sea was positively associated with SST during summer and to a lesser extent by date of ice break-up (earlier break-up associated with faster growth at sea perhaps reflecting earlier sea entry). Other environmental and climate variables that we considered had little measureable effect on early marine scale growth (SW1). Growth during the second through fourth years at sea (SW1-SW4) was primarily associated with Russian pink salmon abundance (negative: SW3 and SW4), wind mixing (negative), Chinook salmon abundance (negative), and SST (positive). Thus, both density dependence and a limited set environmental variables (e.g., SST) appeared to have influenced late marine growth of western Alaska Chinook salmon. These findings are generally

consistent with studies that reported relationships between growth of Chinook salmon and salmon density (e.g., Grachev 1967, Ruggerone and Goetz 2004, Jeffrey et al. 2016) or environmental variables (Wells et al. 2007, McFarlane 2010, Neuswanger et al. 2015).

Influence of growth, environment, and pink salmon on stock productivity

We modeled the lifetime survival (i.e., productivity or number of recruits per spawner) of Chinook salmon as a function of within population density dependence, life stage specific growth, and external environmental processes. The time period of productivity measurements and the accuracy of the productivity estimates varied by stock, and our analysis attempted to account for uncertainty in the underlying estimates of productivity for each stock. Most variables explained relatively little variation in the productivity of Chinook salmon and those variables that did correlate with productivity were sometimes different among the three stocks.

Productivity of Kuskokwim and Nushagak Chinook salmon increased with greater growth during the first year at sea (SW1) and with increasing NPGO, an index of net primary productivity that has recently been associated with salmon growth and survival (Stachura et al. 2013, Kilduff et al. 2015, Ohlberger et al. 2016, Jeffrey et al. 2016). In addition, there was moderate evidence that productivity of both Kuskokwim and Yukon Chinook salmon declined with increasing abundance of Russian pink salmon during the third and fourth years at sea.

We also found that the productivity of all three stocks produced by even-year broods was lower than that of odd-year broods, possibly reflecting interspecific competition with Russian pink salmon that have a strong alternating year pattern of abundance and that have greater abundance and overlap with Yukon, Kuskokwim, and Nushagak Chinook salmon in the Bering Sea and central North Pacific than pink salmon from North America (Myers et al. 2016). Pink salmon abundance in Russia is 1.5 times more abundant in odd-numbered years (Ruggerone et al. 2010, Irvine and Ruggerone 2016) and abundance of maturing pink salmon in the Bering Sea is ~25 times more abundant in odd-numbered years (Davis et al. 2005). Analysis of Chinook salmon diet in the central Bering Sea revealed a 56% reduction in stomach fullness and a 68% reduction in weight of fish and squid consumed during odd- versus even-numbered years, 1991-2000 (Davis 2003). An alternating-year pattern in numbers of Chinook salmon returning to the upper Yukon River has also been documented (JTC 2016). Age-1.4 Chinook salmon produced by even-year broods interact with abundant odd-year pink salmon during their second and fourth years at sea, whereas age-1.4 Chinook salmon produced by odd-year brood only interact with abundant odd-year pink salmon during their third year at sea. Age-1.3 Chinook salmon interact with odd-year pink salmon during the second (even-year broods) or third (odd-year broods) years at sea. Interaction between western Alaska Chinook salmon and Russian pink salmon during the homeward migration is likely negligible

(Ruggerone et al. 2005). Length of age-1.3 and age-1.4 Yukon Chinook salmon produced by even-year broods were consistently smaller than those produced by odd-year broods since the early 1980s (Ruggerone et al. 2009). Our analyses show that scale growth of Yukon, Kuskokwim and Nushagak Chinook salmon during the third and fourth years at sea were inversely correlated with Russian pink salmon abundance. Although we did not detect an inverse correlation between Chinook salmon growth during the second year at sea and pink salmon abundance, scale growth of Yukon Chinook salmon during the second year at sea was consistently lower during odd-numbered years when pink salmon were abundant (Ruggerone et al. 2009). These patterns provide evidence to support the hypothesis that pink salmon exert a negative influence on the growth and productivity of Chinook salmon in western Alaska. Furthermore, female Chinook salmon produced by even year broods may be more strongly influenced by pink salmon because females tend to mature at age 1.4 and most males mature at age 1.3, i.e., age-1.4 female salmon interact with odd-year pinks twice whereas age-1.3 males interact once.

Influence of growth, environment, and pink salmon on age at maturation

As noted above, our findings were consistent with other research showing that growth has a strong influence on the age of maturation: rapid growth tends to lead to earlier maturation (e.g., Healey 1991, Quinn 2005). Overall, few of the oceanographic variables were correlated with age at maturity.

We found some evidence supporting the hypothesis that pink salmon abundance may have influenced age at maturity of Chinook salmon via growth and survival. The percentage of older Chinook salmon returning to the Yukon and Nushagak rivers declined with increasing abundance of Russian pink salmon. Older age at maturity in Kuskokwim Chinook salmon was associated with reduced growth during the second and third years at sea. The percentage of age 6+Chinook salmon tended to be lower among even-year than odd-year broods, possibly reflecting strong odd/even year abundances of Russian pink salmon. This pattern and the alternating year patterns in productivity and growth support the hypothesis that changes in growth, survival, and age at maturity are linked. Although younger age at maturity (age 1.3 versus age 1.4) was associated with faster growth during each life stage in fresh water and at sea (especially during the second and third years at sea), a general decline in growth over time was associated with a decrease in older Chinook salmon, a pattern opposite of that predicted from life history theory. We expected growth and age at maturity to be inversely related.

The unexpected observation of declining growth and age at maturity of Chinook salmon might be explained by relatively high mortality of slower growing salmon during late marine life in recent decades. For age-1.4 salmon, even year broods produce fish that interact with abundant odd-year pink salmon during the second and fourth years at sea, whereas odd-year broods produce fish that interact with

abundant pinks only in the third year at sea. Reduced growth and reduced survival produced by even year broods could lead to a decline in older Chinook salmon. This mechanism would have the greatest effect on female Chinook salmon, which mature primarily at age 1.4 rather than age 1.3. The hypothesized effect of pink salmon on the growth, survival and age of Chinook salmon could help explain the low abundance of female versus male Chinook salmon in western Alaska (Ruggerone et al. 2012, Liller et al. 2013, Saveride and Huang 2014, R. Brown, USFWS, pers. comm.). Furthermore, the declining percentage of older Chinook salmon returning to western Alaska over time (Lewis et al. 2015; this study) is opposite the growing abundance of pink salmon (Ruggerone et al. 2010, Irvine and Ruggerone 2016).

Size-selective harvest, which is known to have occurred in a number of areas, has been identified as another mechanism influencing earlier maturation in Chinook salmon and changes in size and sex ratio on the spawning grounds (e.g., the Yukon River; Bromaghin et al. 2011). Although there is evidence for fishery selection in the age composition data in the Kuskokwim River, exploitation may not be high enough to substantially alter the age composition and sex ratio (Stanton 2015). In the Nushagak River, the commercial fishery tended to select smaller than average Chinook salmon whereas the recreational fishery removed larger than average fish, suggesting that environmental factors are likely influencing reduced size and age at maturation in Nushagak Chinook salmon (Kendall and Quinn 2011, Lewis et al. 2015).

Survival of Chinook salmon in fresh water and first year at sea

Survival and abundance of upper Yukon Chinook salmon originating in Canada appears to be established, in part, in fresh water and the first spring and summer at sea (Murphy et al. 2016). Approximately 73% of the variability in adult Yukon Chinook run size was explained by the estimated abundance of juvenile upper Yukon Chinook salmon in the Bering Sea, based on trawl surveys during 2003-2011. Juvenile abundance was relatively high during 2013-2015, leading the investigators to conclude that Chinook salmon runs will improve beginning in 2016. Although the investigators reported size-selective mortality among the Chinook salmon, significant relationships between juvenile Chinook salmon size and abundance or survival have not been detected.

Our analyses contribute to the emerging understanding of Chinook salmon growth and survival leading up to the Bering Sea survey by Murphy et al. (2016). We found no support for growth and growth-related conditions in fresh water affecting the productivity of Chinook salmon. In contrast, early ice break up and warmer SST during summer contributed to greater growth of Yukon, Kuskokwim and Nushagak Chinook salmon during their first year at sea. Productivity of Kuskokwim and Nushagak Chinook salmon was also associated with higher NPGO and greater growth during the first year at sea.

Survival of Chinook salmon during late marine life

Murphy et al. (2016) estimated that survival from the first fall at sea to adult return in the Yukon averaged 5.2% ± 0.9% during 2003-2011. In other words, approximately 95% of the juvenile Chinook salmon died after the first growing season at sea (i.e., during late marine life).

Our findings are consistent with the hypothesis that high pink salmon abundance may have contributed to the decline in size, productivity and production of older Chinook salmon. Russian pink salmon abundance has been exceptionally high in recent decades, reaching a peak of 450 million fish in 2009 before declining to 200 million in 2013; the decline in 2013 was especially great among eastern Kamchatka pink salmon, which is the dominant stock in the Bering Sea (Irvine and Ruggerone 2016). Commercial catch of Chinook salmon in western Alaska and throughout Alaska and British Columbia has been negatively correlated with pink salmon abundance since 1980 (Ruggerone et al. 2016). Recent evidence from pop-up satellite tagging in the Bering Sea indicates potentially high mortality of large Chinook salmon (59-89 cm) caused by salmon sharks and marine mammals (Seitz and Courtney 2016), suggesting these large and abundant predators may contribute to late marine mortality of Chinook salmon (Nagasawa 1998). Although growth and survival of Chinook salmon is undoubtedly important in fresh water and during early marine life, our findings suggest that reduced growth and high mortality during late marine life may have contributed to the long-term decline in Chinook salmon abundance and productivity and to the paradoxical relationship between slower growth and early maturation in these large Chinook salmon systems.

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DELIVERABLES

Final report:

Ruggerone, G.T., B.M. Connors, B.A. Agler, L.I. Wilson, and D.C. Gwinn. 2016. Growth, age at maturation, and survival of Yukon, Kuskokwim, and Nushagak Chinook salmon. Final report to Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative, Anchorage, Alaska.

Progress Reports:

January 1 to March 31, 2016
July 1 to December 31, 2015
Jan 1 to June 30, 2015
July 1 to December 31, 2014
Jan 1 to June 30, 2014
October 1 to December 31, 2013

Data Sets:

Measurements of Chinook salmon scales collected from the Yukon, Kuskokwim, and Nushagak rivers from the 1960s through 2013. The data set is stored on the ADF&G server using ORACLE:

Bev Agler
ADF&G Division of Commercial Fisheries
Mark, Tag, and Age Lab,
10107 Bentwood Place, Juneau AK 99801
bev.agler@alaska.gov

Presentations:

Have gender-specific growth and maturation at sea influenced the decline of western Alaska Chinook salmon? 17th Annual Salmon Ocean Ecology Meeting. March 2016. Juneau, AK.

Salmon population trends and species interactions in the North Pacific Ocean. Invited keynote presentation. North Pacific Anadromous Fish Commission. May 17-19, 2015. Kobe, Japan.

PROJECT DATA

The data collected by this study involve the Chinook salmon scale measurements described in the methods section of this report (Scale Measurements). Most of the earlier scale measurements were made with previous funding to the Project Team. The overall database for Yukon, Kuskokwim, and Nushagak salmon scales involves approximately one million measurements. The database is archived at the ADF&G Mark, Tag, and Age Lab. Data may be obtained by contacting the Project PIs and Bev Agler of the Mark, Tag, and Age Lab.

ACKNOWLEDGEMENTS

PRESS RELEASE

Abundances of Chinook salmon across the Arctic-Kuskokwim-Yukon (AYK) region, and other regions of Alaska, declined over the past 15 years or more, leading to hardships for people that depend on Chinook salmon for subsistence and income. In an effort to understand factors that have contributed to these declines, we reconstructed indices of Yukon, Kuskokwim, and Nushagak Chinook salmon growth during each life stage in fresh water and the ocean to test leading hypotheses about factors affecting growth as well as hypotheses for how growth and environmental factors affect survival and age at maturation. We were particularly interested in understanding a seemingly paradoxical pattern in Alaskan Chinook salmon stocks. Both the size and age at maturity of adult Chinook salmon declined over the past few decades, a pattern counter to life history theory that predicts age at maturity should be inversely related to growth. We found strong evidence that slower growth (during most life stages, but

especially during the second and third years at sea) leads to delayed maturation of individual fish, as expected. However, we also found evidence indicating that lower percentages of older Chinook salmon (age 6+) were associated with reduced growth during the second and third years at sea and/or increased abundance of Russian pink salmon (potential competitors). Because slower growth should lead to a higher percentage of older Chinook salmon, this finding suggests that reduced late marine growth and competition with pink salmon might have contributed to increased mortality during late marine stages. In support of this hypothesis, we found some evidence for a negative relationship between productivity of Yukon and Kuskokwim Chinook salmon and the abundance of Russian pink salmon. Furthermore, both productivity and percentage of older Chinook salmon produced by even-year broods tended to be lower than that produced by odd-year broods, further suggesting a link to the alternating-year pattern of Russian pink salmon abundance. We discuss these findings in light of other potentially influential environmental factors. Of these variables, sea surface temperature during summer and the North Pacific Gyre Oscillation (NPGO) tended to have the greatest influence on growth at sea and the productivity of the Chinook salmon stocks considered. Our findings, which are based on the most comprehensive analysis of life stage specific patterns in Alaskan Chinook growth to date, highlight the potential for increased mortality during late marine life to influence long-term declines in AYK Chinook salmon abundance and productivity.

FIGURES AND TABLES
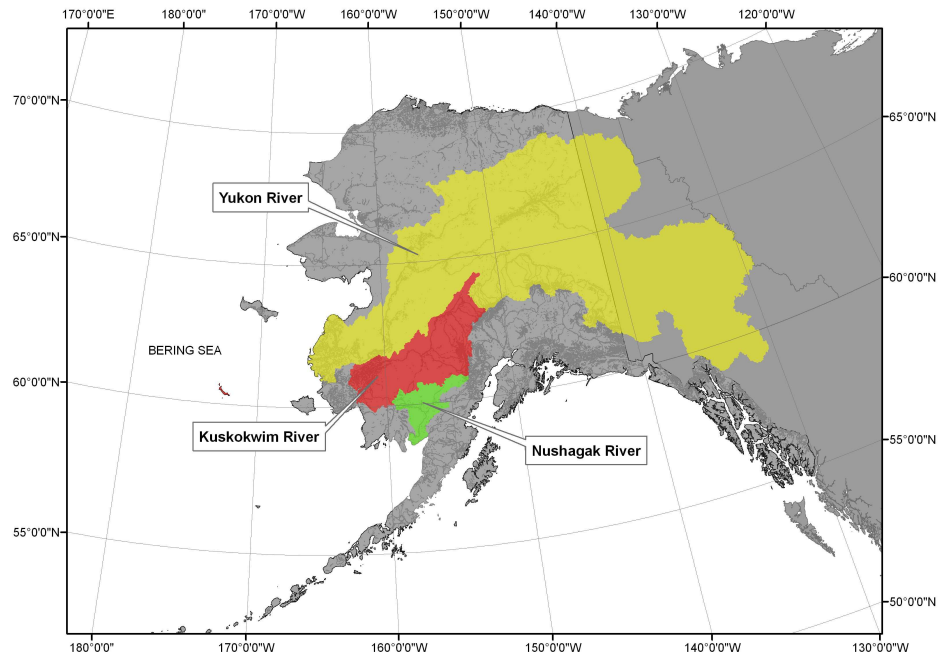
Fig. 1.   Map highlighting the watershed areas of the Yukon, Kuskokwim, and Nushagak rivers in western Alaska that supported the Chinook salmon examined in this study.
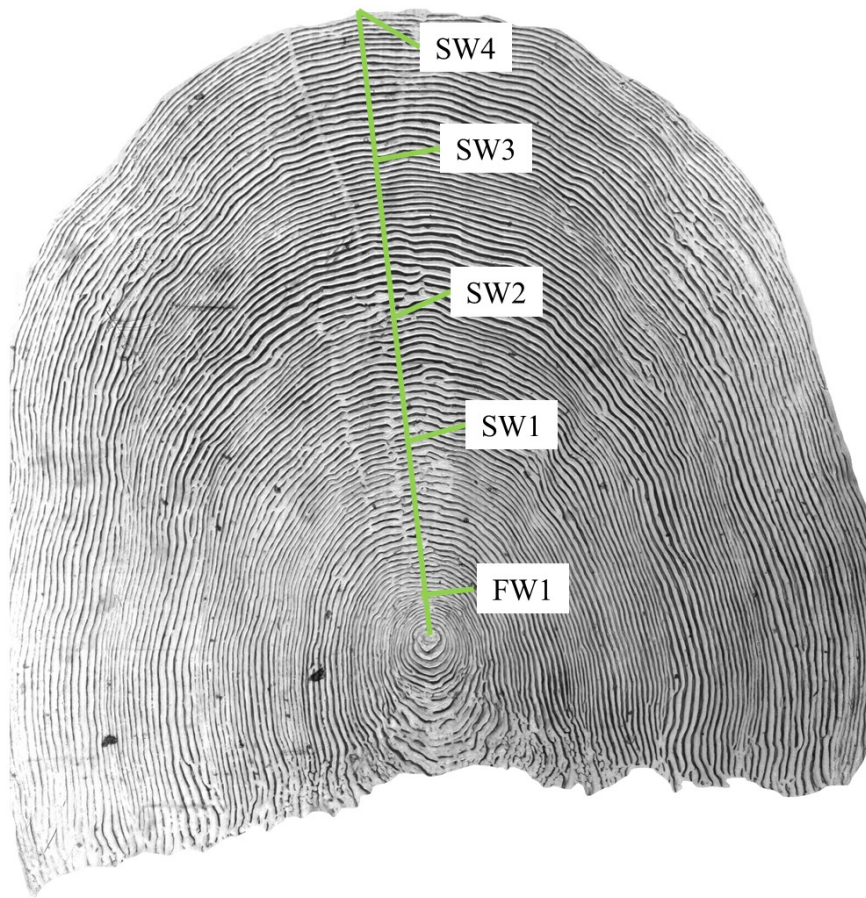
Fig. 2.   Image of an age 1.4 Chinook salmon scale showing the measurement axis, scale circuli, and scale annuli markers: FW1: freshwater growth, SW1: first year at sea, SW2: second year at sea, SW3: third year at sea, and SW4: fourth year at sea. This is an example of a scale used in our study of Chinook salmon from three western Alaska rivers (Yukon, Kuskokwim, and Nushagak).
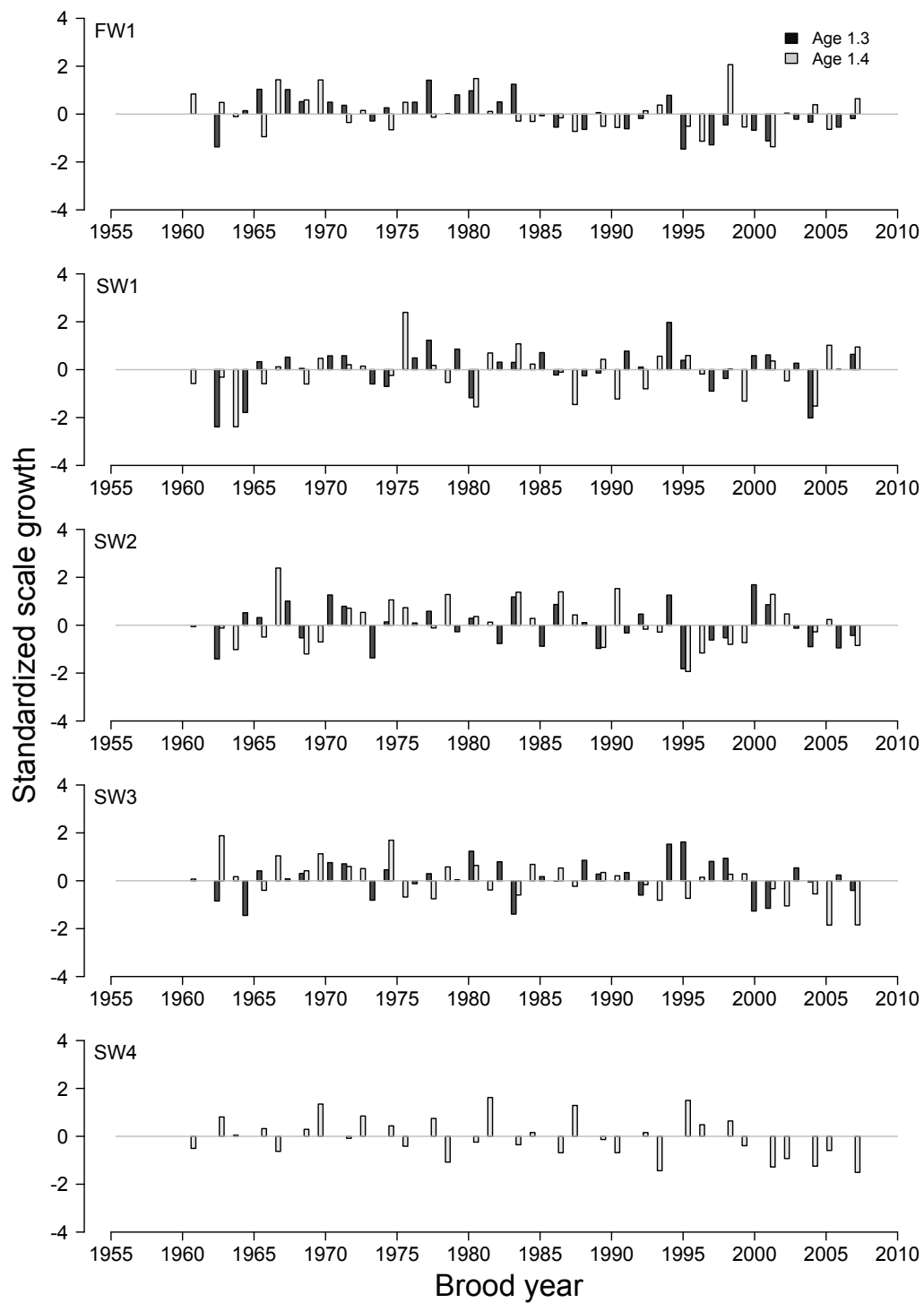
Fig. 3. Mean standardized scale growth over time for age-1.3 (dark grey bars) and -1.4 (light grey bars) Chinook salmon from brood years 1961-2008 in the Yukon River, Alaska. See Appendix A for plots of growth over time by sex and age.
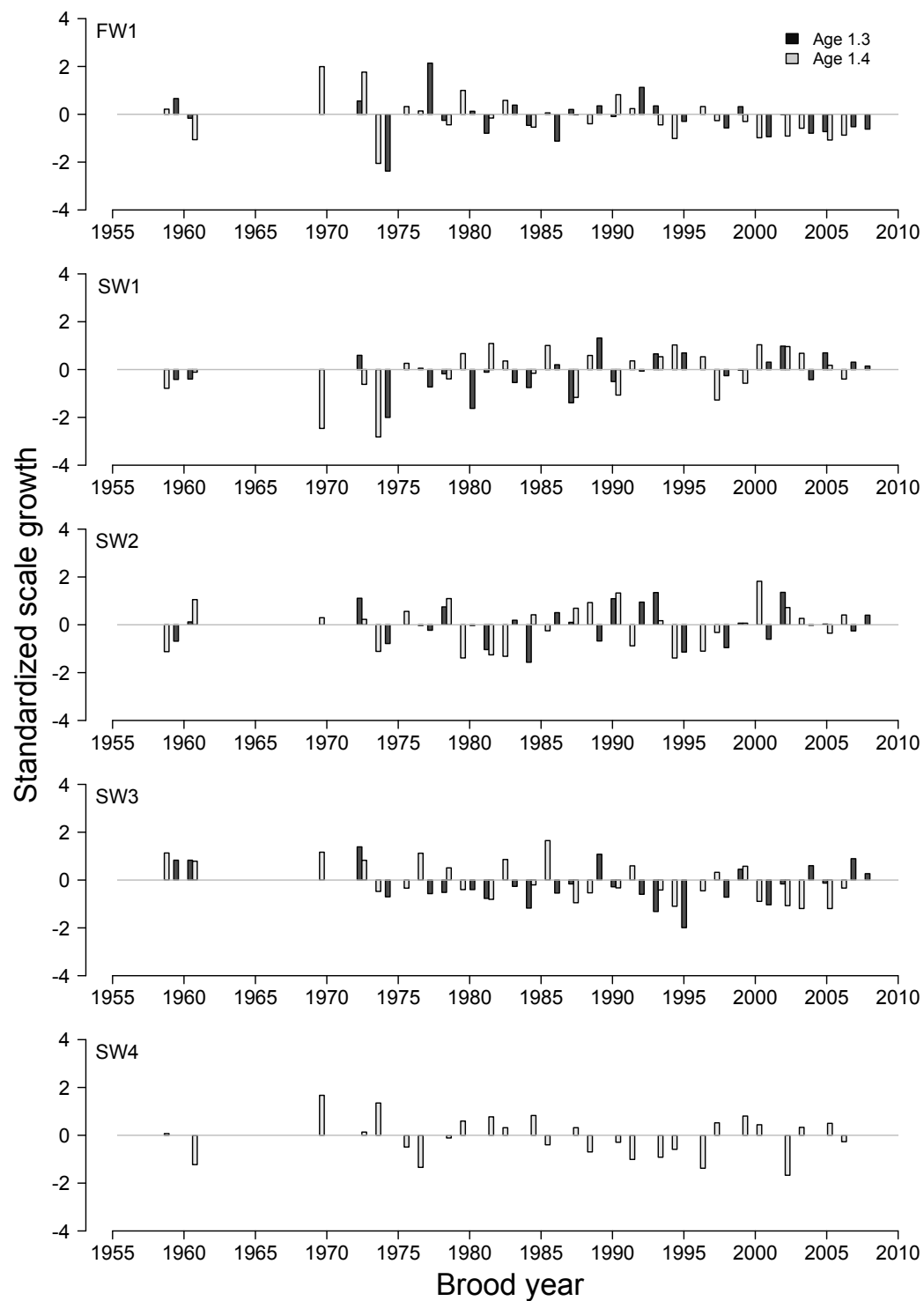
Fig. 4. Mean standardized scale growth over time for age-1.3 (dark grey bars) and -1.4 (light grey bars) Chinook salmon from brood years 1959-2008 in the Kuskokwim River, Alaska. See Appendix A for plots of growth over time by sex and age.
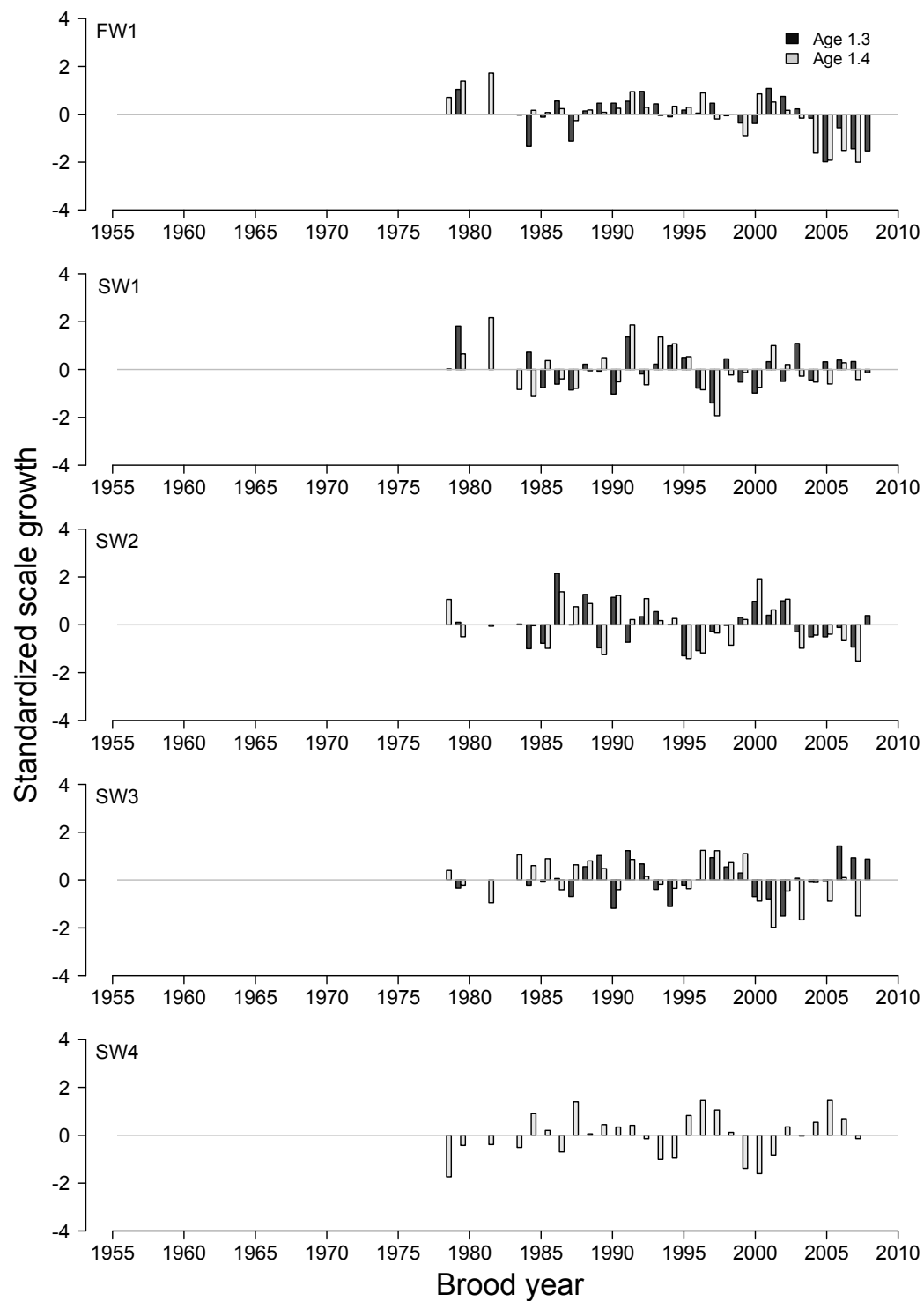
Fig. 5. Mean standardized scale growth over time for age-1.3 (dark grey bars) and -1.4 (light grey bars) Chinook salmon sampled from brood years 1978-2008 in the Nushagak River, Alaska, after escaping the commercial fishery. See Appendix A for plots of growth over time by sex and age.
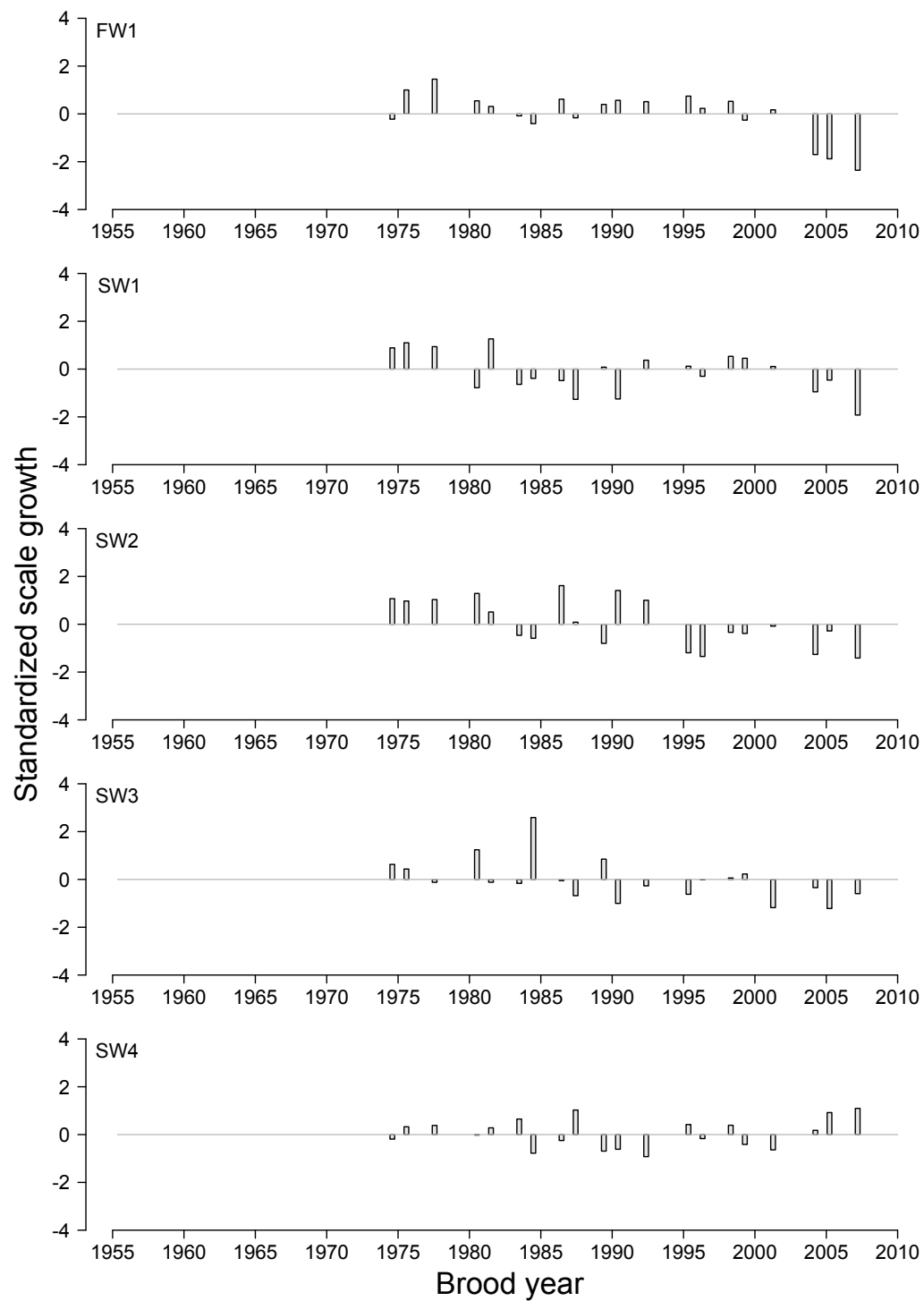
Fig. 6. Mean standardized scale growth over time for age-1.4 Chinook salmon sampled from the commercial fishery in Nushagak Bay, Alaska, brood years 1974-2008. See Appendix A for plots of growth over time by sex and age.
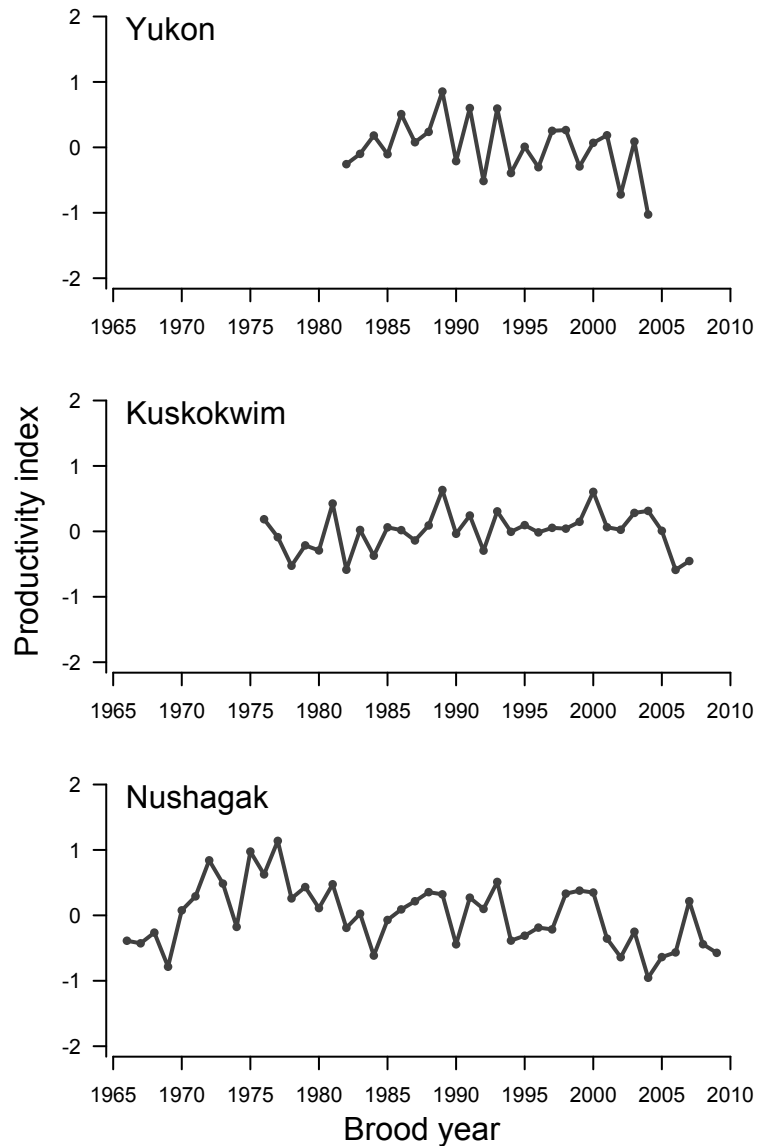
Fig. 7. Productivity over time for each of the three Western Alaska Chinook rivers (Yukon, Kuskokwim, and Nushagak). Productivity values are the residuals of the fit of a Ricker stock recruitment relationship (Log_e R/S).
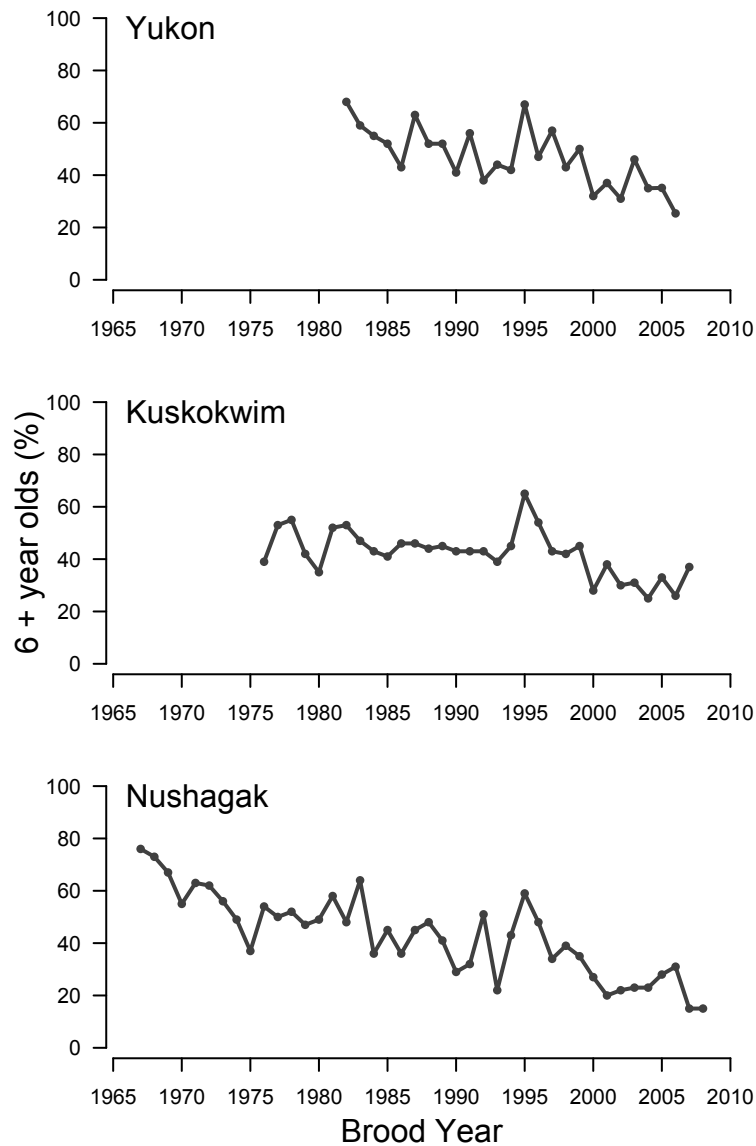
Fig. 8. Average age at maturity of Chinook salmon (percent of total recruits that matured at age 6+ (age 1.4 and older) over time for each of the three Western Alaska rivers (Yukon, Kuskokwim, and Nushagak).
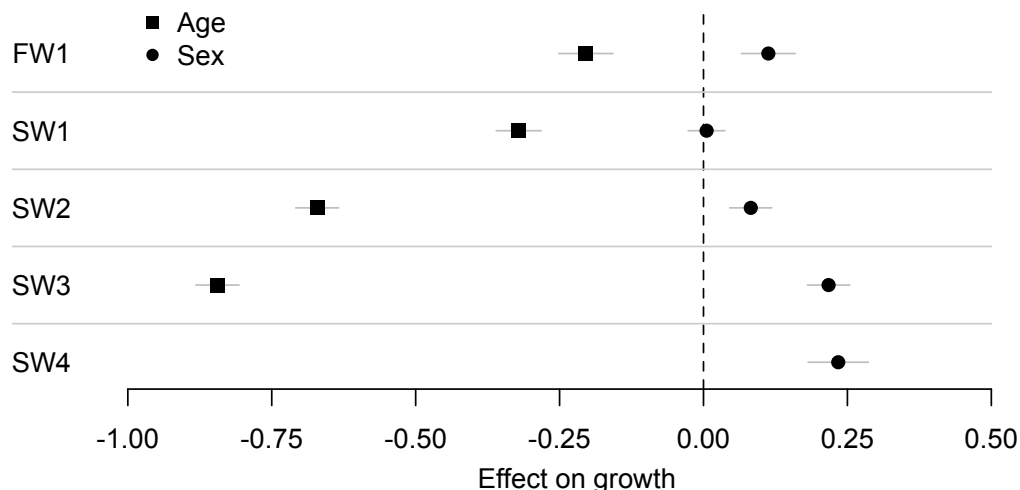
Fig. 9.   Relationships among age at maturity ("Age") and sex ("Sex") and Chinook salmon growth during first year of freshwater growth (FW1) and each year of marine life (SW1-SW4). Estimated relationships are based on multimodel averaged parameter estimates (+/-2 unconditional standard errors).   The "Age" and "Sex" relationships correspond to the difference in growth between age 1.4 and 1.3 (age-1.4 grow slower) and between females and males (females grow faster), respectively. All relationships have a relative variable importance of 1 (with the exception of sex during the first year of marine life [RVI = 0.12]) indicating they have strong support (i.e., appeared in all models with data support). There is no "Age" relationship for SW4 because age-1.3 Chinook salmon do not spend a fourth year at sea. Values based on all three Chinook salmon stocks (Yukon, Kuskokwim, Nushagak).
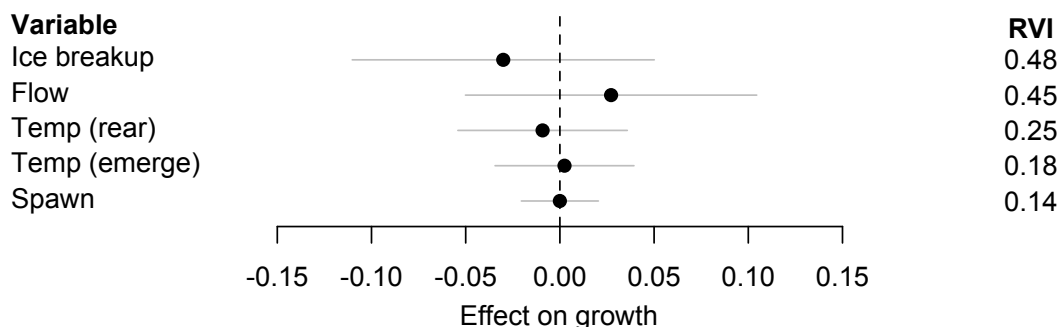
Fig. 10. Effects of ecological variables on Chinook salmon growth during their first year of freshwater growth (FW1). Abbreviations correspond to variables in Table 1. Estimated effects are based on multimodel averaged parameter estimates (+/- 2 unconditional standard errors), and relative variable importance (RVI) of parameters appearing in the top set of hypotheses. All parameters were estimated in standard deviation units to permit meaningful comparisons because independent variables are on different numerical scales.   Values based on all three Chinook salmon stocks (Yukon, Kuskokwim, Nushagak). See Appendix B for the corresponding model selection table.
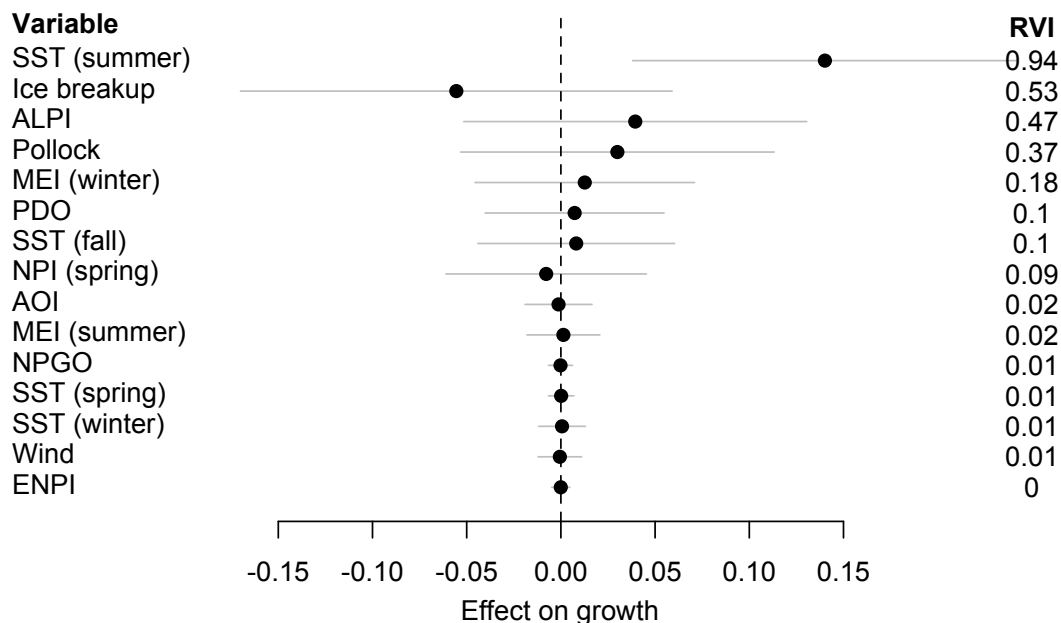
Fig. 11. Effects of ecological variables on Chinook salmon growth during the first year of marine growth (SW1) in a study comparing three stocks from western Alaska (Yukon, Kuskokwim, and Nushagak). The pollock variable is recruitment to age-1. See Appendix B for the corresponding model selection table.
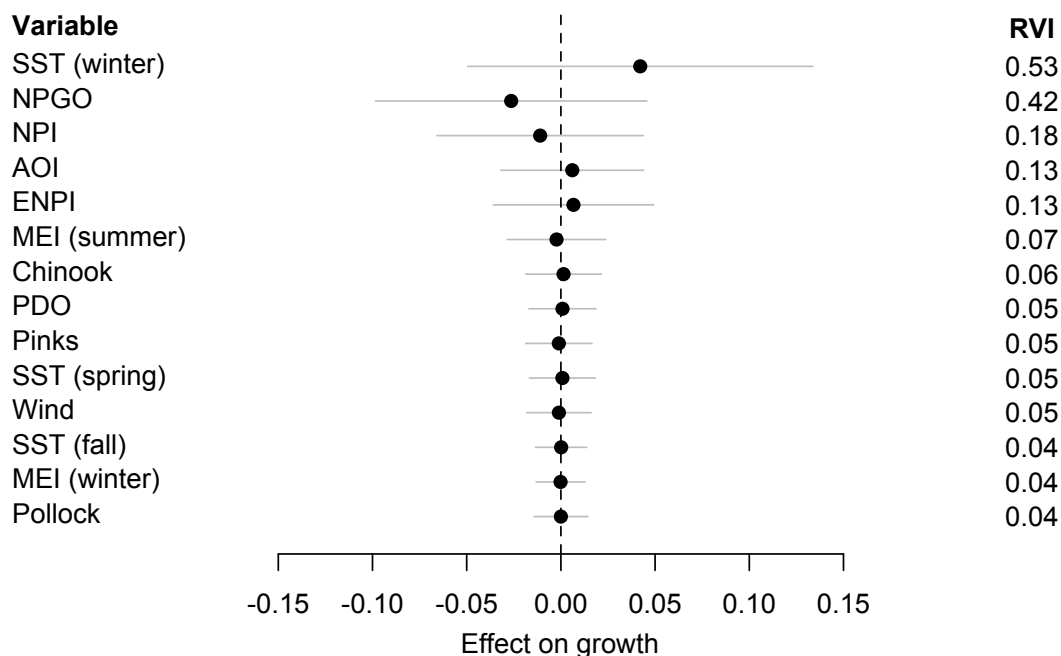
Fig. 12. Effects of ecological variables on Chinook salmon growth during the second year of marine growth (SW2) in a study comparing three stocks from western Alaska (Yukon, Kuskokwim, and Nushagak). The pollock variable is total biomass in the eastern Bering Sea. See Appendix B for the corresponding model selection table.

Variable		RVI
Pinks		1
Wind		0.78
PDO		0.06
Chinook		0.06
Pollock		0.03
AOI		0.02
SST (fall)		0.01
ENPI		0.01
MEI (summer)		0.01
SST (summer)		0.01

-0.15   -0.10   -0.05   0.00   0.05   0.10   0.15
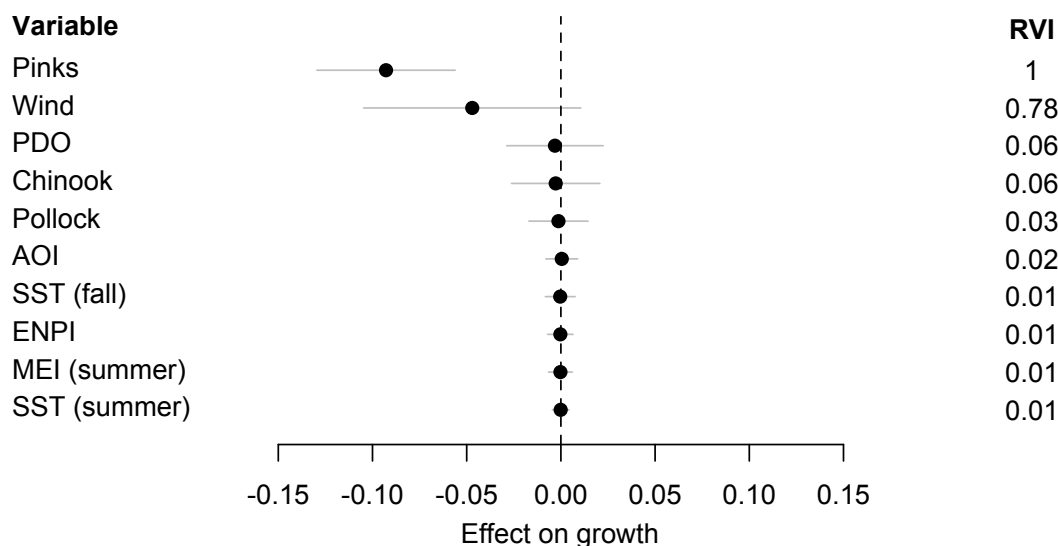
Effect on growth

Fig. 13. Effects of ecological variables on Chinook salmon growth during the third year of marine growth (SW3) in a study comparing three stocks from western Alaska (Yukon, Kuskokwim, and Nushagak). The pollock variable is total biomass in the eastern Bering Sea. See Appendix B for the corresponding model selection table.

Variable		RVI
Pinks		0.68
Chinook		0.57
SST (summer)		0.53
SST (spring)		0.26
SST (fall)		0.22
Wind		0.18
MEI (winter)		0.12
NPI		0.08
ENPI		0.06
MEI (summer)		0.05
Pollock		0.04
AOI		0.04
SST (winter)		0.04

-0.15   -0.10   -0.05   0.00   0.05   0.10   0.15
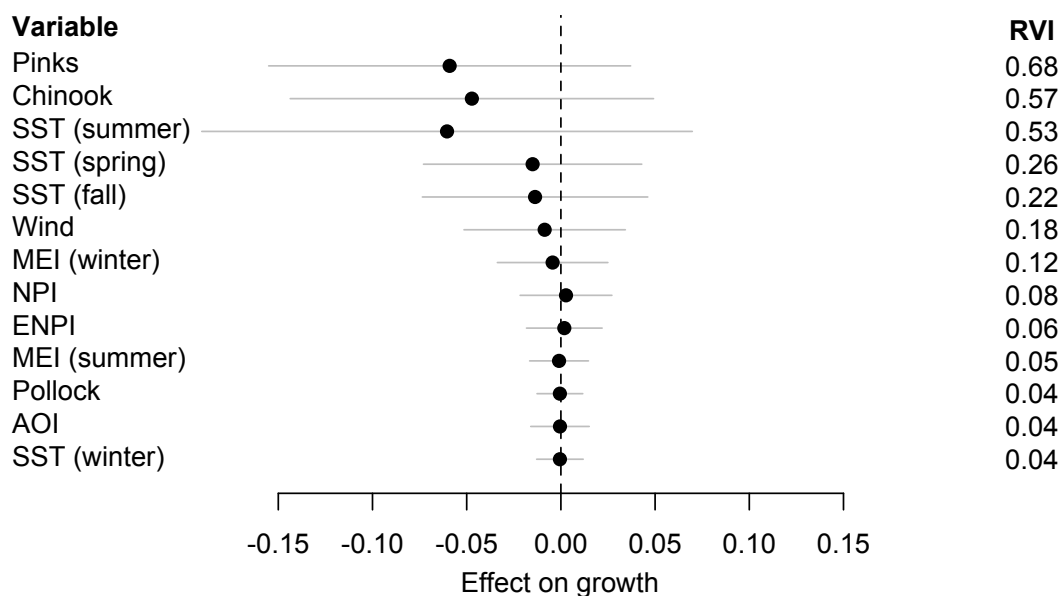
Effect on growth

Fig. 14. Effects of ecological variables on Chinook salmon growth during the fourth year of marine growth (SW4) in a study comparing three stocks from western Alaska (Yukon, Kuskokwim, and Nushagak). The pollock variable is total biomass in the eastern Bering Sea. See Appendix B for the corresponding model selection table.
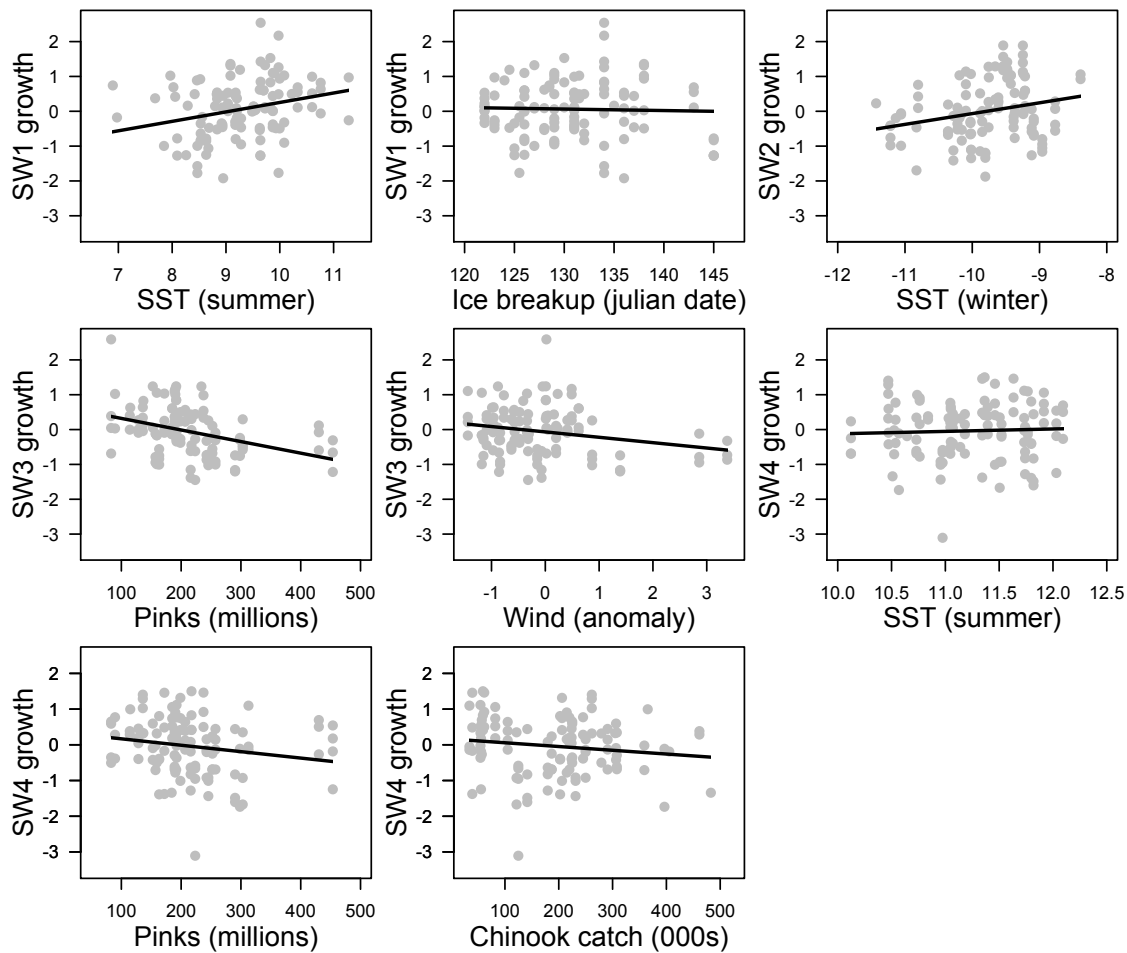
Fig. 15. Relationships among average annual Chinook salmon growth during each life stage and environmental variables with statistical support (i.e., RVIs >0.5). Black horizontal line is the predicted relationship between growth at a given age and each variable (in standardized units). Note that while mean annual growth estimates are plotted here for illustrative purposes, the statistical models were fit to data from individual fish in a hierarchical framework that accounted for the non-independence of observations within stocks and within years. Values based on all three Chinook salmon stocks from western Alaska (Yukon, Kuskokwim, and Nushagak).
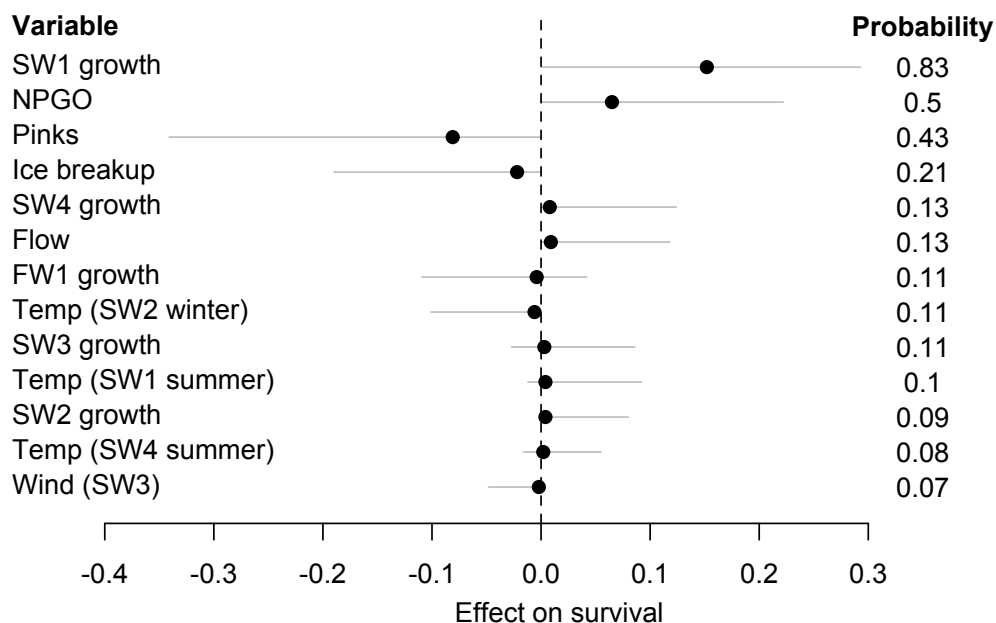
Fig. 16. Effects of life stage specific growth and extrinsic environmental variables on Kuskokwim River, Alaska Chinook salmon survival. Abbreviations correspond to life stage specific growth and variables in Table 1. Parameter mean and 95% Bayesian credible intervals are based on model averaged posterior samples. The covariate probabilities are the mean of the posterior samples of the inclusion parameters, which indicates the support for the associated hypothesis (probabilities ≥ 0.5 indicate that including the parameter in the model results in optimal predictive properties; Barbieri and Berger 2004). All parameters were estimated in standard deviation units to allow meaningful comparisons of the independent variables, which have different numerical scales.

Fig. 17. Effects of life stage specific growth and extrinsic environmental variables on Nushagak River, Alaska Chinook salmon survival. The solid black points and probabilities are based on analyses that were restricted to brood years where there were estimates of growth available. The grey points and probabilities are based on analyses that considered environmental influences on survival with all available years of stock and recruitment data.
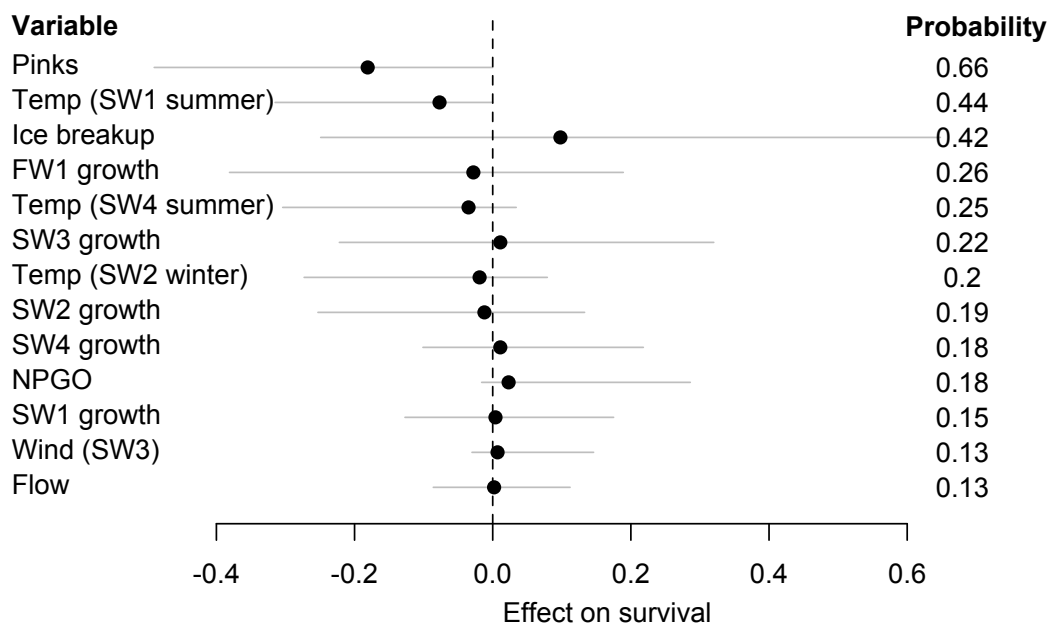
Fig. 18. Effects of life stage specific growth and extrinsic environmental variables on Yukon River, Alaska Chinook salmon survival.
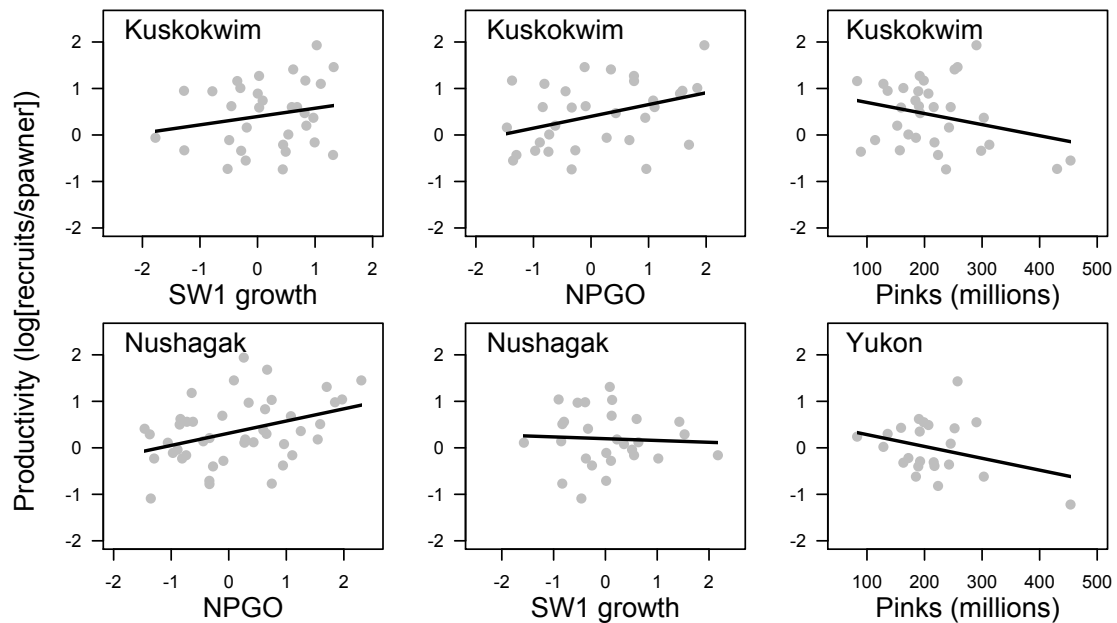
Fig. 19. Relationships among Chinook salmon productivity (natural logarithm of recruits produced per spawner) and growth and environmental covariates with statistical support (i.e., inclusion probabilities >0.5). The black horizontal line is the predicted relationship between productivity and each variable (in standardized units). Although productivity is plotted here for illustrative purposes, the models that were actually fit to the data simultaneously accounted for within stock density dependence, the influence of all covariates, process variation in recruitment and age at maturity, and observation error in estimates of spawner abundance and age composition.

Variable		RVI
SW2 growth		0.92
Temp (SW2 winter)		0.72
SW3 growth		0.68
Pinks		0.35
Temp (SW1 summer)		0.34
Temp (SW4 summer)		0.19
Chinook		0.09
SW1 growth		0.07
FW1 growth		0.06
NPGO		0.06
Wind (SW3)		0.06

Effect on age at maturity
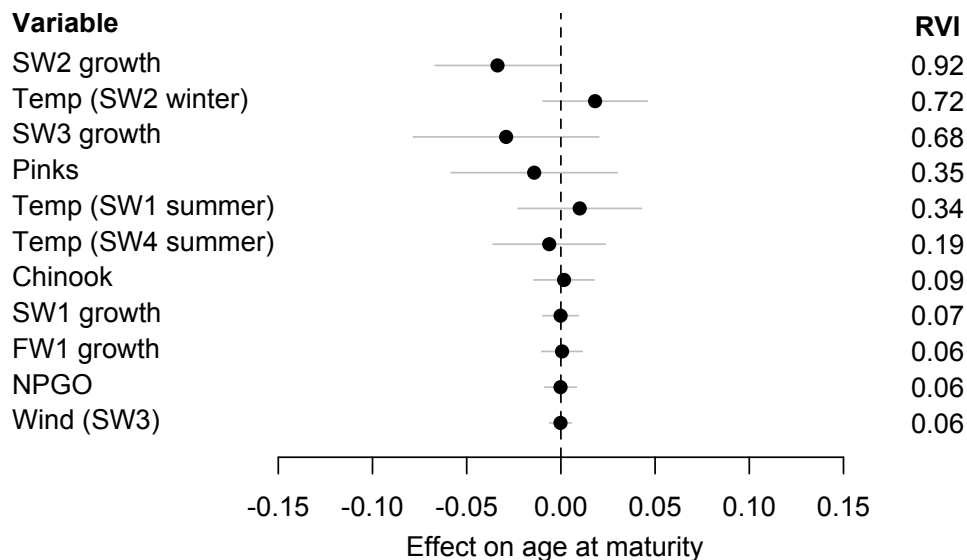
Fig. 20. Effects of ecological variables and growth on Kuskokwim Chinook salmon age at maturity (as indexed by percent of recruits from a given brood year that matured at age 6+. Abbreviations correspond to variables in Table 1. Estimated effects are based on multimodel averaged parameter estimates (+/- 2 unconditional standard errors), and the relative variable importance (RVI) of parameters appearing in the top set of hypotheses. All parameters were estimated in standard deviation units to permit meaningful comparisons because the independent variables are on different numerical scales. See Appendix E for the corresponding model selection table.
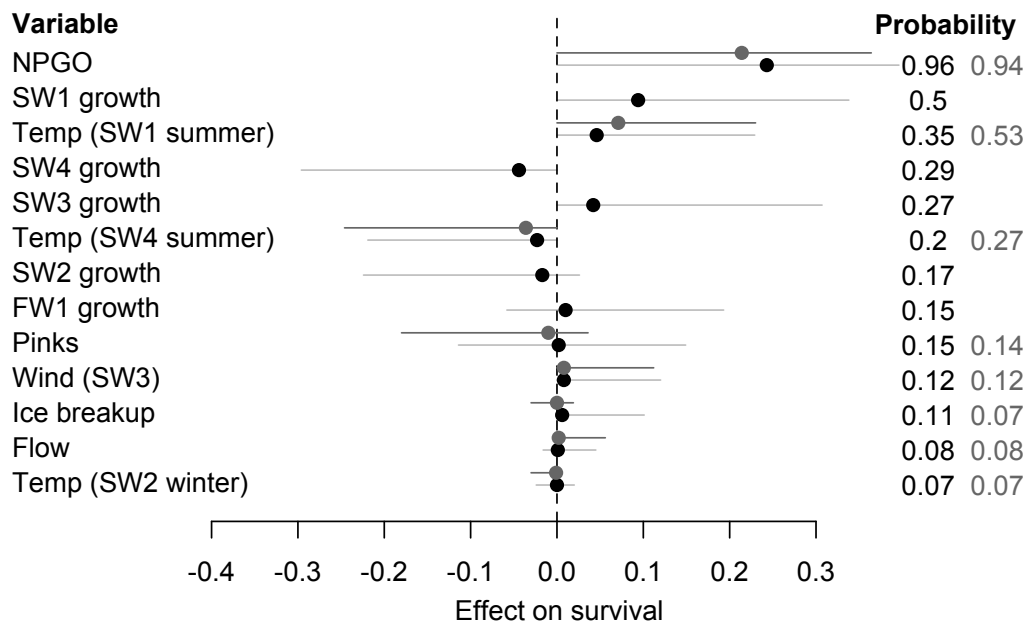

Variable		RVI	
Pinks		0.6	0.7
SW3 growth		0.34	
Wind (SW3)		0.34	0.44
Temp (SW2 winter)		0.27	0.38
FW1 growth		0.24	
Temp (SW4 summer)		0.24	0.23
NPGO		0.19	0.32
SW2 growth		0.18	
SW1 growth		0.15	
Temp (SW1 summer)		0.14	0.23
Chinook		0.13	0.2

Effect on age at maturity
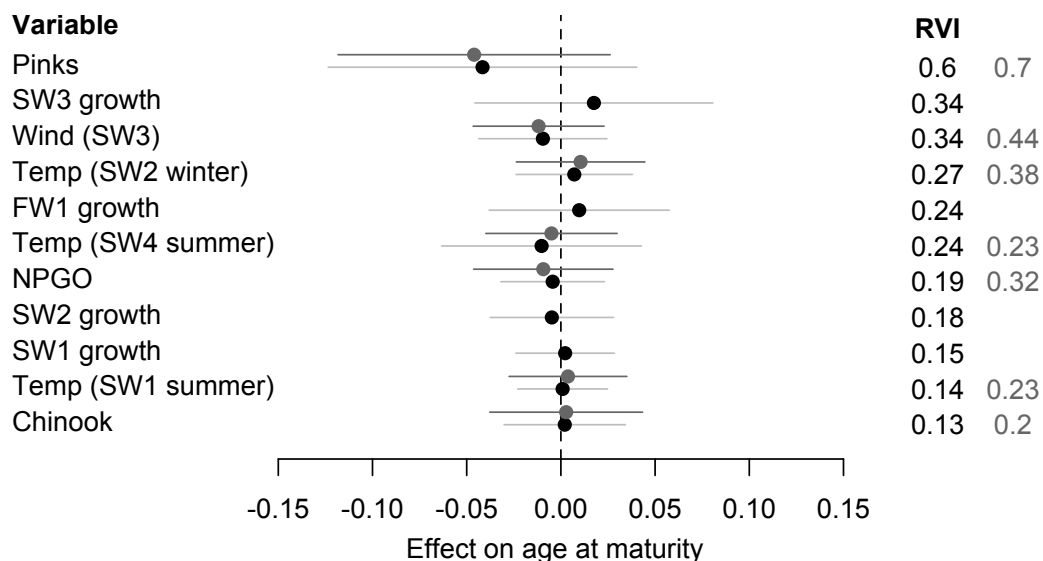
Fig. 21. Effects of ecological variables and growth on Nushagak Chinook salmon age at maturity (as indexed by percent of recruits from a given brood year that matured at age 6+). The effects and relative variable importance (RVI) in light grey are based on analyses of the entire time series of age at maturity while those in black are based on analyses restricted to brood years for which there were corresponding growth estimates.
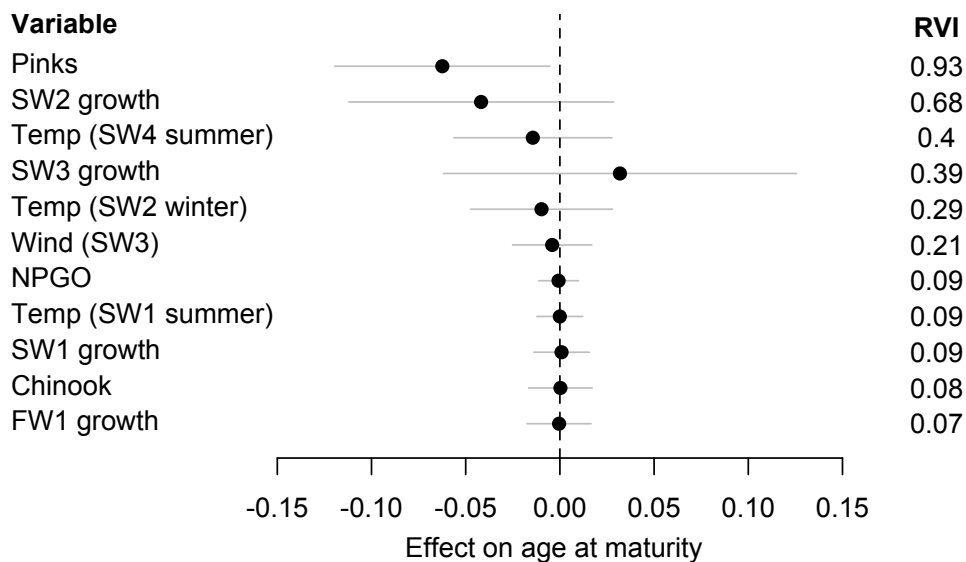
Fig. 22. Effects of ecological variables and growth on Yukon Chinook salmon age at maturity (as indexed by percent of recruits from a given brood year that matured at age 6+).
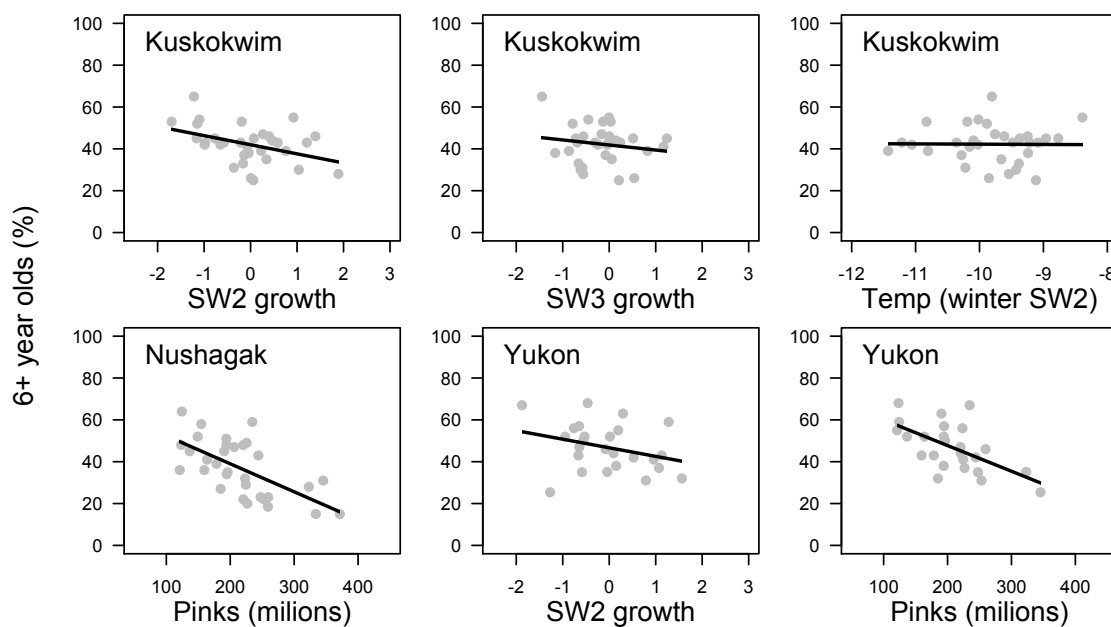
Fig. 23. Relationships between Chinook salmon age at maturity (as indexed by percent of recruits from a given brood year that matured at age 6+) and those variables with statistical support (i.e., RVI >0.5). The black horizontal line is the predicted relationship between age at maturity and each variable (in standardized units).

Table 1. Potential influential environmental variables considered in the study of Yukon, Kuskokwim, and Nushagak Chinook salmon growth, survival and age at maturity. "X"s indicate life stages (FW1, SW1, SW2, SW3, SW4) in which the variable is hypothesized to influence Chinook salmon growth, survival, or age at maturation.

Variable description	Abbreviation	FW	SW1	SW2	SW3	SW4	Source	Reference	Notes
Summer air temperature. Proxy for river temperature during rearing; known to increase Chinook growth	**Temp** (emerge or rear)	X					National Weather Service Forecast Office (http://w2.weather.gov/climate/xmacis.php?wfo=pafg)	Ohlberger et al. 2016	Used air temperatures in May for emergence and June-Sep for rearing. Based on available data, Fairbanks, Bethel and King Salmon were used as the indices for air temperature for the Yukon, Kuskokwim and Nushagak, respectively.
Discharge. Proxy for summer discharge. Hypothesized to reduce growth and productivity during residence in fresh water.	**Flow**	X					USGS (http://waterdata.usgs.gov/nwis/)	Neuswanger et al. 2015	Used data on cubic ft per sec from the upper Yukon (Eagle) and Kuskokwim (confluence with Crooked Creek) for the Kuskokwim and Nushagak. We averaged 1985-1995 for missing Kuskokwim data in 1990.
Spawner abundance. Proxy for intra-specific competition in fresh water.	**Spawn**	X					ADFG and others (see text)		
Timing of ice breakup in river basin. Early ice out hypothesized to increase growth and productivity in fresh water and first year at sea.	**Ice breakup**	X	X				Alaska-Pacific River Forecast Center, NOAA (http://aprfc.arh.noaa.gov)	Ohlberger et al. 2016	Used the timing of ice break-up at Dawson for Yukon salmon and Bethel for Kuskokwim and Nushagak salmon. Missing Bethel values in 1964 and 1965 replaced by avg in 1960-1970.
Sea surface temperature as an index of biotic and abiotic conditions experienced during marine life. Hypothesized to increase growth and productivity.	**SST** (summer, fall, winter and spring)		X	X	X	X	NOAA (http://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl)	Braun et al. 2015; Sharma and Liermann 2010	Used regional continental shelf values for 1st year marine life: northern Bering Sea values for the Yukon and southern Bering Sea values for Kuskokwim and Nushagak. Thereafter, used offshore Bering Sea values.

Variable description	Abbreviation	FW	SW1	SW2	SW3	SW4	Source	Reference	Notes
Eastern Bering Sea Pollock as index of key prey	**Pollock**		X				NOAA (http://www.beringclimate.noaa.gov/data/index.php)	Farley et al. 2009	Used age-1 pollock recruitment.
Arctic Oscillation Index. Sea level pressure variability north of 20°N in winter and index of biotic and abiotic conditions.	**AOI**		X	X	X	X	NOAA (http://www.beringclimate.noaa.gov/data/index.php)	Stachura et al. 2013	
Multivariate El Nino-Southern Oscillation Winter Index. Variability of 6 variables over the tropical Pacific in winter. Index of biotic and abiotic conditions.	**MEI** (winter or summer)		X	X	X	X	NOAA (http://www.esrl.noaa.gov/psd/enso/mei/table.html)	Wolter and Timlin 1998; Stachura et al. 2013; Jeffrey et al. 2016	Winter and summer MEI effects considered. Positively correlated with Chinook size.
Pacific Decadal Oscillation. NP SST variability north of 20°N. Index of biotic and abiotic conditions. Hypothesized to have a positive effect.	**PDO** (winter or summer)		X	X	X	X	University of Washington http://research.jisao.washington.edu/pdo/PDO.latest	Mantua and Hare 2002; Stachura et al. 2013	Considered winter and summer PDO effects.
East Pacific-North Pacific Index. Teleconnection index with positive phase associated with a southward shift and intensification of the Pacific jet stream measured in spring summer. Index of biotic and abiotic conditions.	**ENPI** (summer)		X	X	X	X	NOAA (http://www.beringclimate.noaa.gov/data/index.php)	Stachura et al. 2013	
Aleutian Low Pressure Index. Index of relative intensity of Aleutian Low pressure system in winter. Hypothesized to have positive effect on	**ALPI**		X	X	X	X	Fisheries and Oceans Canada (http://www.pac.dfo-mpo.gc.ca/science/species-especes/climatology-ie/cori-irco/indices/alpi.txt)	Beamish et al. 1997; Stachura et al. 2013	

Variable description	Abbreviation	FW	SW1	SW2	SW3	SW4	Source	Reference	Notes
salmon.									
Strong Winds Index. Wind velocity in the SE Bering Sea. Index of biotic and abiotic conditions.	**Wind**		X	X	X	X	NOAA (http://www.beringclimate.noaa.gov/data/index.php)	Ohlberger et al. 2016	
North Pacific Index. Aleutian Low between Apr-July. Index of biotic and abiotic conditions.	**NPI**		X	X	X	X	NOAA (http://www.beringclimate.noaa.gov/data/index.php)	Ohlberger et al. 2016	
North Pacific Gyre Oscillation. 2nd dominant pattern of sea surface height variability in the NE Pacific.	**NPGO**		X	X	X	X	Di Lorenzo et al. 2008 (http://www.o3d.org/npgo/)	Stachura et al. 2013; Kilduff et al. 2015; Ohlberger et al. 2016; Jeffrey et al. 2016	NPGO is strong indicator of fluctuations in mechanisms driving planktonic ecosystem dynamics & evidence indicates it influences Chinook production.
Eastern Bering Sea Pollock. Index of potential interspecific competitor.	**Pollock**			X	X	X	NOAA (http://www.beringclimate.noaa.gov/data/index.php)		Used total estimated pollock biomass in Eastern Bering Sea.
Regional Chinook abundance. Index of potential intraspecific competitors.	**Chinook**			X	X	X	ADFG (http://www.adfg.alaska.gov/), Ruggerone et al. 2016	Ruggerone et al. 2016	Used commercial catch in from Western Alaska.
Russian pink salmon abundance. Index of potential interspecific competitors during 2nd-4th years at sea.	**Pinks**			X	X	X	Irvine and Ruggerone 2016	Ruggerone et al. 2016	Russian pink salmon, and in particular, Eastern Kamchatka pink salmon, are primary pink salmon stocks in the Bering Sea.

Table 2. Number of Chinook salmon scales measured for each brood year, stock, age group, and gender for the study of Yukon, Kuskokwim, and Nushagak Chinook salmon.

Brood year	Yukon Age-1.3		Yukon Age-1.4		Kuskokwim Age-1.3		Kuskokwim Age-1.4		Nushagak escapement Age-1.3		Nushagak escapement Age-1.4		Nushagak catch Age-1.4	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
1958							25	24						
1959					24	22	14	24						
1960			25	21	25	21	24	19						
1961	2		25	25	21	4								
1962	12	10	23	25										
1963	32	1	25	25										
1964	30	12	22	24										
1965	35	11	25	25										
1966	24	24	24	26										
1967	24	19	25	21										
1968	29	13	23	30										
1969	25	7	25	22			4	5						
1970	25	24	22	24	23	23								
1971	23	24	23	23			22	26					49	
1972	28	12	30	25	28	8	24	30					50	
1973	7	6	25	20	9	3	18	25					15	17
1974	24	23	25	25	9	12							14	19
1975	26	26	23	22			25	25					24	25
1976	23	22	27	25	25	6	24	22						
1977	25	20	26	27	24	5	25	25					18	24
1978	39	9	28	23	30	20	25	26			10	16		
1979	26	2	23	24	32	4	26	25	19	2	3	9	25	25
1980	21	5	23	24	25	16	4	16	2				17	25
1981	25	25	27	25	26	11	24	17			10	17	25	26
1982	26	5	31	22	31	4	22	25	4					
1983	26	8	15	17	24	22	21	26			5	16	17	24
1984	15	6	27	27	24	14	21	22	3	4	11	10	1	6
1985	29	18	27	23	25	16	12	18	22	24	21	25	24	25
1986	30	17	28	26	23	21	10	22	26	25	23	30	25	25
1987	27	18	20	25	29	4	7	10	24	26	25	29	24	25
1988	25	18	24	22	20	3	22	12	25	24	23	30	26	27
1989	23	21	27	26	35	10	25	25	25	25	26	31	25	25
1990	14	2	5	18	27	10	22	21	12	14	9	11	25	25
1991	27	25	19	25	27	15	15	13	17	23	15	26	30	23
1992	24	27	25	26	16		15	20	22	3	26	30	19	25
1993	27	23	24	25	27	17	23	23	27	24	25	26		
1994	14	7	25	17	17	1			26	26	25	25	1	8
1995	12	2	23	25			8	5	28	25	19	26	28	26
1996	19	3	23	22	7		24	17	16	6	18	22	30	25
1997	30	8	18	26	37	2	24	17	20	15	14	20	24	29
1998	40	8	24	23	40	5	23	25	27	22	24	25	19	31
1999	28	4	25	24	37	8	25	25	19	20	19	28	25	26
2000	25	25	25	25	25	24	24	25	25	16	19	26	24	25
2001	25	26	25	20	25	8	5	14	26	25	14	29	26	26
2002	30	16	25	230	15	9	14	23	13	25	10	31		
2003	28	55	25	25	29	17	26	25	29	25	9	22	10	7
2004	25	6	25	25	25	9	16	25	14	9	13	22	15	10
2005	25	25	25	25	25	18	13	25	25	25	17	26	16	16
2006	25	25	25	25	25	6	11	24	25	25	13	25	6	25
2007	25	25	25	25	28	20	14	23	25	25	13	25	12	17
2008	25	17			26	13			25	25				
Sum	1174	735	1154	1350	970	431	726	819	571	508	459	658	689	662

APPENDICES

Appendix A. Chinook growth over time by sex and age.

Fig. A1. Standardized growth over time for male age-1.3 Chinook salmon from the Kuskokwim River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).

Fig. A2. Standardized growth over time for male age-1.4 Chinook from the Kuskokwim River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
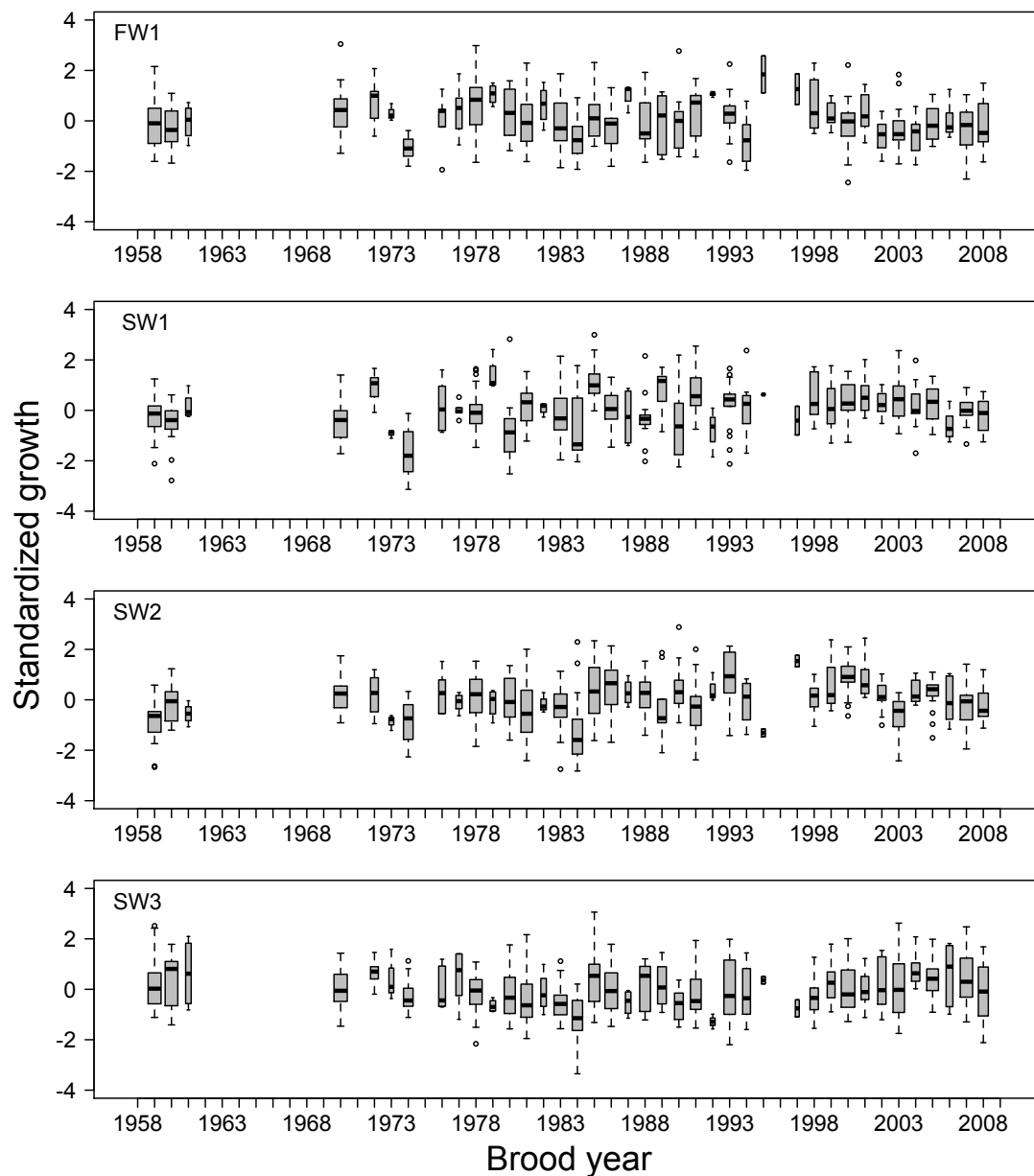
Fig. A3. Standardized growth over time for female age-1.3 Chinook from the Kuskokwim River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
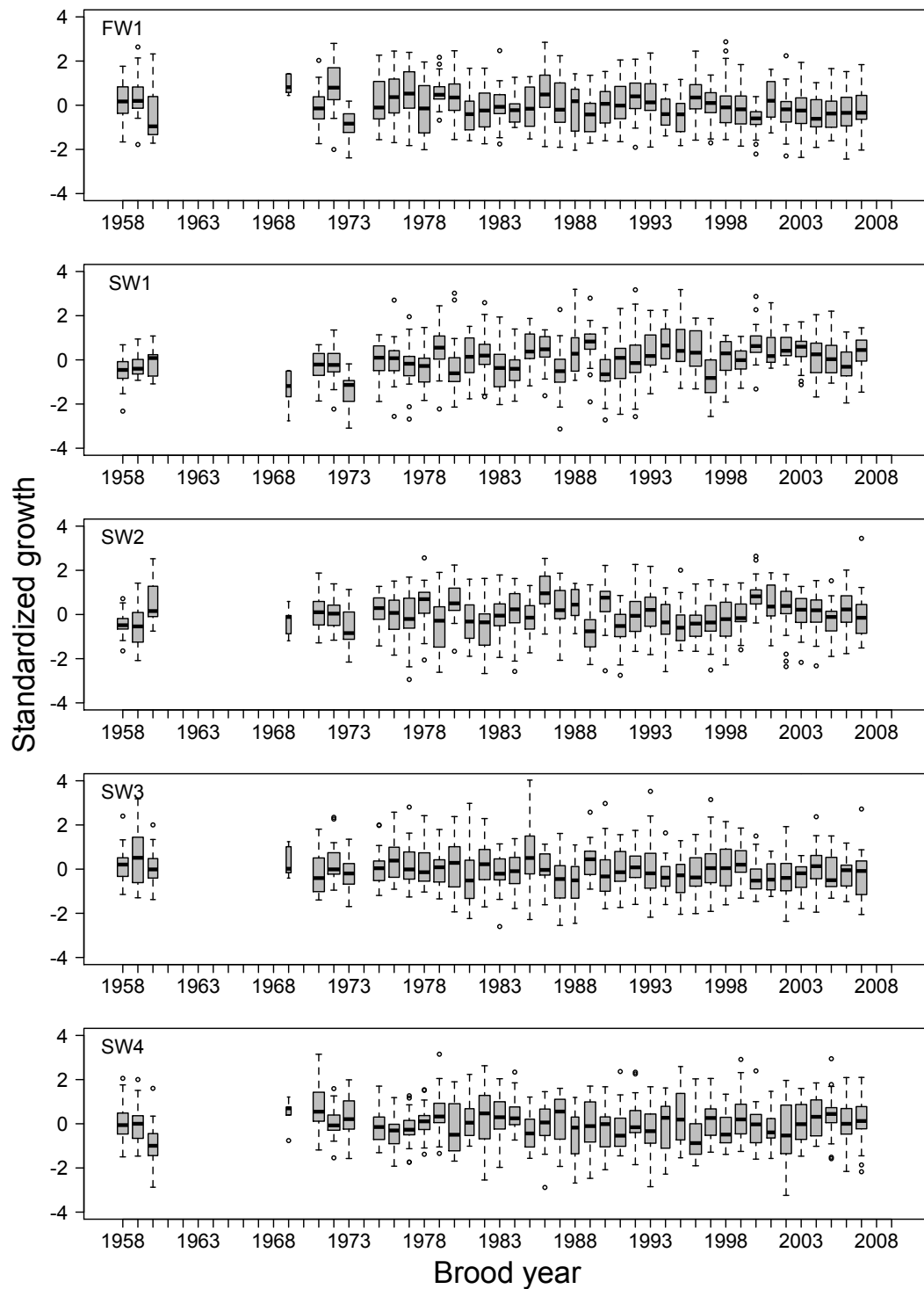
Fig. A4. Standardized growth over time for female age-1.4 Chinook from the Kuskokwim River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
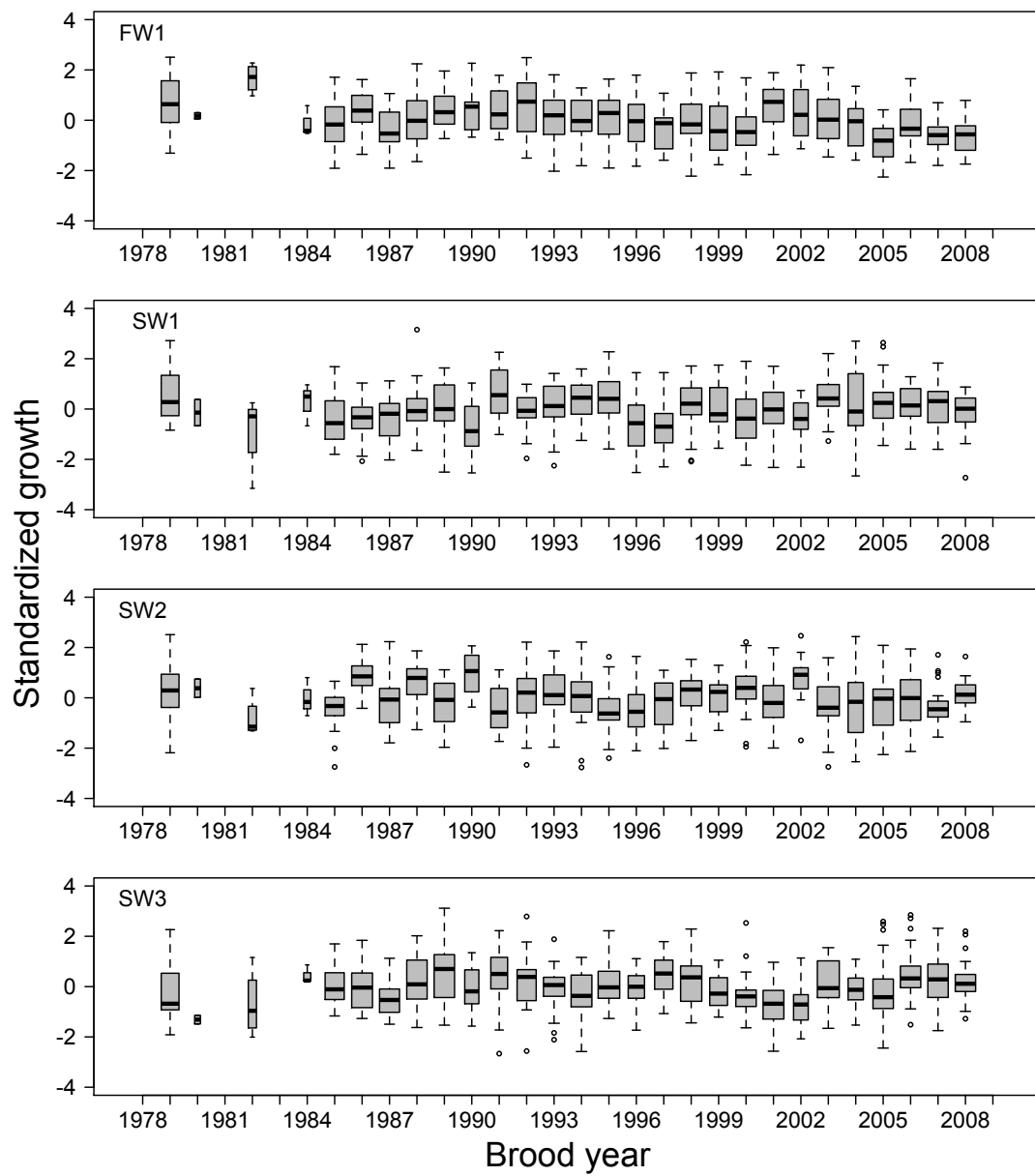
Fig. A5. Standardized growth over time for male age-1.3 Chinook from the Nushagak River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
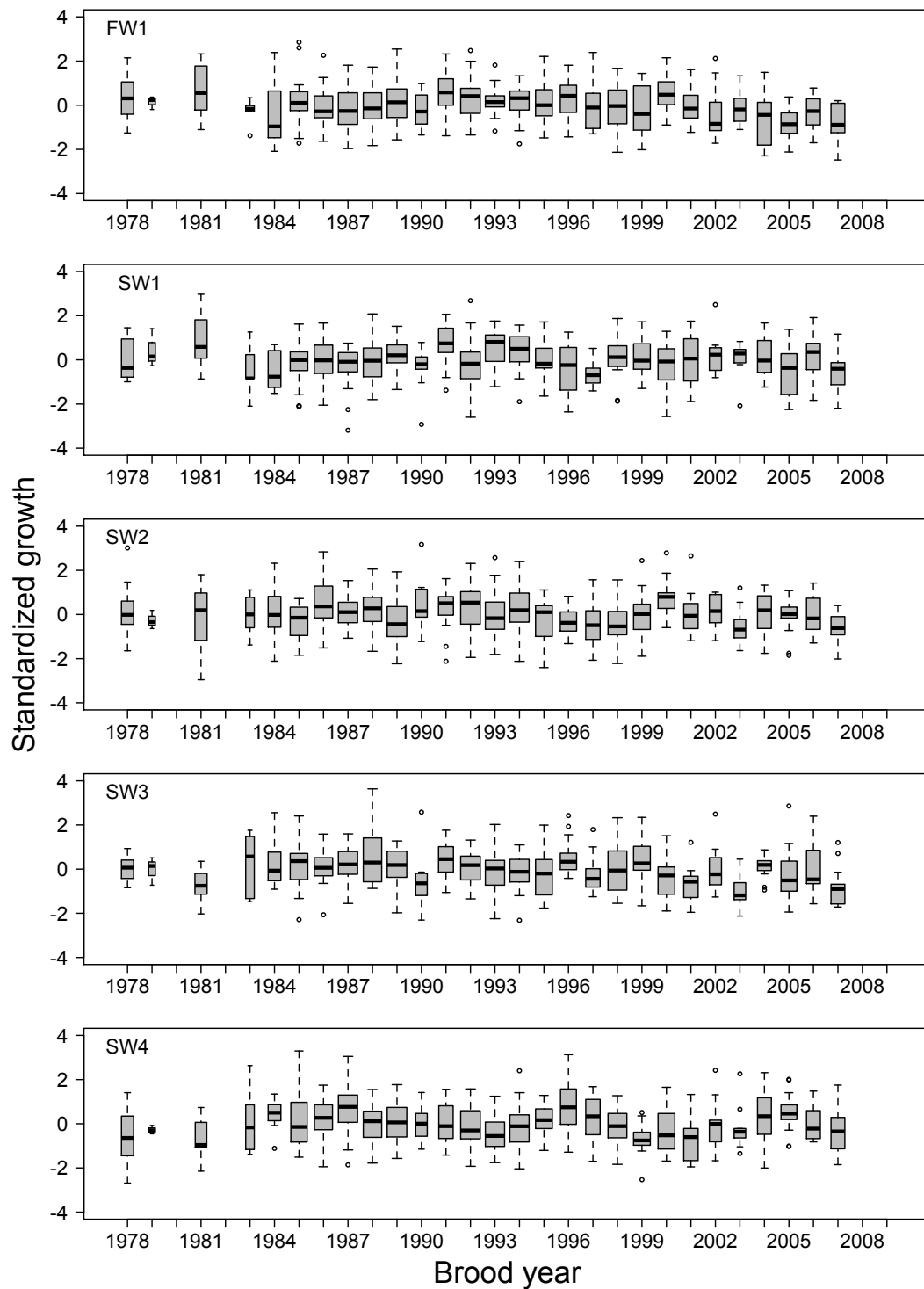
Fig. A6. Standardized growth over time for male age-1.4 Chinook from the Nushagak River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
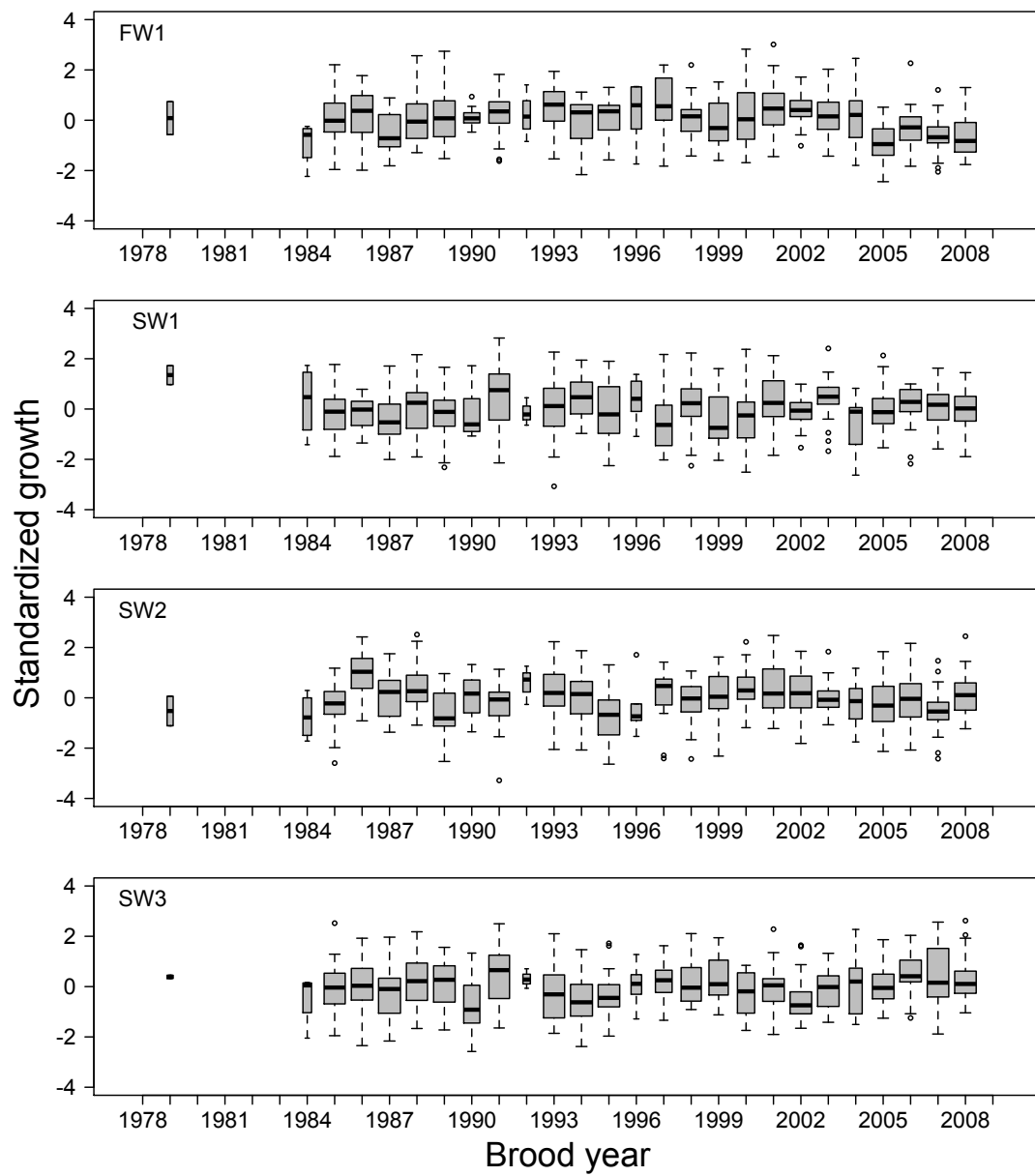
Fig. A7. Standardized growth over time for female age-1.3 Chinook from the Nushagak River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
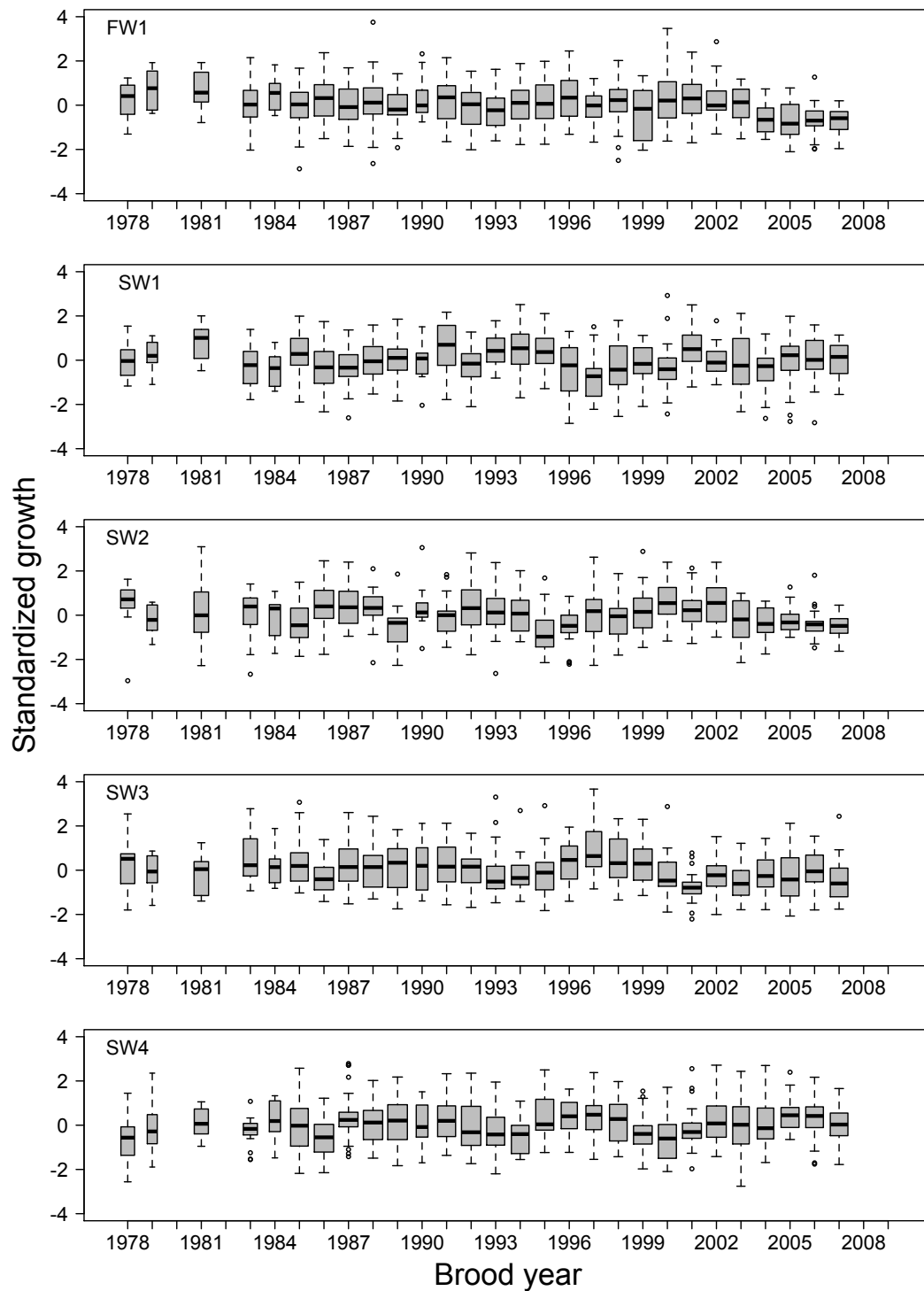
Fig. A8. Standardized growth over time for female age-1.4 Chinook from the Nushagak River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
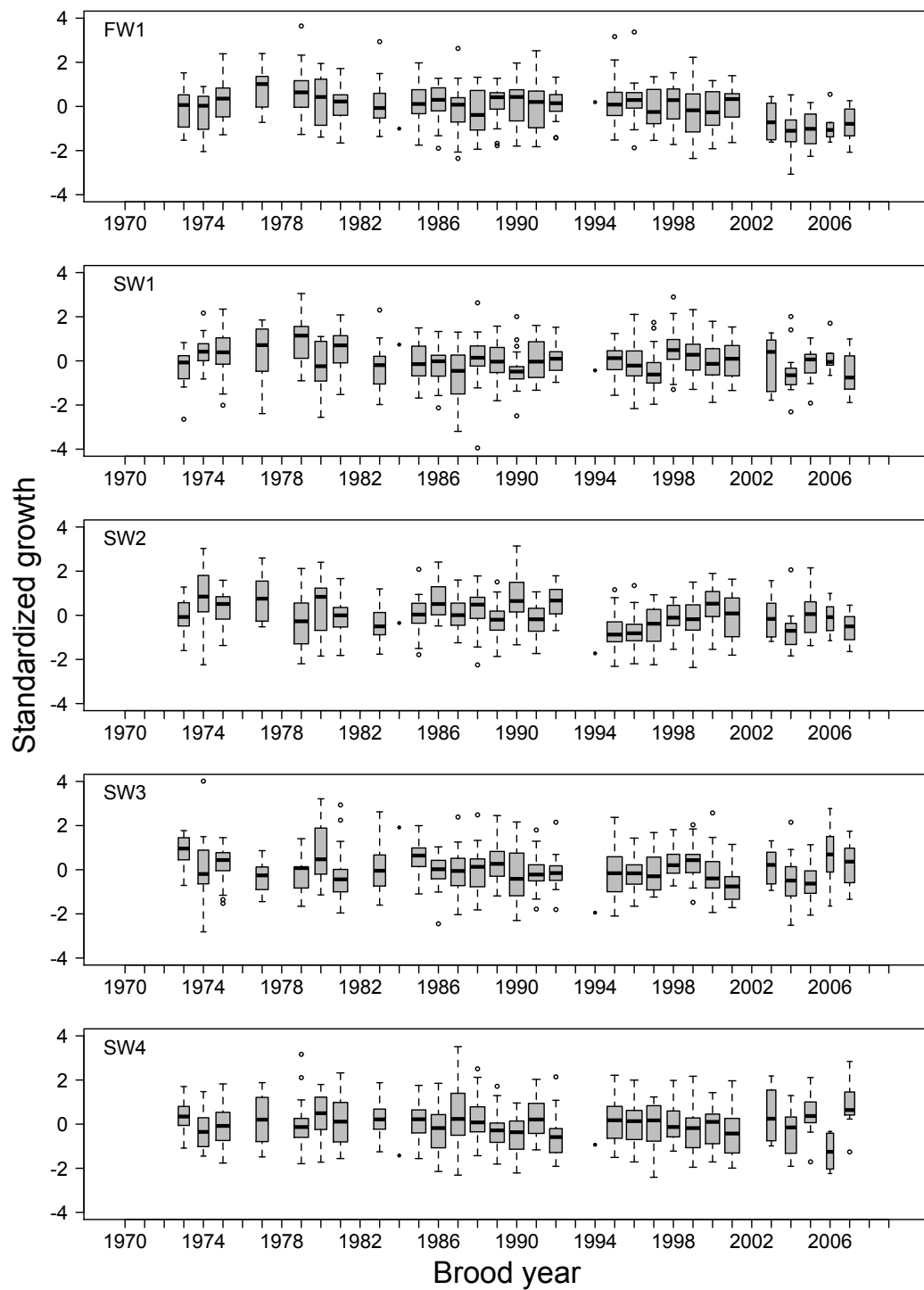
Fig. A9. Standardized growth over time for male age-1.4 Chinook from the Nushagak River, Alaska (based on scales collected in commercial gillnet fisheries). Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
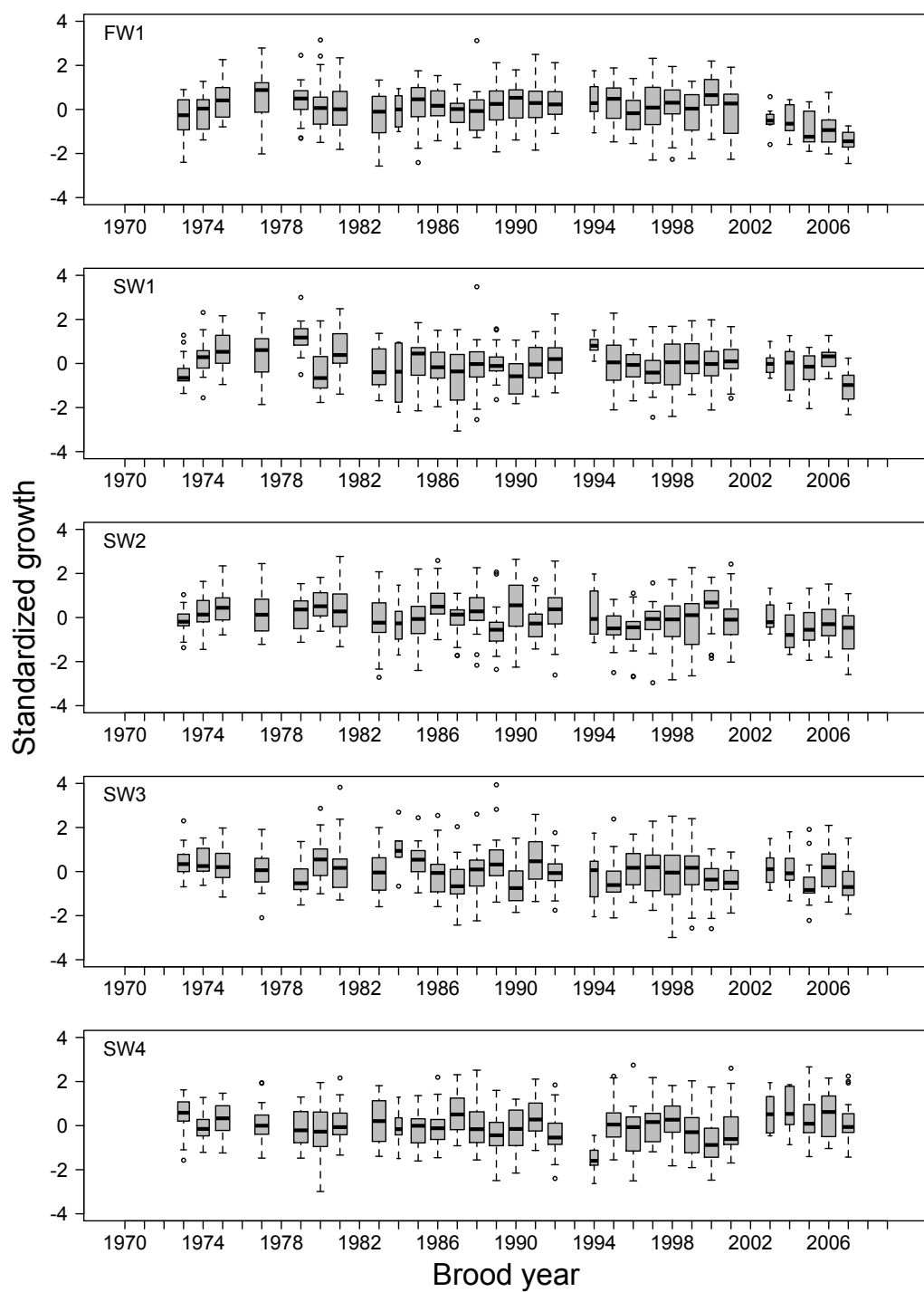
Fig. A10. Standardized growth over time for female age-1.4 Chinook from the Nushagak River, Alaska (based on scales collected in commercial gillnet fisheries). Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
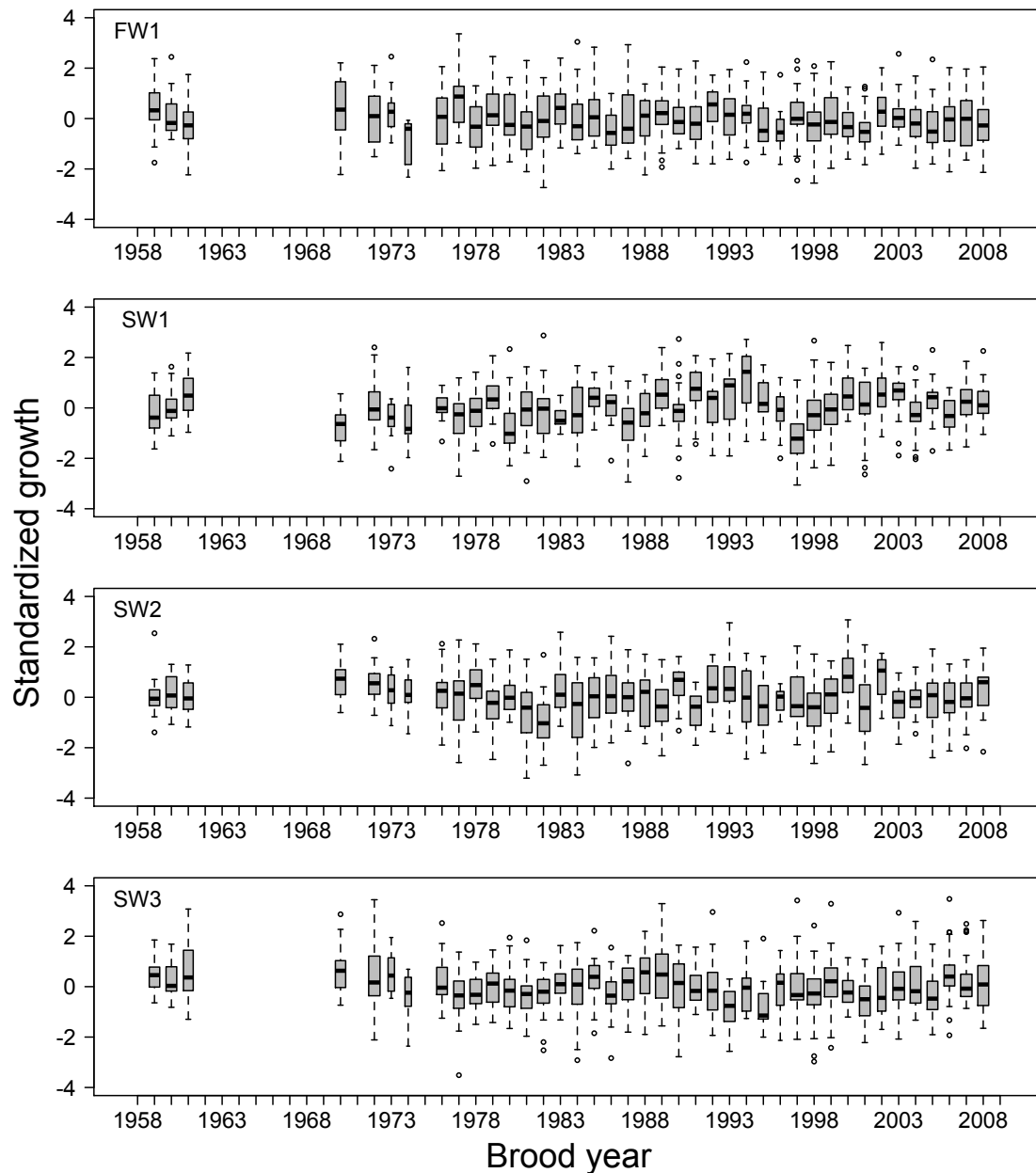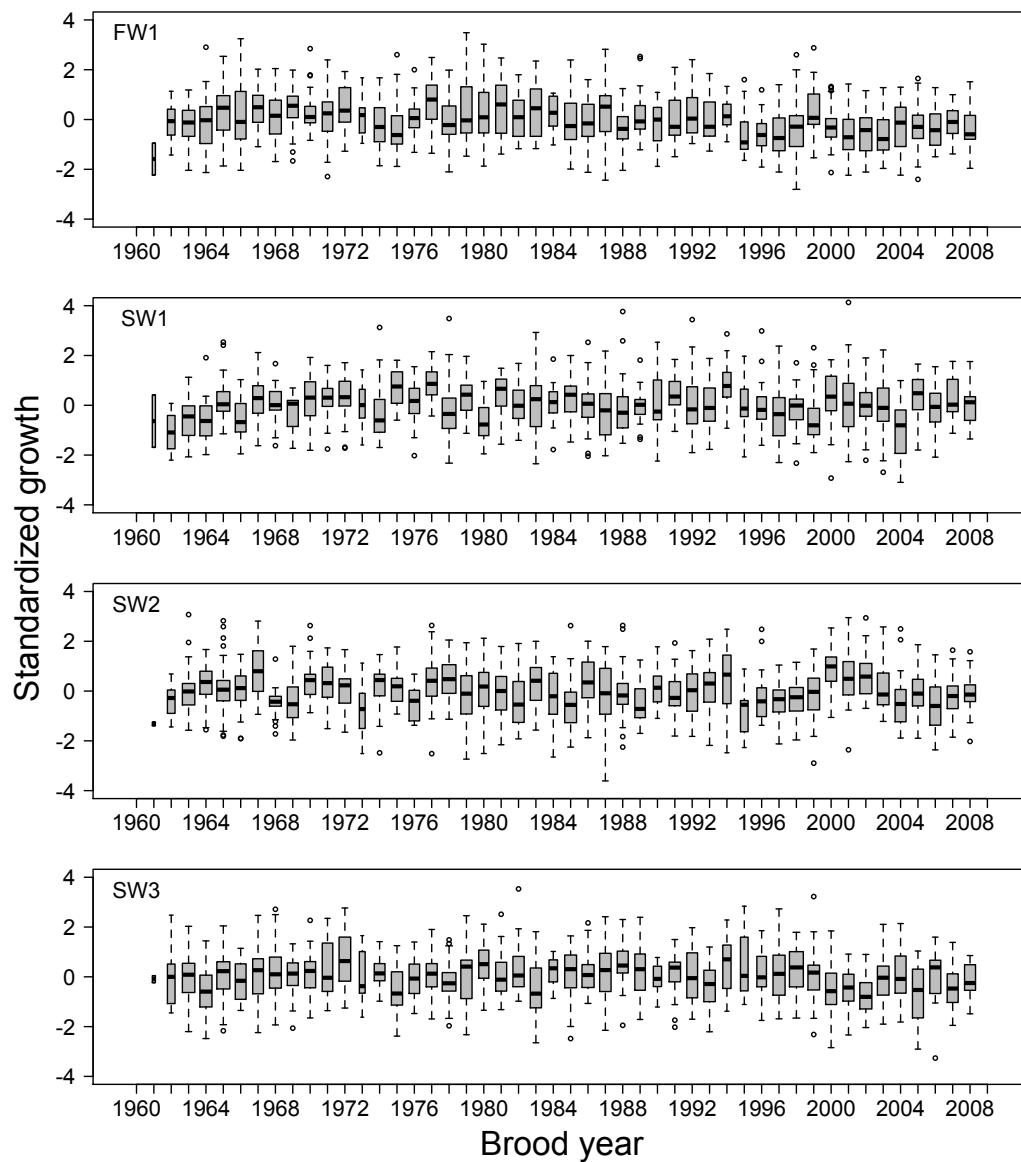
Fig. A11. Standardized growth over time for male age-1.3 Chinook from the Yukon River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
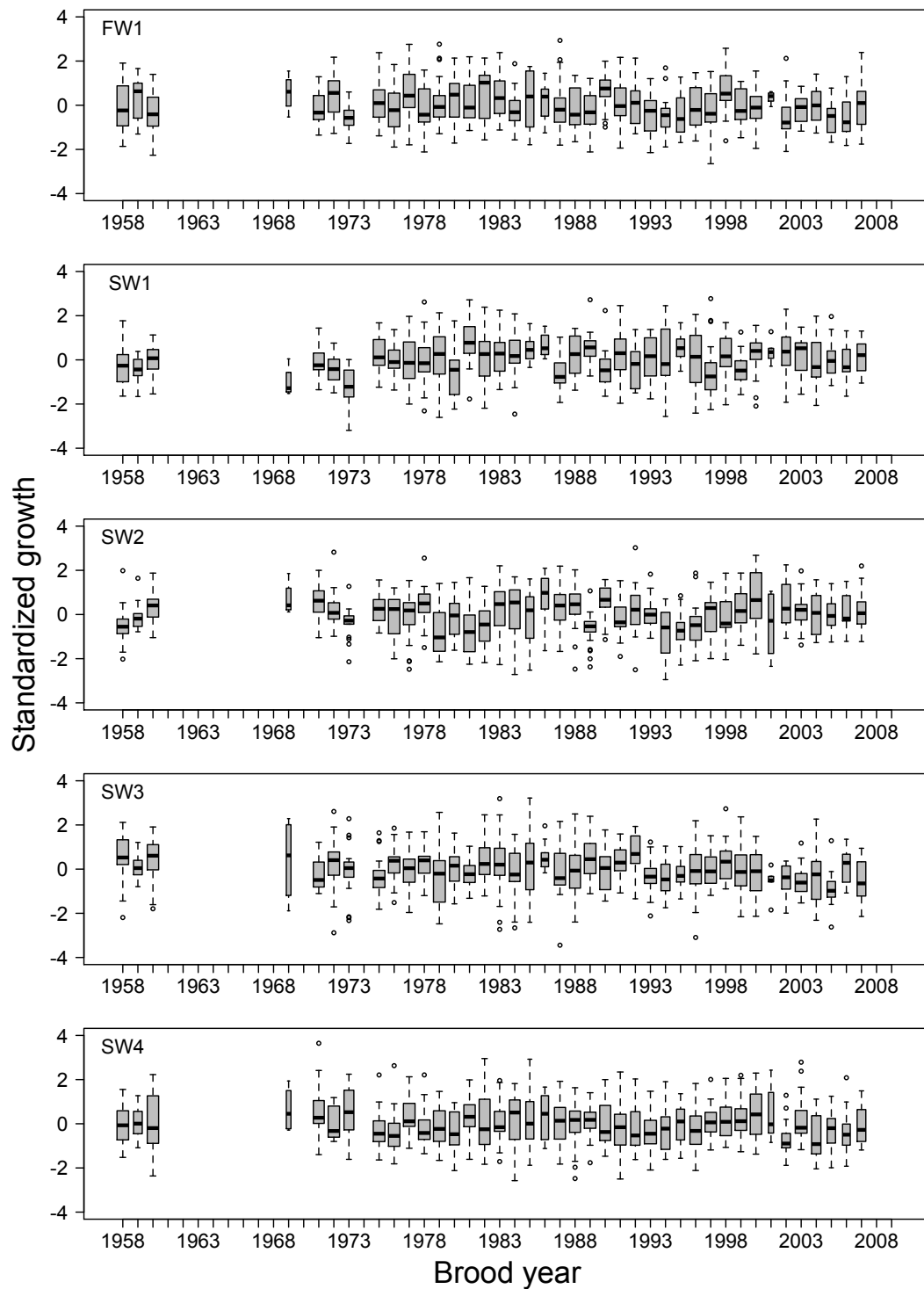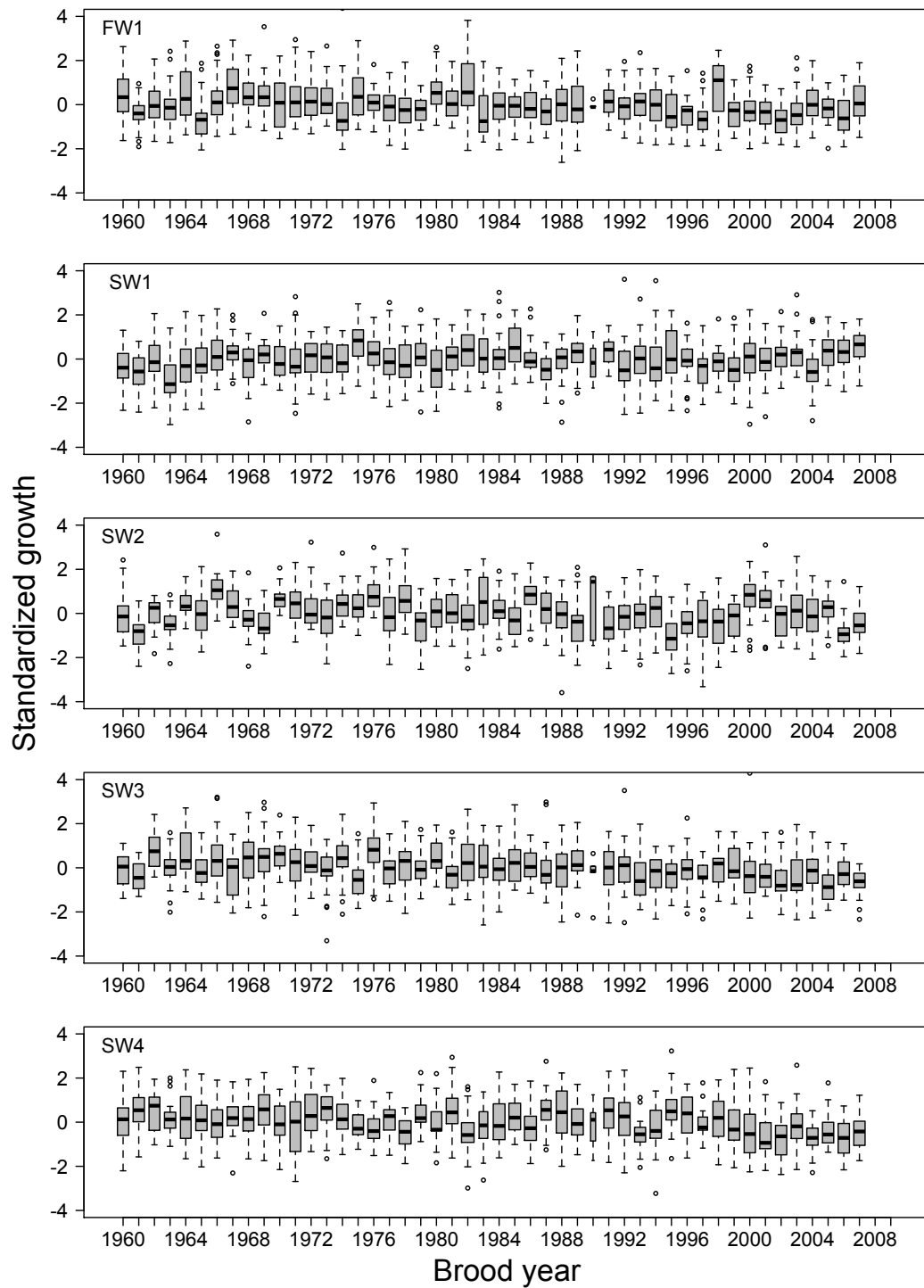
Fig. A12. Standardized growth over time for male age-1.4 Chinook from the Yukon River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
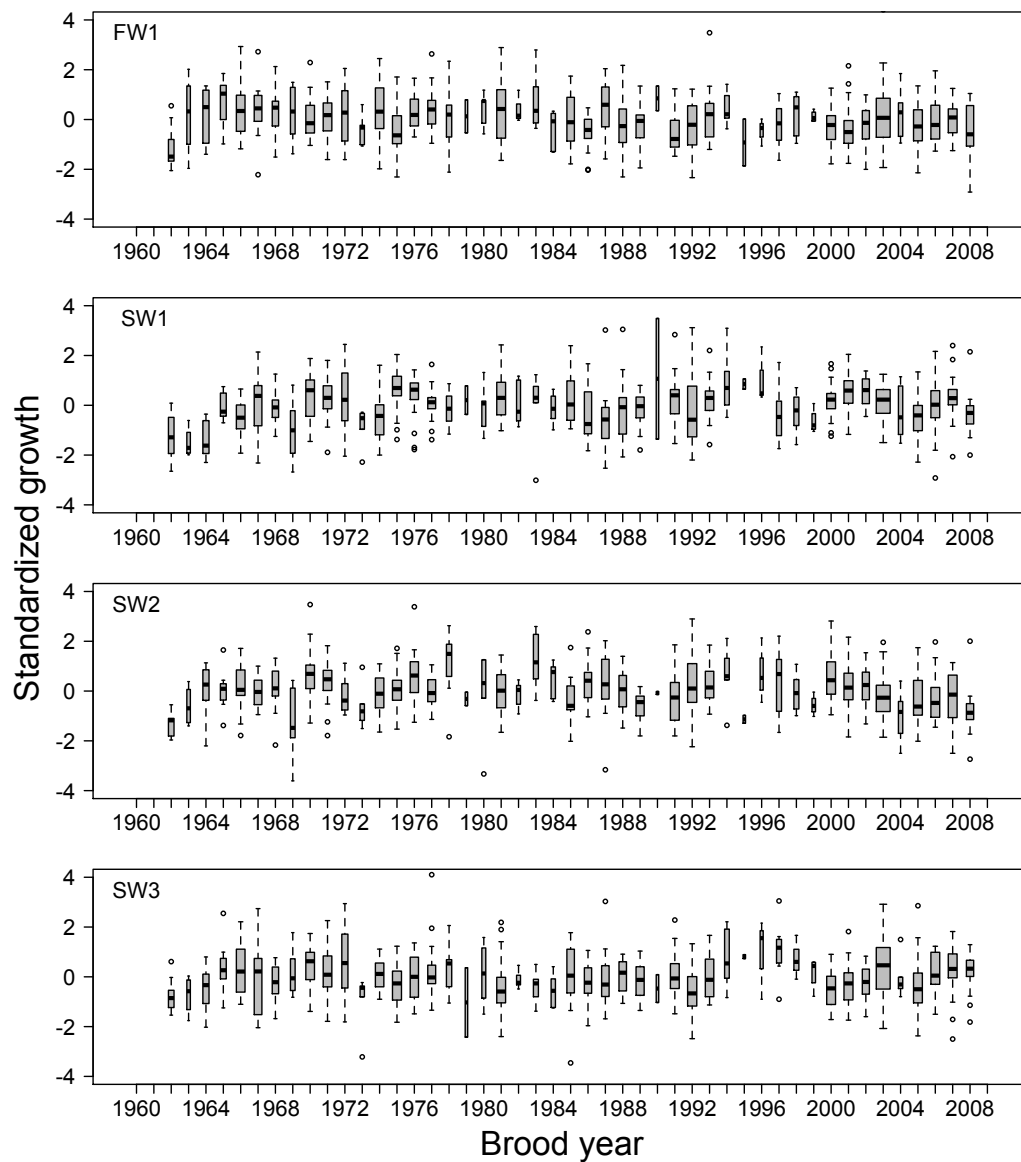
Fig. A13. Standardized growth over time for female age-1.3 Chinook from the Yukon River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).
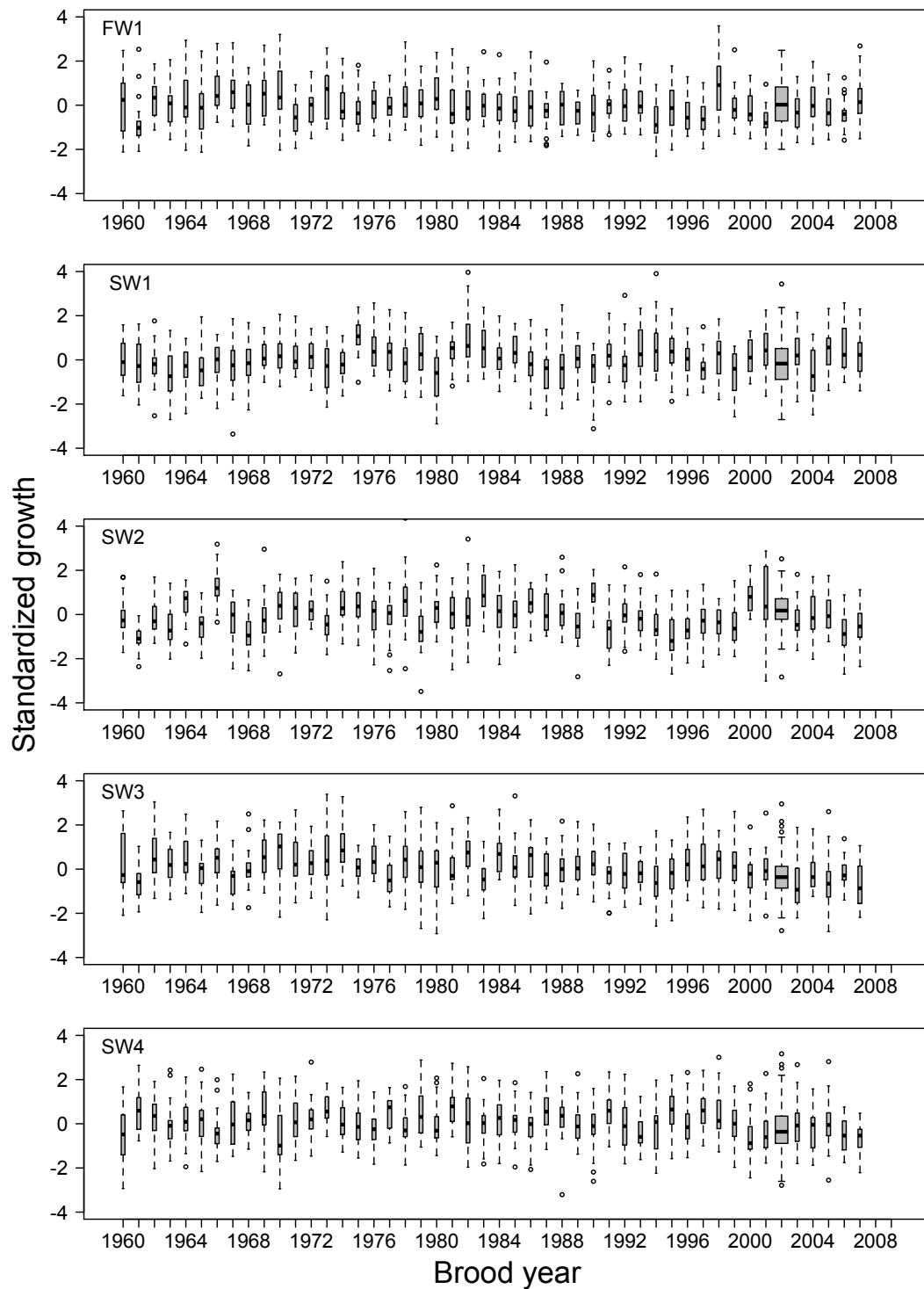
Fig. A14. Standardized growth over time for female age-1.4 Chinook from the Yukon River, Alaska. Width of the boxplots is a function of the relative sample size (wider boxes indicate larger sample size).

Appendix B. Model selection tables for analyses of ecological influences on growth.

Table B1. Summary of model selection statistics for analyses of hypotheses related to ecological effects on growth in fresh water in Chinook salmon in three Alaskan rivers (Yukon, Kuskokwim, and Nushagak). An "X" indicates the variable was included in the model for that row. Models for each set of hypotheses are ordered by increasing values of the small- sample Akaike information criterion (AICc) with the top ten models shown. Also shown are the log likelihoods (LL), differences in AICc from the AICc of the top model (ΔAICc), and Akaike model weights (w_i).

Age	Temp (emerge)	Temp (rear)	Flow	Ice breakup	Spawn	Sex	LL	Δ AICc	w_i
X			X	X		X	-10098	0.00	0.21
X		X		X		X	-10098	1.32	0.11
X						X	-10100	1.56	0.10
X			X			X	-10099	1.56	0.10
X				X		X	-10099	1.76	0.09
X	X		X			X	-10099	2.48	0.06
X		X				X	-10100	2.68	0.06
X		X	X			X	-10099	3.25	0.04
X	X			X		X	-10099	3.32	0.04
X	X					X	-10100	3.52	0.04

Table B2. Summary of model selection statistics for analyses of hypotheses related to ecological effects on growth of Chinook salmon from three rivers in western Alaska (Yukon, Kuskokwim, and Nushagak) in the first year at sea. Top ten models shown.

Age	ALPI	AOI	ENPI (sum)	Ice breakup	MEI (sum)	MEI (win)	NPI (sum)	NPGO	PDO	Pollock	Sex	SST (fall)	SST (sum)	SST (spr)	SST (win)	Wind	LL	Δ AICc	w_i
X	X			X									X				-12762	0.00	0.18
X	X									X			X				-12762	0.29	0.16
X				X		X							X				-12763	1.80	0.08
X									X	X			X				-12763	2.60	0.05
X						X				X			X				-12764	2.90	0.04
X				X							X		X				-12764	3.18	0.04
X				X					X				X				-12764	3.52	0.03
X				X						X			X				-12764	3.72	0.03
X				X								X	X				-12764	3.74	0.03
X										X	X		X				-12764	3.88	0.03

Table B3. Summary of model selection statistics for analyses of hypotheses related to ecological effects on growth of Chinook salmon from three rivers in western Alaska (Yukon, Kuskokwim, and Nushagak) in the second year at sea. Top ten models shown.

Age	AOI	Pinks	ENPI (sum)	SST (fall)	MEI (sum)	MEI (win)	NPI (sum)	NPGO	PDO	Pollock	Sex	SST (spr)	Chinook	Wind	SST (win)	LL	Δ AICc	w_i
X								X			X				X	-12463	0.00	0.24
X							X				X				X	-12465	3.64	0.04
X											X				X	-12466	3.84	0.03
X			X								X				X	-12465	4.54	0.02
X											X		X		X	-12465	4.55	0.02
X	X							X			X					-12465	4.84	0.02
X								X			X					-12466	5.01	0.02
X		X									X				X	-12465	5.04	0.02
X	X										X				X	-12465	5.16	0.02
X							X				X					-12466	5.26	0.02

Table B4. Summary of model selection statistics for analyses of hypotheses related to ecological effects on growth of Chinook salmon from three rivers in western Alaska (Yukon, Kuskokwim, and Nushagak) in the third year at sea. Top ten models shown.

Age	AOI	ENPI (sum)	SST (fall)	MEI (sum)	MEI (win)	NPI (sum)	PDO	Pinks	Pollock	Sex	SST (spr)	SST (sum)	Chinook	Wind	SST (win)	LL	Δ AICc	w_i
X								X		X				X		-12629	0.00	0.78
X							X	X		X						-12631	4.99	0.06
X								X		X			X			-12631	5.16	0.06
X								X	X	X						-12632	6.43	0.03
X	X							X		X						-12633	7.84	0.02
X			X					X		X						-12633	8.42	0.01
X		X						X		X						-12633	8.74	0.01
X								X		X						-12634	8.77	0.01
X				X				X		X						-12633	8.99	0.01
X								X		X		X				-12634	9.98	0.01

Table B5. Summary of model selection statistics for analyses of hypotheses related to ecological effects on growth of Chinook salmon from three rivers in western Alaska (Yukon, Kuskokwim, and Nushagak) in the fourth year at sea. Top ten models shown.

AOI	ENPI (sum)	SST (fall)	MEI (sum)	MEI (win)	NPI (sum)	Pinks	Pollock	Sex	SST (spr)	SST (sum)	Chinook	Wind	SST (win)	LL	Δ AICc	w_i
						X		X		X	X	X		-7238	0.00	
		X				X		X				X		-7239	2.60	
						X			X	X	X	X		-7240	3.58	
								X		X	X	X		-7241	3.63	
		X						X		X	X	X		-7240	3.81	
						X		X	X				X	-7240	3.87	
				X		X		X					X	-7240	4.12	
					X			X		X	X	X		-7240	4.29	
	X							X		X	X	X		-7240	4.42	
						X		X	X			X		-7240	4.47	

Appendix C. Model code for age-structured Ricker stock-recruitment model with growth and environmental covariates.

```
model {
 # priors for SR portion
 lnalpha ~ dunif(0, 4)                # prior for log of alpha
 beta ~ dunif(0,10)                   # prior for beta
 tau.R ~ dgamma(0.01,0.01)            # white noise process error
 rho ~ dunif(-0.99, 0.99)             # autocorrelation coefficient
 log.resid.0 ~ dnorm(0, tau.red)      # starting residual for AR1 process
 for(i in 1:5){eta[i] ~ dunif(-1,1) } # priors for growth effects
 for(i in 1:9){phi[i] ~ dunif(-1,1)}  # priors for extrinsic effects
 for(i in 1:15){
 w[i] ~ dbern(.5)                     # priors for parameter inclusion probs
        }

 # Ricker SR with Growth effects, Extrinsic effecs and AR1 process
 for (y in (A+a.min):nRyrs) {
   log.R[y] ~ dnorm(log.R.mean.2[y], tau.R)
   R[y] <- exp(log.R[y])
   log.R.mean.1[y] <- lnalpha + log(S[y-a.max]) - beta * S[y-a.max] +
         growth.effects[y-a.max] + extr.effects[y-a.max]

 growth.effects[y-a.max] <- w[1]*eta[1]*cFW1[y-a.max] + w[2]*eta[2]*cSW1[y-a.max] +
   w[3]*eta[3]*cSW2[y-a.max] + w[4]*eta[4]*cSW3[y-a.max] + w[5]*eta[5]*cSW4[y-a.max]

 extr.effects[y-a.max] <- w[6]*phi[1]*iceoff[y-a.max] + w[7]*phi[2]*summertempSW1[y-a.max] +
        w[8]*phi[3]*wintertempSW2[y-a.max] + w[9]*phi[4]*windSW3[y-a.max] +
        w[10]*phi[5]*summertempSW4[y-a.max] +
        w[11]*phi[6]*pinks[y-a.max] + w[12]*phi[7]*npgo[y-a.max] +
        w[13]*phi[8]*flow[y-a.max]

   log.resid.a[y] <- log.R[y] - log.R.mean.1[y]
}

log.R.mean.2[A+a.min] <- log.R.mean.1[A+a.min] + w[15]*rho * log.resid.0

for (y in (A+a.min+1):nRyrs) {
  log.R.mean.2[y] <- log.R.mean.1[y] + w[15]*rho * log.resid.a[y-1]
}

#derived quantities
tau.red <- tau.R * (1 - rho * rho)
sigma.red <- 1 / sqrt(tau.red)
sigma.R <- 1 / sqrt(tau.R)
alpha <- exp(lnalpha)
log.resid <- log.resid.a[(A+a.min):nRyrs]

# First `a.max` years of recruits, for which there is no spawner link
mean.log.R0 ~ dnorm(0, 1E-4)
mean.R0 <- exp(mean.log.R0)
tau.R0 ~ dgamma(0.1,0.1)
sigma.R0 <- 1/sqrt(tau.R0)
for (y in 1:a.max) {
  log.R[y] ~ dnorm(mean.log.R0, tau.R0)
  R[y] <- exp(log.R[y])
}

# biological reference points: derived quantities
lnalpha.c <- lnalpha + (sigma.R * sigma.R)/2/(1-rho * rho)
S.max <- 1/beta
```

```
  S.eq <- lnalpha.c * S.max
  S.msy <- S.eq * (0.5 - 0.07 * lnalpha.c)
  U.msy <- lnalpha.c * (0.5 - 0.07 * lnalpha.c)

  # Maturity schedule: we assume that the age proportions are constant through time
  prob[1] ~ dbeta(1,1)
  prob[2] ~ dbeta(1,1)
  prob[3] ~ dbeta(1,1)
  pi[1]<- prob[1]
  pi[2] <- prob[2] * (1 - pi[1])
  pi[3] <- prob[3] * (1 - pi[1] - pi[2])
  pi[4] <- 1 - pi[1] - pi[2] - pi[3]

  # Calculate the numbers at age matrix
  for (t in 1:Y) {
   for(a in 1:A){
     N.ta[t,a] <- R[t+A-a] * pi[a]
   }
  }

  ## OBSERVATION SUBMODEL ##
  # multinomial scale sampling
  for (t in 1:Y) {
   for (a in 1:A) {
     q[t,a] <- N.ta[t,a]/N[t]
   }
   x[t,1:A] ~ dmulti(q[t,1:A], n[t])
  }

  for (t in 1:Y) {
   # get observation tau's from assumed CV's
   log.sigma.C[t] <- sqrt(log((C.cv[t]^2) + 1))
   log.tau.C[t] <- 1/log.sigma.C[t]^2
   log.sigma.S[t] <- sqrt(log((S.cv[t]^2) + 1))
   log.tau.S[t] <- 1/log.sigma.S[t]^2

   # catch model
   U[t] ~ dunif(0.01, 0.99)
   N[t] <- sum(N.ta[t,1:A])
   S[t] <- N[t] * (1 - U[t])

   C[t] <- N[t] * U[t]
   log.C[t] <- log(C[t])
   C.obs[t] ~ dlnorm(log.C[t], log.tau.C[t])

   # escapement model

   log.S[t] <- log(S[t])
   S.obs[t] ~ dlnorm(log.S[t], log.tau.S[t])
  }
}
```

Appendix D. Sensitivity of recruitment covariate parameter estimates to assumptions about uncertainty in estimates of escapement, harvest, and age proportion.

Table D1. Parameter inclusion probabilities for the Kuskokwim River, Alaska, under a range of assumptions about input data precision. Parameters with inclusion probabilities ≥ 0.5 (i.e., when included in the model result in optimal predictive abilities; Barbieri and Berger 2004) are highlighted in bold. See equations 3 and 4 for covariates.

Param.	Harvest CV			Escapement CV			Age sample size		
	0.5x	1x	2x	0.5x	1x	2x	0.5x	1x	2x
η_1	0.12	0.11	0.13	0.12	0.11	0.11	0.13	0.11	0.10
η_2	**0.84**	**0.83**	**0.85**	**0.59**	**0.83**	**0.95**	**0.59**	**0.83**	**0.95**
η_3	0.09	0.09	0.11	0.09	0.09	0.11	0.10	0.09	0.09
η_4	0.10	0.11	0.10	0.14	0.11	0.14	0.12	0.11	0.09
η_5	0.13	0.13	0.13	0.15	0.13	0.11	0.16	0.13	0.09
φ_1	0.20	0.21	0.20	0.48	0.21	0.11	0.41	0.21	0.10
φ_2	0.10	0.10	0.10	0.19	0.10	0.08	0.16	0.10	0.07
φ_3	0.12	0.11	0.09	0.12	0.11	0.08	0.13	0.11	0.10
φ_4	0.08	0.07	0.07	0.09	0.07	0.06	0.09	0.07	0.05
φ_5	0.09	0.08	0.08	0.09	0.08	0.09	0.09	0.08	0.08
φ_6	0.42	0.43	0.41	0.32	0.43	0.40	0.09	0.43	0.11
φ_7	**0.52**	**0.50**	0.41	0.19	**0.50**	**0.67**	0.24	**0.50**	0.49
φ_8	0.13	0.13	0.12	0.20	0.13	0.08	0.16	0.13	**0.78**
ρ	**0.83**	**0.83**	**0.78**	**0.67**	**0.83**	**0.71**	**0.69**	**0.83**	**0.93**

Table D2. Parameter inclusion probabilities for the Nushagak River, Alaska, under a range of
assumptions about input data precision. Parameters with inclusion probabilities $\geq$ 0.5
(i.e., when included in the model result in optimal predictive abilities; Barbieri and Berger
2004) are highlighted in bold.

Param.	Harvest CV			Escapement CV			Age sample size		
	0.5x	1x	2x	0.5x	1x	2x	0.5x	1x	2x
η_1	0.16	0.16	0.15	0.21	0.16	0.21	0.23	0.16	0.14
η_2	**0.54**	**0.52**	0.48	0.20	**0.52**	0.20	0.22	**0.52**	0.69
η_3	0.16	0.16	0.17	0.22	0.16	0.22	0.16	0.16	0.16
η_4	0.29	0.29	0.32	0.52	0.29	0.52	0.45	0.29	0.25
η_5	**0.56**	**0.56**	**0.59**	**0.75**	**0.56**	**0.75**	**0.67**	**0.56**	**0.43**
φ_1	0.10	0.10	0.10	0.11	0.10	0.11	0.14	0.10	0.08
φ_2	0.11	0.10	0.11	0.13	0.10	0.13	0.10	0.10	0.12
φ_3	0.19	0.19	0.21	0.20	0.19	0.20	0.16	0.19	0.15
φ_4	0.10	0.11	0.11	0.14	0.11	0.14	0.12	0.11	0.09
φ_5	0.19	0.20	0.23	0.29	0.20	0.29	0.24	0.20	0.14
φ_6	0.15	0.15	0.14	0.19	0.15	0.19	0.17	0.15	0.15
φ_7	0.65	**0.65**	**0.60**	0.37	**0.65**	0.37	0.36	**0.65**	**0.75**
φ_8	0.09	0.09	0.09	0.10	0.09	0.10	0.09	0.09	0.09
ρ	**0.89**	**0.87**	**0.84**	**0.65**	**0.87**	**0.65**	**0.75**	**0.87**	**0.93**

Table D3. Parameter inclusion probabilities for the Yukon River, Alaska, under a range of
assumptions about input data precision. Parameters with inclusion probabilities ≥0.5
(i.e., when included in the model result in optimal predictive abilities; Barbieri and Berger
2004) are highlighted in bold.

Param.	Harvest CV			Escapement CV			Age sample size		
	0.5x	1x	2x	0.5x	1x	2x	0.5x	1x	2x
η_1	0.26	0.26	0.24	0.29	0.26	0.13	0.30	0.26	0.23
η_2	0.16	0.15	0.15	0.18	0.15	**0.85**	0.18	0.15	0.16
η_3	0.19	0.19	0.19	0.33	0.19	0.11	0.21	0.19	0.18
η_4	0.22	0.22	0.21	0.25	0.22	0.10	0.22	0.22	0.21
η_5	0.19	0.18	0.17	0.21	0.18	0.13	0.21	0.18	0.17
φ_1	0.43	0.42	0.43	**0.54**	0.42	0.20	0.43	0.42	0.39
φ_2	0.46	0.44	0.41	**0.57**	0.44	0.10	0.47	0.44	0.38
φ_3	0.20	0.20	0.19	0.21	0.20	0.09	0.22	0.20	0.20
φ_4	0.13	0.13	0.13	0.13	0.13	0.07	0.12	0.13	0.13
φ_5	0.27	0.25	0.21	0.22	0.25	0.08	0.24	0.25	0.23
φ_6	**0.64**	**0.66**	**0.66**	**0.72**	**0.66**	**0.41**	**0.71**	**0.66**	**0.59**
φ_7	0.17	0.18	0.21	0.31	0.18	0.41	0.17	0.18	0.18
φ_8	0.13	0.13	0.12	0.13	0.13	0.12	0.14	0.13	0.11
ρ	**0.70**	**0.69**	**0.67**	**0.77**	**0.69**	**0.78**	**0.74**	**0.69**	**0.61**

Table E1. Summary of model selection statistics for analyses of hypotheses related to growth and extrinsic environmental influences on Kuskokwim River, Alaska, Chinook salmon age at maturity. An "X" indicates variables included in the model for that row. Models for each set of hypotheses are ordered by increasing values of the small-sample Akaike information criterion (AICc) with top ten models shown. Also shown are log likelihoods (LL), differences in AICc from the AICc of the top model (ΔAICc), and Akaike model weights (w_i).

FW1	SW1	SW2	SW3	Temp (Sum SW1)	NPGO	Temp (Win SW2)	Wind	Pinks	Temp (Sum SW4)	Chinook	LL	Δ AICc	w_i
		X	X	X		X					48.49	0.00	0.16
		X	X			X	X				48.05	0.88	0.10
		X	X			X					46.18	1.30	0.08
		X	X				X				45.55	2.56	0.04
		X	X			X				X	46.94	3.09	0.03
		X		X		X					45.13	3.40	0.03
		X		X		X			X		46.77	3.43	0.03
		X				X			X		45.01	3.64	0.03
		X	X			X			X		46.57	3.82	0.02
	X	X	X			X					46.54	3.89	0.02

Table E2. Summary of model selection statistics for analyses of hypotheses related to growth and extrinsic environmental influences on Nushagak River, Alaska Chinook salmon age at maturity. An "X" indicates variables included in the model for that row. Models for each set of hypotheses are ordered by increasing values of the small-sample Akaike information criterion (AICc) with top ten models shown. Also shown are log likelihoods (LL), differences in AICc from the AICc of the top model (ΔAICc), and Akaike model weights (w_i).

FW1	SW1	SW2	SW3	Temp (Sum SW1)	NPGO	Temp (Win SW2)	Wind	Pinks	Temp (Sum SW4)	Chinook	LL	Δ AICc	w_i
								X			24.93	0.00	0.04
							X	X			26.29	0.27	0.03
		X						X			25.79	1.26	0.02
					X			X			25.62	1.61	0.02
X							X	X			27.06	2.00	0.01
					X		X	X			27.02	2.06	0.01
	X						X	X			26.93	2.25	0.01
		X						X			25.25	2.33	0.01
		X							X		25.25	2.34	0.01
					X			X			25.22	2.40	0.01

Table E3. Summary of model selection statistics for analyses of hypotheses related to growth and extrinsic environmental influences on Yukon River, Alaska, Chinook salmon age at maturity. An "X" indicates variables included in the model for that row. Models for each set of hypotheses are ordered by increasing values of the small-sample Akaike information criterion (AICc) with top ten models shown. Also shown are log likelihoods (LL), differences in AICc from the AICc of the top model (ΔAICc), and Akaike model weights (w_i).

FW1	SW1	SW2	SW3	Temp (Sum SW1)	NPGO	Temp (Win SW2)	Wind	Pinks	Temp (Sum SW4)	Chinook	LL	Δ AICc	w_i
		X						X	X		32.70	0.00	0.14
		X						X			30.34	1.20	0.07
		X					X	X	X		33.80	1.72	0.06
			X			X		X			31.62	2.15	0.05
		X				X		X	X		33.37	2.57	0.04
			X			X	X	X			33.37	2.57	0.04
		X				X		X			31.32	2.76	0.03
			X					X			29.36	3.18	0.03
		X						X	X	X	32.83	3.67	0.02
X		X						X	X		32.81	3.69	0.02