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AYK – Norton Sound Chinook Growth & Production

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Summary

Harvests of Unalakleet Chinook salmon in Norton Sound, Alaska, declined significantly during 1999-2009 in response to fewer returning salmon. Factors affecting the decline in abundance are largely unknown. However, growth of salmon in freshwater and the ocean is generally thought to influence salmon survival. Therefore, we examined historical Chinook salmon catch trends and developed growth indices of age-1.3 and age-1.4 Unalakleet Chinook salmon during each life stage in freshwater and the ocean using measurements of scale growth sampled from returning adult salmon, 1981-2009. Growth trends of Unalakleet Chinook salmon were compared with harvests, climate shifts, environmental variables, and Chinook life history. This investigation represents a continuation of previous Chinook salmon scale growth research involving Yukon and Kuskokwim Chinook salmon.

Harvest Trends of Unalakleet and Western Alaska Chinook Salmon

Harvests of Unalakleet, Yukon, and Kuskokwim Chinook salmon rapidly increased in the mid-1970s, then rapidly declined in the late 1990s, apparently in response to the 1976/77 ocean regime shift and the 1997/98 El Niño event, respectively. Abundance of Bristol Bay Chinook salmon (Nushagak District) also appeared to have been affected by these events. The rapid responses of Chinook salmon abundance to climate change suggest late life stages were primarily affected, at least initially. However, abundance of Arctic-Yukon-Kuskokwim (AYK) Chinook salmon remained low for at least 10 years following the 1997/98 El Niño event, suggesting that some unknown factor(s) continued to adversely affect Chinook salmon abundance.

Scale Growth Patterns and Relationships

We searched for growth patterns of Unalakleet Chinook salmon that might be related to changes in climate, environmental conditions, and Chinook salmon abundance. Growth indices of age-1.3 and age-1.4 Unalakleet Chinook salmon in freshwater and the ocean extended back to the late 1970s. Annual scale growth did not show distinct patterns over time for most life stages, although there was a tendency for growth during the second year at sea (SW2) to be low after the 1989 ocean regime shift, a pattern that was also observed in length-at-age of Bristol Bay sockeye salmon. Growth was not associated with harvests, which reflect abundance trends. Overall, Chinook scale growth was correlated with relatively few environmental and climate variables (e.g., seasonal SST, air temperature, barometric pressure, ice cover, wind mixing, PDO, Aleutian Low, Arctic Oscillation), but there was a tendency for growth to be positively correlated with seasonal sea surface temperature in the Bering Sea.

Scale growth of age-1.3 Unalakleet Chinook salmon was correlated with scale growth of age-1.3 and age-1.4 Yukon Chinook salmon during the second and third years at sea but not during other life stages. Scale growth of age-1.4 Unalakleet Chinook salmon was correlated with age-1.3 and age-1.4 Yukon Chinook salmon only during the second year at sea. Growth of Unalakleet Chinook salmon, like Yukon Chinook, was not correlated

with that of Kuskokwim Chinook salmon. These findings suggest that the distribution at sea of Yukon and Unalakleet Chinook was more similar than it was with Kuskokwim Chinook salmon, possibly reflecting the proximity of the rivers.

Previous studies indicated that Chinook salmon growth and survival was influenced by competition with pink salmon. Alternating-year patterns in Chinook salmon growth at sea were detected and may reflect direct and/or indirect interactions with pink salmon, which are exceptionally abundant in the Bering Sea during odd-numbered years. Alternating-year growth patterns of Unalakleet Chinook salmon were similar to Yukon Chinook during the second year at sea (both had high odd-year growth) but opposite during the third year at sea. Additional research is needed to further identify and describe the food webs in each ocean habitat and season that leads to these alternating-year patterns.

Growth of age-1.3 and age-1.4 Unalakleet Chinook salmon during each life stage was significantly and positively correlated with growth during the previous year. This pattern is consistent with observations of Yukon and Kuskokwim Chinook salmon growth. The pattern appears to reflect the dependence of Chinook salmon on larger and more mobile prey (fishes and squid) and the ability of larger Chinook to capture these prey and grow faster.

Female Unalakleet Chinook salmon were larger than males at a given age. Scale measurements demonstrated that greater growth of females began during the first year at sea. Additionally, female Chinook salmon were older than males, on average. Faster growth and older age-at-maturation of female Unalakleet Chinook salmon is consistent with observations of Yukon and Kuskokwim Chinook salmon. Large size and older age of mature female Chinook salmon likely reflects the importance of size to female Chinook salmon, whose reproductive potential (number and size of eggs) is linked to adult size.

Chinook length-at-age and age-at-maturation have both declined during the past 20 years. Adult female Chinook salmon returning to the river are less abundant than male salmon, in part because female Chinook salmon risk greater mortality at sea while maturing at an older age. For example, female Chinook salmon, especially those exceeding 55 cm, were captured more frequently than male Chinook salmon in the pollock fishery. The declining age-at-maturation is unexpected given that length-at-age has also declined, e.g., reduced growth typically leads to older age-at-maturation. These factors, in addition to the 1997/1998 El Niño event, have reduced the reproductive potential of female Chinook salmon and have likely contributed to the low abundance of Unalakleet, Yukon, and Kuskokwim Chinook salmon, all of which exhibited similar patterns of growth, life history, and population trends.

Introduction

Harvests of Chinook salmon in Norton Sound, Alaska, have declined significantly since 1999. Most Chinook salmon return to rivers in eastern Norton Sound, primarily the Unalakleet and Shaktoolik rivers (Fig. 1), where subsistence and commercial harvests declined 47% and 99%, respectively, during 2005-2009 compared with harvests prior to 1999 (Kent and Bergstrom 2009). Both the Unalakleet and Shaktoolik Chinook salmon stocks are classified as a Stocks of Concern by the State of Alaska because they have failed to produce anticipated harvests (Munro and Volk 2010). Factors causing the decline are unknown and AYK SSI identified the cause of the decline as a high priority issue (AYK SSI 2006).

Growth is a key factor affecting survival and life history characteristics of Pacific salmon (e.g., Healey 1986, Henderson and Cass 1991, Friedland et al. 2006, Farley et al. 2007, Ruggerone and Goetz 2004, Ruggerone et al. 2007a). Faster growing salmon are able to better avoid predators and survive winter when prey availability is low (Juanes 1994, Beamish and Mahnken 2001). Relatively rapid early marine growth of Bristol Bay and Chignik sockeye salmon occurred immediately after the mid-1970s ocean regime shift (Hare and Mantua 2000) that led to substantially greater abundances of salmon throughout northern areas (Ruggerone et al. 2005, 2007a, 2010a). However, adult length-at-age of Bristol Bay sockeye salmon was unusually low after the 1989 climate shift and may have contributed to the significant and rapid decline of Kvichak sockeye salmon (Ruggerone and Link 2006).

Growth may be especially important to Chinook salmon, which are relatively old and large at maturation. Faster growing Chinook salmon tend to mature at an earlier age and experience less risk of mortality, but younger adult female salmon are smaller and they tend to produce fewer and smaller eggs (Healey 1986, Quinn et al. 2004, Kent and Bergstrom 2009). As a result, female Chinook salmon tend to mature at an older age compared with male Chinook salmon. This pattern represents an important tradeoff between survival and reproductive potential. Greater growth of Chinook salmon during early marine life may also affect survival. For example, both early marine scale growth and survival of Puget Sound Chinook salmon exhibited an alternating-year pattern that was inversely related to the dominant odd-year run of pink salmon, whose progeny appear to reduce prey availability for subyearling Chinook salmon (Ruggerone and Goetz 2004; unpublished scale data). Yukon River and Kuskokwim River Chinook salmon scale patterns also revealed an alternating-year pattern of growth, but this pattern primarily occurred during the second year at sea, apparently because they began to overlap the region occupied by abundant Asian pink salmon during their second year (Ruggerone et al. 2009a, Myers et al. 2009).

Our recent analysis of Yukon River and Kuskokwim River Chinook salmon scale patterns revealed several new findings. Annual growth at sea was highly dependent on previous-year growth, including growth in freshwater (Ruggerone et al. 2009a,b). This pattern may reflect the importance to Chinook salmon of large prey, such as forage fishes and squid, and the greater ability of larger Chinook salmon to capture larger prey.

Female Chinook salmon were larger-at-age than male salmon, a finding that is opposite of that for most sockeye and chum salmon. However, the most striking finding was that differential growth between female and male salmon began during early life and continued thereafter. Earlier maturing Chinook salmon grew faster than late maturing salmon. Scale analyses indicated that the growth of age-1.3 Yukon and Kuskokwim River Chinook salmon began to exceed that of age-1.4 Chinook salmon in freshwater. These life history traits possibly reflect an evolutionary response of these salmon to their fluctuating environment and may represent traits that enhance survival and reproductive success. These findings highlight the importance of growth and size of Chinook salmon and their strategy to produce numerous large eggs.

The goal of this investigation was to evaluate potential effects of annual and seasonal growth of Unalakleet Chinook salmon on their abundance and life history characteristics, and to evaluate environmental influences on Chinook salmon growth. The investigation relied upon measurements of Chinook salmon scales collected since 1981 by the Alaska Department of Fish and Game (ADF&G). Scale radii are known to be correlated with salmon body size (Clutter and Whitesel 1956, Henderson and Cass 1991, Fukuwaka and Kaeriyama 1997, Ruggerone et al. 2010b).

Specific objectives of the investigation were to create indices of annual growth during each life stage of age-1.3 and age-1.4 Unalakleet Chinook salmon, 1981-2009[1], share these data with interested collaborators, and to test the following hypotheses:

1) Unalakleet Chinook salmon growth during each life stage (including freshwater) was correlated with index of Unalakleet Chinook salmon abundance.

2) Unalakleet Chinook salmon growth during each life stage shifted in response to major ocean-climate events (1989 regime shift and the 1997 El Niño event) and seasonal sea surface temperature (SST).

3) Unalakleet Chinook growth at sea exhibited an alternating-year pattern that was inversely related to pink salmon abundance.

4) Unalakleet Chinook growth was correlated with that of Yukon and/or Kuskokwim Chinook salmon growth, indicating common factors affected growth across broad regions and/or overlapping distributions of the stocks at sea.

5) Chinook growth at each life stage (freshwater through each year at sea) was associated with adult age and gender.

[1] The original objective was to measure scales through the 2007 return year, but we extended the time series to 2009.

Methods

Scale Collection and Measurements

Adult Chinook salmon scales from the Unalakleet River were obtained from the Alaska Department of Fish and Game (ADF&G) archives in Anchorage and Nome, Alaska. Scales have been collected annually for quantifying age composition since 1969, but scales were only available back to the 1981 season. Approximately 62% of the 1,893 scales measured in the study were from commercial catch samples, 33% were from test fishery operations, and 4% were from escapement samples (Table 1). Commercial and test fish harvests are typically conducted with 8.25 inch and 5.875 inch (stretched measure) set gillnets, respectively (Kohler et al. 2005). Escapement samples (2007-2009 sample years) were obtained using a beach seine. Commercial catches typically occurred near the mouth of the Unalakleet River, whereas most test fish samples originated from within the river. Samples from the test fishery occurred throughout the time series, whereas commercial catch samples only occurred prior to 2002.

The goal was to measure 50 scales from each of the two dominant age groups (ages 1.3 and 1.4)[2] of Unalakleet Chinook salmon with equal numbers of each gender. However, no scales were available in 1999, and few scales were available in several additional years (Table 1). Scales were selected for measurement only when: 1) we agreed with the age determination previously made by ADF&G, 2) the scale shape indicated the scale was removed from the preferred area (Koo 1962), and 3) circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis.

Scale measurements followed procedures described by Hagen et al. (2001). After selecting a scale for measurement, the scale was scanned from a microfiche reader and stored as a high resolution digital file. High resolution imaging (3352 x 4425 pixels) allowed the entire scale to be viewed and provided enough pixels between narrow circuli to ensure accurate measurements of circuli spacing. The digital image was loaded in Optimate image processing software to collect measurement data using a customized macro. The scale image was displayed on digital LCD monitors, and the scale measurement axis was defined as the longest axis extending from the scale focus to the scale edge. Distance (mm) between circuli was measured 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). Because most Chinook salmon return during spring (e.g., June), some fish exhibited little or no SWPL growth. Data associated with the scale, such as date of collection, location, sex, fish length and capture method, were included in the dataset.

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[2] Age was designated by European notation, i.e. the number of winters spent in freshwater before going to sea, 1 winter = age-1.X, followed by the number of winters spent at sea, three winters = age-X.3 or four winters = age-X.4.

Development of Standardized Scale Growth Datasets

Unequal numbers of male and female Chinook salmon scales were available for measurement in most years. Female Chinook salmon were much less common among age-1.3 Chinook salmon, and male Chinook salmon were less common among age-1.4 Chinook salmon, owing to differences in age at maturation. Male and female Chinook salmon may experience different growth rates, especially in the ocean. Therefore, scale growth indices were developed to equally weight male and female scale growth during each year while utilizing all available scale measurement data:

$$\text{Annual mean growth (Z)} = [n_M \text{ (Growth } Z_M) + n_F \text{ (Growth } Z_F)] / [n_M + n_F],$$

where n_M and n_F are sample sizes of male and female salmon, and Growth Z_M and Growth Z_F are normalized mean growth of male and female salmon, respectively. Normalized growth is the number of standard deviations (SD) above or below the long-term mean.

In order to remove the effects of time trends and to highlight differences in growth between even- and odd-numbered years while testing for a possible effect of pink salmon, we calculated the first difference of each Chinook scale growth variable:

$$\text{Differenced growth } (DG_i) = G_i - G_{i-1}, \text{ where G is scale growth in year i.}$$

If the previous year was missing, then scale growth was differenced with the next available year while also maintaining difference between even- and odd-numbered-years.

Most Chinook salmon were sampled from the commercial fishery, but some were sampled from the test fishery that often used smaller mesh set gillnets. ANOVA using the entire Age Sex Length (ASL) database during years when samples were collected from both commercial and test fishery activities indicated that length-at-age of Chinook in the commercial catch was significantly longer than those captured in the test fishery ($P < 0.05$). Therefore, correction factors were applied Chinook lengths measured from fish sampled from the test fishery to standardize all measurements to commercial catch values. The age and gender-specific correction factors were applied to 29% of the ASL measurements (test fishing samples). The corrections ranged from 1.0 (age-1.2 males) to 1.06 (age-1.3 females).

ANOVA was used to test whether sampling gear (commercial versus test fishing gear influenced annual scale growth measurements. This analysis was restricted to years in which samples from both gear types were available. Three factor ANOVAs (gear, age, year) did not reveal significant differences in scale growth of fish captured by the two gear types ($P > 0.05$) during the later stages of life (SW3, SW4, SWPL) when adult body size is determined; therefore, a correction factor was not applied to scale growth measurements. The effect of mesh size could have influenced body size and associated scale growth measurements (Ruggerone et al. 2007b), but insufficient data were available on the mesh size used to capture each fish sampled with commercial and test fishing gear. Different mesh sizes may have contributed to variability in measurements described below.

Some Unalakleet Chinook salmon had an abnormal focus that reduced the number of circuli in the freshwater zone. Statistical tests indicated freshwater growth associated with the abnormal focus was slightly greater than growth in normal scales ($P < 0.05$). Previous analyses indicated FW1 growth of scales with abnormal focus was not different among Kuskokwim Chinook salmon, but it was slightly greater among Yukon Chinook salmon ($P < 0.05$; Ruggerone et al. 2007b). No effect was observed in adjacent life stages. Fish having an abnormal focus were excluded from statistical analyses involving FW1.

Environmental Data

Bering Sea climate data were obtained from http://www.beringclimate.noaa.gov. Additional sea surface temperature (SST) data were derived from COADS data provided by the US National Center for Atmospheric Research and the US National Oceanic and Atmospheric Administration (Woodruff et al. 1998; http://dss.ucar.edu/datasets/ds540.1/data/msga.form.html). Monthly air temperature at Nome were obtained from http://climate.gi.alaska.edu.

Results and Discussion

Abundance of Unalakleet and Western Alaska Chinook salmon

Harvests of Unalakleet Chinook salmon by subsistence and commercial fishermen were used as an index of abundance since the early 1960s because spawning escapement was not consistently monitored until 1996 (Kent and Bergstrom 2009). During the entire period of record (1961-2009), harvests averaged approximately 4,900 Chinook salmon. Harvests tended to be below average from 1964 to 1977 (avg. 2,785 fish), above average from 1978 to 1998 (avg. 7,840 fish), and below average from 1999 to 2009 (avg. 2,574 fish; Fig. 2).

The relatively abrupt harvest increase in the mid-1970s corresponded with the 1976/1977 ocean regime shift that also influenced greater abundance of other western Alaska Chinook salmon stocks (Fig. 2) and Bristol Bay sockeye salmon (Ruggerone et al. 2007a). The decline in Unalakleet Chinook harvests beginning in 1999 corresponded with the abrupt decline of other Chinook populations in western Alaska (Ruggerone et al. 2009a). This decline appeared to be related to the 1997/1998 El Niño event (Kruse 1998, Fig. 2). However, abundance of western Alaska Chinook salmon has remained relatively low from 1999 through 2009 even though oceanographic characteristics of the El Niño event have not persisted. It is noteworthy that adult abundance of Chinook salmon changed rapidly in response to the 1976/77 and 1997/98 climate events, suggesting that large shifts in abundance and survival were largely influenced during late marine life rather than early life. This observation is opposite of the general view that salmon abundance trends are set during early marine life rather than late marine life.

Trends in average ocean age-at-maturation of male and female Chinook salmon were examined. During the mid-1970s to late 1980s, Chinook salmon tended to spend 3.5 to nearly 4.0 years in the ocean, on average (mean of male and female salmon) (Fig. 3). However, years spent in the ocean declined markedly to approximately 2.8 to 3.7 years during 1990 to 2009. Ocean age was especially low in the early 1990s and again in the mid-2000s.

Smaller (younger) female Chinook salmon produce fewer and smaller eggs than bigger (older) Chinook salmon (Kent and Bergstrom 2009). Female Chinook salmon tend to represent less than 50% of the total returning to spawn in the Unalakleet, Yukon, and Kuskokwim rivers (Ruggerone et al. 2007b, Kent and Bergstrom 2009). Thus, the combination of smaller length-at-age (see below), younger age-at-maturation, fewer returning adults, and low percentage of female versus male adult Chinook salmon contributes to the relatively low reproductive potential of Unalakleet Chinook salmon during the past 20 years. The decline in both age-at-maturation and length-at-age is unusual because slower growing Chinook salmon tend to mature at an older age rather than earlier age.

Annual Growth Trends by Life Stage

Indices of age-1.3 and age-1.4 Chinook salmon scale growth in freshwater and the ocean extend back to the late 1970s (Figs 4, 5, 6, 7). Annual scale growth did not show distinct patterns over time for most life stages. There was a slight tendency for growth in freshwater to be somewhat high in the late 1970s and early 1980s, especially during the spring migration of smolts. SW1 growth tended to be relatively low in the 1980s and highly variable in the 1990s. SW2 growth tended to be high in the late 1970s and 1980s, then below average in the 1990s, possibly reflecting changes in the ocean associated with the 1989 ocean regime shift. SW2 growth in the 2000s was not consistent among age-1.3 and age-1.4 salmon. SW3 growth tended to be below average during the 1990s, especially among age-1.3 salmon. As in earlier life stages, growth during SW4 tended to be highly variable in the late 1990s. Growth during the homeward migration (SWPL) tended to be above average in the 1980s and early 1990s and below average beginning in the late 1990s, especially among age-1.3 salmon.

Trends in mean length of age-1.3 male Chinook and age-1.4 female Chinook salmon were examined after standardizing all lengths to commercial catch gear (Fig. 8). Length of age-1.4 female Chinook salmon declined significantly from the late 1970s to 2009 ($df = 1, 23$; $F = 6.107$; $P = 0.022$). Age-1.3 male Chinook salmon tended to decline over time, but the relationship was not statistically significant.

Comparison of Age-1.3 and Age-1.4 Chinook Salmon Growth

Scale growth of age-1.3 and age-1.4 Unalakleet Chinook salmon that co-existed in freshwater and marine habitats during each life stage were compared using correlation analysis. Growth of age-1.3 and age-1.4 Unalakleet Chinook salmon were positively correlated during the second and third years at sea and during spring of the smolt migration (Table 2). Scale growth of the two age groups tended to be positively correlated during freshwater and the first year at sea but the relationships were not statistically significant ($P > 0.05$). It is noteworthy that correlation of age-1.3 and age-1.4 Chinook growth from the Yukon and Kuskokwim rivers during the first year at sea was also low, possibly reflecting high mortality that may occur during early marine life (Ruggerone et al. 2007b).

Comparison of Unalakleet, Yukon and Kuskokwim Chinook Salmon Growth

Scale growth of age-1.3 Unalakleet Chinook salmon was significantly correlated with scale growth of age-1.3 and age-1.4 Yukon Chinook salmon during the second and third years at sea but not during other life stages (Table 2). Scale growth of age-1.4 Unalakleet Chinook salmon was correlated only with age-1.3 and age-1.4 Yukon Chinook salmon during the second year at sea. Growth of Unalakleet Chinook salmon, like Yukon Chinook, was not correlated with that of Kuskokwim Chinook salmon. Thus, growth at sea of Unalakleet and Yukon Chinook salmon tended to be correlated with each other but not with Kuskokwim salmon (Ruggerone et al. 2007). This finding suggests that the distribution at sea of Yukon and Unalakleet Chinook likely overlaps during the second and third years at sea, but these two stocks may have less overlap with Kuskokwim Chinook salmon. The mouths of Unalakleet and Yukon rivers are close (~200 km) but they are both relatively distant from the Kuskokwim River (520-720 km). Genetic samples collected at sea could be used to test the hypothesis that the ocean distribution of Unalakleet and Yukon Chinook salmon overlaps more with each other than with Kuskokwim Chinook salmon.

Climate Shifts, Chinook Salmon Abundance and Growth

We did not find statistically significant and meaningful relationships between harvests of Unalakleet Chinook salmon and their scale growth during each life stage. The lack of significant relationships may reflect the dependence of scale growth on growth that occurred during the previous year, as noted below and in previous studies (Ruggerone et al. 2009b). The lack of a distinct relationship between Chinook salmon harvests and growth was also observed among Yukon and Kuskokwim Chinook salmon (Ruggerone et al. 2009a). Nevertheless, growth of Chinook salmon was found to have a strong influence on age-at-maturation and gender-specific growth.

Annual growth of Unalakleet Chinook salmon scales were compared with the environmental conditions (seasonal SST, air temperature, barometric pressure, ice cover, wind mixing), climate indices (PDO, Aleutian Low, Arctic Oscillation), and climate events in 1976/77, 1989, and 1997/98 climate events. Scale growth was correlated with relatively few environmental and climate variables. Key variables that may have influenced annual scale growth are shown in Table 3. Growth during the first year in freshwater (FW1) was positively correlated with Nome air temperature during spring. Growth during the first year in saltwater (SW1) was positively correlated with SST (January-April) measured at Mooring 2 in the southeastern Bering Sea. Growth during the second year in saltwater (SW2) was correlated with a variety of variables, including SST in the southeastern Bering Sea during May, SST (January-April) measured at Mooring 2, and number of days of ice present at Mooring 2 after March 15 (negative correlation with ice). SW2 growth also tended to be low after the 1989 regime shift, including years after the 1997 El Niño. Growth during the third year in saltwater (SW3) was negatively correlated with winter SST in the western North Pacific Ocean, but it is possible this relationship was spurious. Growth during the fourth year in saltwater (SW4) was positively correlated with wind mixing at Mooring 2 during June and July, and negatively correlated with conditions following the 1997/1998 El Niño.

Growth in Relation to Asian Pink Salmon

Previous studies indicated that Chinook salmon growth and survival was influenced by competition with pink salmon (Grachev 1967; Ruggerone and Goetz 2004; Ruggerone and Nielsen 2005, Ruggerone et al. 2009a). We tested the hypothesis that Unalakleet Chinook salmon scale growth was influenced by Asian pink salmon, which are exceptionally abundant in the central Bering Sea during odd- versus even-numbered years (Ruggerone et al. 2003; Davis et al. 2005). For example, during the 1990s, catch per unit effort (CPUE) in Japanese research nets during odd-numbered years indicated that pink salmon were 580% more abundant than sockeye salmon and 87% more abundant than chum salmon (Davis et al. 2005). However, chum salmon in the Bering Sea exhibited an alternating pattern of abundance that was opposite of pink salmon. Chum salmon were 134% more abundant during even-numbered years. We did not expect competition between Unalakleet Chinook salmon and western Alaska pink salmon, which were much less abundant and were primarily present as maturing fish in even-numbered years. It was possible, however, that pink salmon fry contributed to the diet and growth of yearling Chinook salmon, therefore we also examined growth in freshwater.

Differenced scale growth was not statistically different between odd- and even-numbered years in freshwater (FW1) and the first year at sea (SW1; $P > 0.05$). Thus, the potential beneficial effect of pink salmon (prey) in freshwater was not detected (see Ruggerone et al. 2010b). However, growth during the second and third years at sea was greater during odd-numbered years for both age-1.3 and age-1.4 Chinook salmon (two-factor ANOVA (odd/even year, age; $df = 1, 43$; $F = 7.76$ & 8.55; $P < 0.01$). For age-1.4 salmon, growth during the fourth year at sea (age-1.4) was significantly lower during odd-numbered years ($df = 1, 20$; $F = 11.79$; $P = 0.003$) but higher during the homeward migration (SWPL; $df = 1, 20$; $F = 10.96$; $P = 0.004$). For age-1.3 Chinook salmon, growth during the homeward migration of age-1.3 salmon did not vary with odd- and even-numbered years ($P > 0.05$).

Adult length of age-1.4 Chinook salmon was significantly greater in odd-numbered return years (df = 1, 23; $F = 6.509$; $P = 0.018$), based on analysis of the entire Age-Sex-Length database. For age-1.3 salmon, length did not vary with odd- and even-numbered years. The greater length of age-1.4 Chinook salmon returning in odd-numbered years was consistent with greater scale growth that occurred among these fish during SW3, SW4, and SWPL but not with their growth during SW2. Somewhat high growth of age-1.3 Chinook salmon during odd-numbered years of SW2 and SW3 effectively cancelled each other out, leading to no apparent differences in adult length during even- and odd-numbered years.

Alternating-year growth patterns of Unalakleet Chinook salmon were similar to Yukon Chinook during SW2 (both had high odd-year growth) but opposite during the third year at sea (Ruggerone et al. 2009a). Myers et al. (2009) reported that prey consumption of Chinook salmon during July in the Aleutian Basin was approximately 100% higher in even- versus odd-years, 1991-2000. The large majority of these Chinook were ocean age-2 fish, corresponding to the third season at sea (SW3). Thus, the diet data were consistent with SW3 growth of Yukon Chinook but opposite that of the Unalakleet Chinook growth. However, SW3 growth of Unalakleet and Yukon Chinook were positively correlated over time (see Table 2). Multiple regression showed that the alternating-year pattern of these two stocks during the third year at sea was opposite, as noted above, i.e., the odd/even year variable was significant and negatively correlated ($n = 22$, $R^2 = 0.56$, $P < 0.001$). One explanation for this unique pattern is that growth conditions during the 22-year period were positively correlated over broad regions of the ocean, but that the primary foraging grounds of the two stocks differed and led to the opposite alternating-year pattern. This pattern may reflect, for example, foraging in the Aleutian Basin versus the continental slope or shelf.

Greater growth of Chinook salmon during odd-numbered years at sea may reflect the higher trophic level of Chinook compared with pink salmon and the cascading trophic effect numerous pink salmon likely had on higher trophic level prey that Chinook salmon consume (Ruggerone et al. 2009a). However, there was some evidence that this alternating-year pattern depended on ocean age and ocean habitat occupied by the salmon (e.g., Ruggerone et al. 2009a, Myers et al. 2009). The region occupied by AYK Chinook salmon is broad and spans multiple ocean habitats. However, detailed information about the abundance of salmon in these habitats and variation in distribution across seasons and years is lacking.

Growth Dependence on Earlier Growth

Life stage growth of age-1.3 and age-1.4 Unalakleet Chinook salmon was significantly and positively correlated with growth during the previous year ($P < 0.05$; Fig. 9). Serial autocorrelation was non-significant. The amount of variability in scale growth explained by growth during the previous year was approximately 20%, except for the third year at sea (40%).

These relationships were consistent with those observed in Yukon and Kuskokwim Chinook salmon. In the previous analysis, both mean growth of the population and growth of individual Chinook salmon were dependent on growth during the previous year (Ruggerone et al. 2007b, 2009a). The dependence of growth on prior growth was an unusual finding compared with analyses of individual Bristol Bay sockeye growth where there was no significant positive correlation between scale growth of adjacent life stages (Ruggerone, unpublished analyses). Ruggerone et al. (2005) reported a significant negative correlation between mean growth of the population in the second year versus first year at sea. They suggested the negative relationship reflected the need to grow fast in the second year if growth in the first year was below average.

Sexual Dimorphism

Two factor ANOVA (sex, age) indicated that adult female Chinook salmon returning at ages-1.2, -1.3 -1.4, and -1.5 were significantly longer than male salmon (Fig. 10; $df = 1, 6545$; $F = 173.4$; $P < 0.001$). Although the interaction between age and gender was significant ($F = 20.75$, $P < 0.001$), female Chinook remained larger on average at each age at maturation. On average, female Chinook salmon were 71 mm, 56 mm, 28 mm, and 10 mm longer than male salmon at ages-1.2, -1.3, -1.4, and -1.5, respectively. Thus, the greater size-at-age differential of female versus male Unalakleet Chinook salmon declined with age. This pattern is consistent with Yukon and Kuskokwim Chinook salmon, except male age-1.5 Chinook salmon tended to be larger than female salmon in these two rivers (Ruggerone et al. 2007b).

ANOVA was used to identify the life stage(s) at which female Chinook salmon became longer than male salmon. Among age-1.3 and age-1.4 Unalakleet Chinook salmon, female scale radii exceeded that of male salmon beginning in the first year at sea (Table 4, Fig. 11). Differential growth was not detected during the second year at sea. For age-1.3 salmon, female scale growth was significantly greater than male growth during the third year at sea (SW3), whereas scale growth of age-1.4 female salmon was greater during the fourth year at sea (Table 4; Fig. 11). Greater growth of female versus male Unalakleet Chinook salmon during early life stages was consistent with that of Kuskokwim and Yukon Chinook salmon, although the life stage in which differential growth began varied by age and stock (Ruggerone et al. 2007b).

These unique findings of sexual dimorphism among AYK Chinook salmon provide important information about the life history strategy of Chinook salmon. The data show that characteristics of age-1.3 and age-1.4 Chinook salmon begin to establish during early life.

Life Stage Growth of Age-1.3 and Age-1.4 Chinook Salmon

Faster growing salmon tend to mature at an earlier age (Fig. 11). Therefore, scale measurements and a two-factor ANOVA (sex, age) were used to determine the life stage at which growth of age-1.3 Unalakleet Chinook salmon began to exceed that of age-1.4 salmon. Growth of age-1.3 Chinook salmon began to exceed that of age-1.4 salmon during the first year at sea (SW1) and annual growth continued to be greater among age-1.3 Chinook salmon during each subsequent year at sea (Fig. 11; Table 5). The greatest growth differential occurred during the second year at sea, suggesting that growth during the second year may be key to determining whether the fish matured after three or four winters at sea. However, as noted above, age-at-maturation has become earlier over time even though growth during the second year at sea has declined over time.

These observations of Unalakleet growth and age were generally consistent with those of Yukon and Kuskokwim Chinook salmon. Growth of Yukon age-1.3 Chinook salmon began to exceed that of age-1.4 salmon during freshwater, whereas faster growth of age-1.3 Chinook from the Kuskokwim River began during the first year at sea (Ruggerone et al. 2007b).

Conclusions

Harvests of Unalakleet, Yukon and Kuskokwim Chinook salmon rapidly increased immediately after the 1976/77 ocean regime shift, then declined soon after the 1997/98 El Niño event and remained low. The rapid responses of Chinook salmon abundance to climate change suggested that late life stages were primarily affected, at least initially. The harvest patterns also suggested that ocean climate factors have been key factors leading to both greater and lower harvests during the past 50 years.

Relationships between annual growth of Chinook salmon scales, Chinook abundance, and environmental factors, such as the ocean regime shifts, were complicated by the high dependency of growth on previous-year growth. This finding was also observed in Yukon and Kuskokwim Chinook salmon. Nevertheless, scale growth measurements revealed key information about the life history of Unalakleet Chinook salmon, which in turn provides information on factors affecting Chinook salmon abundance.

Alternating-year patterns in Chinook salmon growth at sea were detected and may reflect direct and/or indirect interactions with pink salmon, which are exceptionally abundant in the Bering Sea during odd-numbered years. Alternating-year growth patterns of Unalakleet Chinook salmon were similar to Yukon Chinook during the second year at sea (both had high odd-year growth) but opposite during the third year at sea. Additional research is needed to further identify and describe the food webs in each ocean habitat and season that lead to these alternating-year patterns.

Female Unalakleet Chinook salmon were longer than male salmon at a given age. Scale measurements demonstrated that greater growth of female Chinook salmon began during the first year at sea. Additionally, female Chinook salmon were older than male Chinook salmon. Faster growth and older age-at-maturation of female versus male Unalakleet Chinook salmon was consistent with that observed in Yukon and Kuskokwim Chinook salmon (Ruggerone et al. 2007b). Rapid growth and large size of female Chinook salmon likely reflects the importance of size to female Chinook salmon, whose reproductive potential (number and size of eggs) is linked to adult size (e.g., Kent and Bergstrom 2009).

Sampling of fisheries and spawning areas indicate fewer female than male Chinook salmon are returning to the Unalakleet River (Kent and Bergstrom 2009) and to the Yukon and Kuskokwim rivers (Olsen et al. 2006a, 2006b, Ruggerone et al. 2010c). The low abundance of female versus male Chinook salmon reflects greater mortality associated with older age at maturation (Ruggerone et al. 2007b), and possibly greater risk taking by females while attempting to feed and grow rapidly (Holtby and Healey 1990). Greater residence time of female Chinook in the ocean exposed them for longer periods to mortality risks, including capture in the pollock fishery. For example, Ianelli (2007) reported that more female than male Chinook salmon were captured in the pollock fishery, especially among salmon exceeding 55 cm (females: 57% of total)[3].

Age-at-maturation of Unalakleet Chinook salmon has declined even though length-at-age has also declined. This pattern is opposite of what is expected because faster growth is associated with earlier maturation (e.g., this study; Ruggerone et al. 2007b). This relationship deserves further analysis.

We suggest that the life history characteristics of AYK Chinook salmon, in conjunction with the 1997/1998 El Niño event, were key factors influencing the decline of Unalakleet and other AYK Chinook salmon. Characteristics of female Chinook salmon seem to be especially important because egg number and egg size support future returns. Younger age-at-maturation, reduced length-at-age, and fewer female versus male adult Chinook salmon have likely reduced the reproductive potential of Chinook salmon and contributed to the continued low abundance of Chinook salmon since the late 1990s.

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Table 1. Annual scale sample sizes of age-1.3 and age-1.4 Unalakleet River, Alaska, Chinook salmon, 1981-2009. Also shown are the proportion of total scales that were from female salmon, had resorbed focus, and were taken in the commercial fishery.

Year	Age-1.3				Age-1.4			
	Total scales	% female	% resorbed	% commercial	Total scales	% female	% resorbed	% commercial
1981	29	0.17	0.21	0.86	46	0.46	0.13	0.89
1982	40	0.20	0.05	0.88	27	0.74	0.11	0.81
1983	38	0.18	0.03	0.82	59	0.53	0.00	0.85
1984	53	0.45	0.02	0.58	50	0.50	0.00	0.70
1985	33	0.21	0.00	0.48	50	0.50	0.00	0.58
1986	49	0.29	0.00	0.78	55	0.45	0.00	0.91
1987	17	0.18	0.06	0.71	65	0.58	0.02	0.69
1988	46	0.22	0.00	0.96	62	0.47	0.06	0.98
1989	53	0.36	0.08	0.60	54	0.52	0.13	0.80
1990	44	0.34	0.05	0.73	53	0.53	0.02	0.94
1991	45	0.44	0.11	0.89	44	0.64	0.02	0.89
1992	9	0.33	0.22	0.67	5	0.80	0.40	0.80
1993	40	0.33	0.03	0.53	52	0.58	0.06	0.73
1994	50	0.50	0.00	0.78	47	0.60	0.02	0.94
1995	17	0.18	0.12	0.65	60	0.57	0.00	0.57
1996	53	0.49	0.00	0.08	39	0.56	0.08	0.79
1997	16	0.19	0.00	0.69	56	0.46	0.04	0.34
1998	32	0.47	0.06	0.69	13	0.62	0.08	0.85
1999	0	NA	NA	NA	0	NA	NA	NA
2000	38	0.32	0.03	0.63	30	0.43	0.03	0.80
2001	6	0.17	0.00	0.17	44	0.68	0.09	0.48
2002	24	0.00	0.08	0.00	3	0.33	0.33	0.00
2003	11	0.09	0.09	0.00	1	1.00	0.00	0.00
2004	4	0.00	0.00	0.00	4	1.00	0.00	0.00
2005	4	0.25	0.00	0.00	17	0.53	0.06	0.00
2006	10	0.10	0.10	0.00	0	NA	NA	NA
2007	31	0.32	0.06	0.00	20	0.60	0.00	0.00
2008	52	0.19	0.00	0.00	19	0.89	0.05	0.00
2009	29	0.14	0.03	0.00	45	0.69	0.07	0.00
Total	873	0.30	0.04	0.54	1020	0.56	0.05	0.68

Table 2. Correlations (r) between age-1.3 and age-1.4 Unalakleet River, Alaska, Chinook salmon and age-1.3 and age-1.4 Yukon River and Kuskokwim River Chinook salmon that coexisted in the habitats. Significant correlations are shown in bold (P < 0.05).

		Growth Zone	Unalakleet Age-1.3						Unalakleet Age-1.4						
			FW1	FWPL	SW1	SW2	SW3	SWPL	FW1	FWPL	SW1	SW2	SW3	SW4	SWPL
Unalakleet	Age 14	FW1	0.30												
		FWPL		**0.72**											
		SW1			0.31										
		SW2				**0.88**									
		SW3					**0.61**								
		SW4													
		SWPL						0.38							
Yukon	Age 1.3	FW1	0.02						0.24						
		FWPL		-0.02						-0.21					
		SW1			-0.03						-0.10				
		SW2				**0.58**						**0.61**			
		SW3					**0.48**						0.32		
		SWPL						0.04							-0.12
	Age 14	FW1	0.10						0.14						
		FWPL		0.28						0.23					
		SW1			0.14						0.18				
		SW2				**0.61**						**0.72**			
		SW3					**0.54**						0.35		
		SW4												0.09	
		SWPL						-0.26							0.07
Kuskokwim	Age 1.3	FW1	0.03						-0.06						
		FWPL		**-0.54**						**-0.47**					
		SW1			0.24						0.24				
		SW2				-0.35						0.23			
		SW3					-0.16						-0.18		
		SWPL						0.04							0.07
	Age 14	FW1	0.10						-0.37						
		FWPL		-0.35						-0.25					
		SW1			0.31						0.07				
		SW2				0.25						-0.14			
		SW3					-0.08						-0.30		
		SW4												0.01	
		SWPL						0.02							-0.01

Table 3. Correlations between annual scale growth of Unalakleet River, Alaska, Chinook salmon and key environmental and climate variables.

Life Stage	Variable	n	Correlation (r)	P-value
FW1	Nome air temperature, May-June	29	0.39	0.070
SW1	SST @ Mooring 2, Jan-Apr	29	0.33	0.076
SW2	SST SE Bering Sea, May	29	0.61	< 0.001
	SST @ Mooring 2, Jan-Apr	29	0.46	0.012
	Ice days after 15 March, Mooring 2	29	-0.52	0.003
	1989 shift & 1997 El Nino	29	-0.34	0.060
SW3	SST, West Pacific, Dec-March	29	-0.52	0.004
SW4	1997/1998 El Nino	23	-0.46	0.025
	Wind Mixing, Mooring 2, JunJul	23	0.52	0.010

Table 4. ANOVA test results to determine whether scale growth of Unalakleet River, Alaska, Chinook salmon at each life stage was influenced by gender. Tests conducted on both age-1.3 and age-1.4 Chinook salmon. The larger gender is identified. See Fig. 11 for associated analyses.

	Age-1.3				Age-1.4			
Stage	Larger Sex	n	F-value	P-value	Larger Sex	n	F-value	P-value
FW1		836	2.54	0.111	M	974	8.10	0.004
FWPL		873	0.63	0.428		1020	0.03	0.868
SW1	F	873	8.70	0.003	F	1020	6.40	0.011
SW2		873	0.28	0.598		1020	0.51	0.474
SW3	F	873	18.53	<0.001		1020	2.10	0.148
SW4		NA			F	1020	19.31	<0.001
SWPL		873	0.00	0.966	F	1020	7.22	0.007
SWPL Max		873	0.59	0.443	F	1020	3.71	0.054

Table 5. Two factor ANOVAs (age, sex) to determine whether scale growth at each life stage varied with adult age of Unalakleet River, Alaska, Chinook salmon. Percentage difference is the difference in age-1.3 growth relative to age-1.4 growth. Scales having abnormal scale focus were excluded from the analysis of FW1 scale growth. See Table 4 and Fig. 11 for associated analyses.

	n		%		
Stage	age-1.3	age-1.4	difference	F-value	P-value
FW1	836	974	-0.6	0.36	0.551
FWPL	873	1020	5.6	0.12	0.732
SW1	873	1020	5.2	41.60	<0.001
SW2	873	1020	12.0	172.36	<0.001
SW3	873	1020	7.3	63.58	<0.001
SWPL	873	1020	2.2	33.83	<0.001
SWPL Max	873	1020	3.8	17.20	<0.001

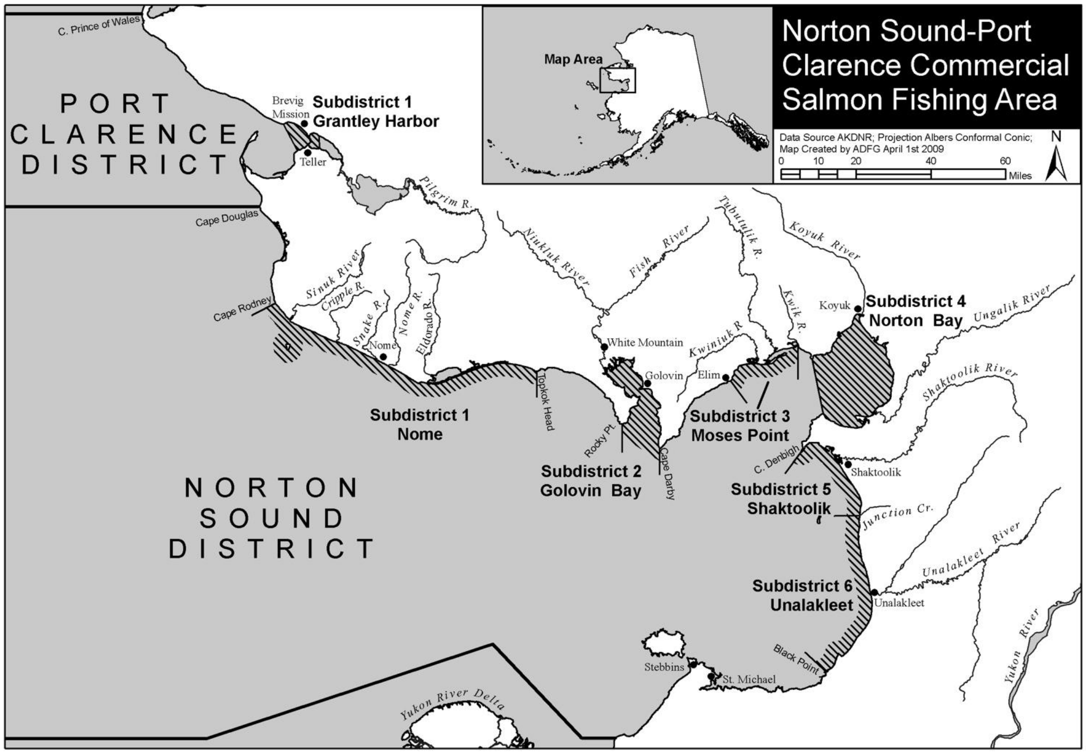

Fig. 1. Map of salmon fishing subdistricts in Norton Sound and the location of Unalakleet River, Alaska (S. Kent, ADF&G, personal communication).

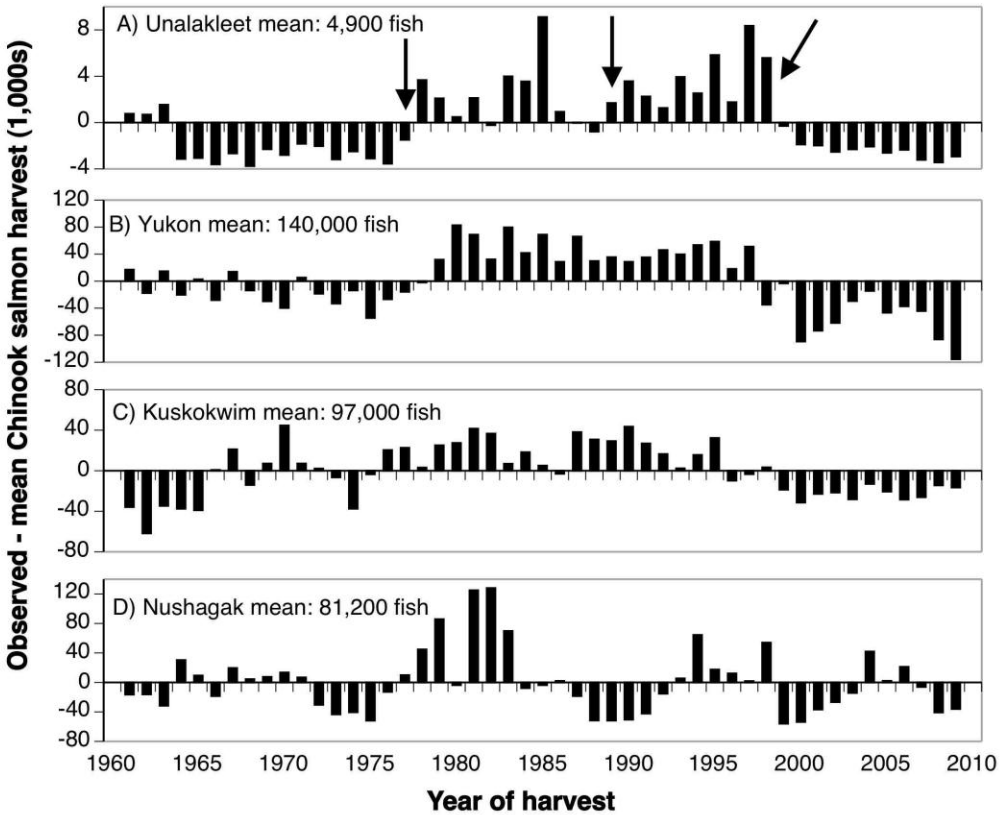

Fig. 2. Catch trends of A) Unalakleet River, B) Yukon River, C) Kuskokwim River, and D) Nushagak River Chinook salmon, 1961-2009. Values include commercial, subsistence, and sport harvests. Kuskokwim River subsistence catches prior to 1988 were adjusted by a factor of 1.47 (based on the ratio of 5 years after method change versus 5 years prior to change). Arrows identify 1976/77 and 1989 climate regime change and 1997/98 El Niño event. Data sources: Bue and Hayes 2006, Whitmore et al. 2005, Ruggerone et al. 2007b, Kent and Bergstrom 2009, and www.cf.ADF&G.state.ak.us/region3/rgn3home.php.

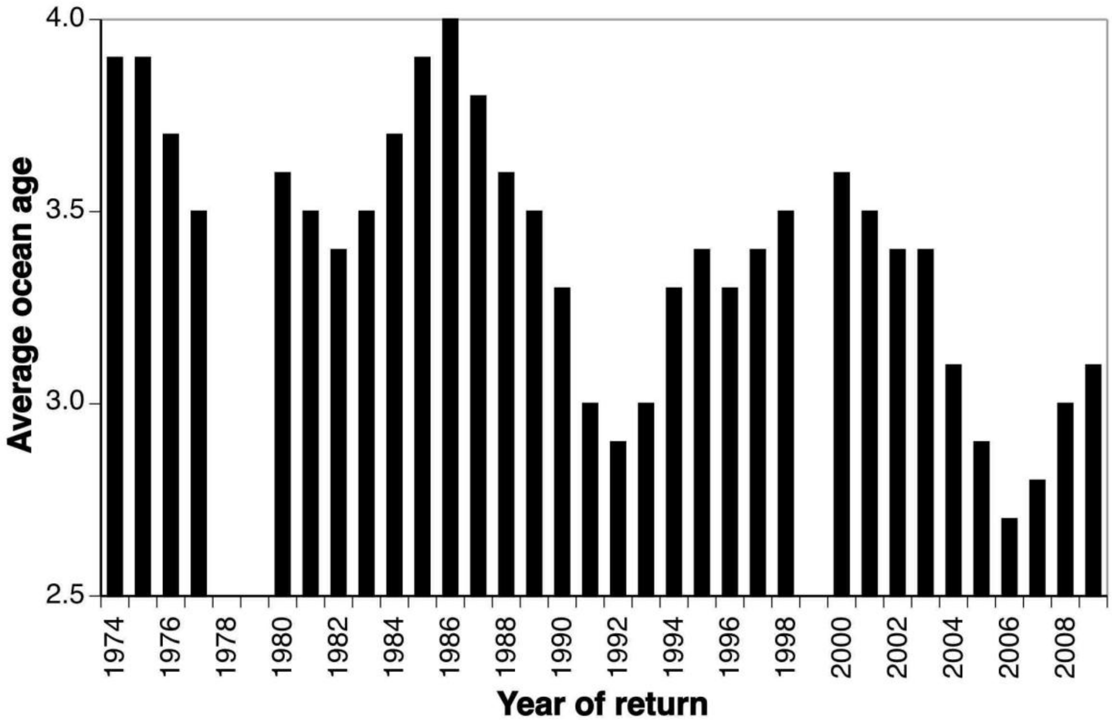

Fig. 3. Average ocean age of male and female Chinook salmon collected in the Unalakleet River, Alaska, 1974-2009. Values are based on the moving three-year average of mean ocean age of male and female salmon (equal weight). Ocean age of male and female salmon was highly correlated (r = 0.98), although female salmon were older on average (see below).

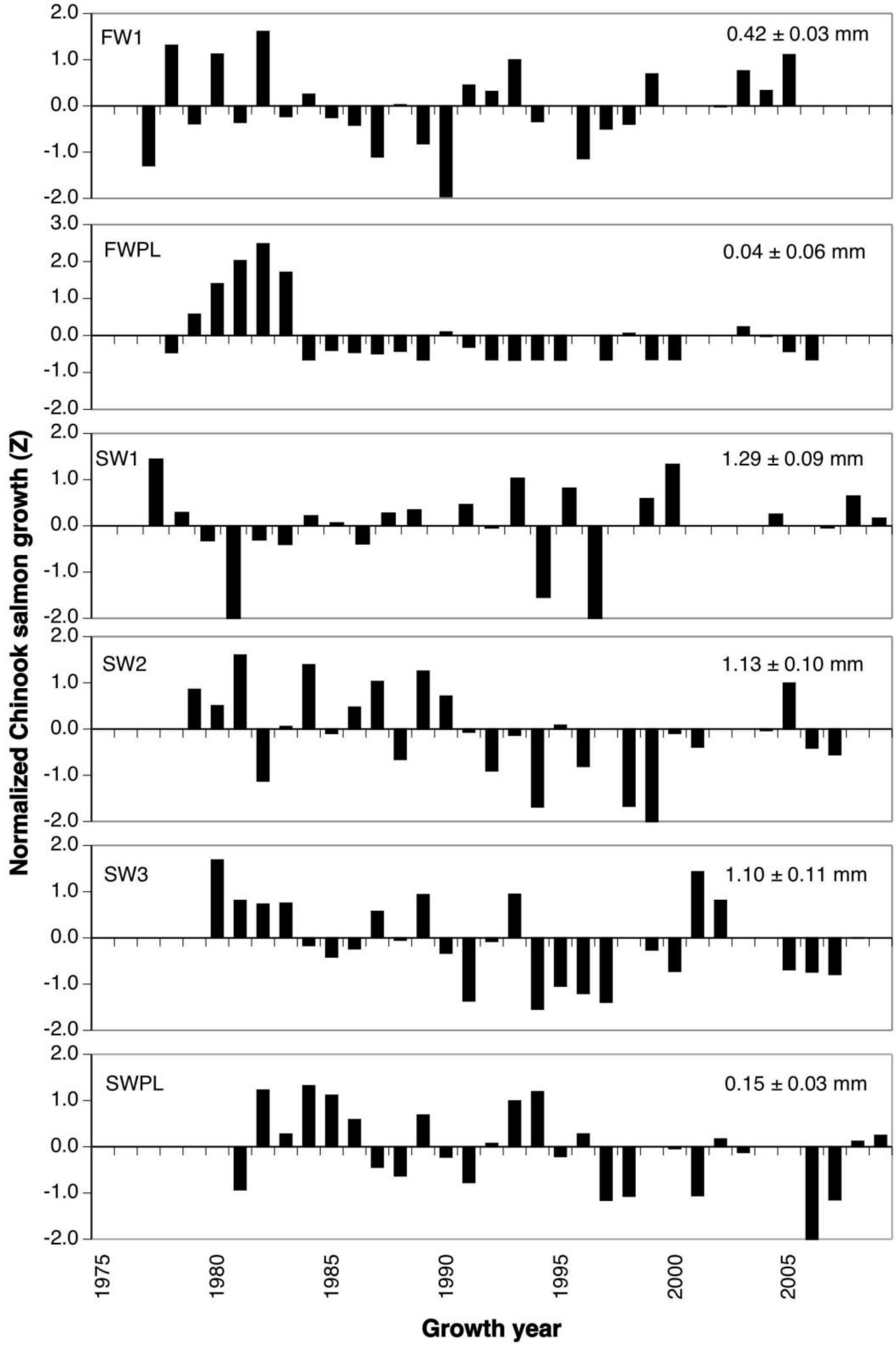

Fig. 4. Mean annual growth of age-1.3 Unalakleet River Chinook salmon during each life stage, growth years 1977-2009. Values are standard deviations above and below the long-term mean. The long-term unweighted mean of male and female scale measurements are shown. No values for years associated with brood years 1999, 2001, 2004, and 2005.

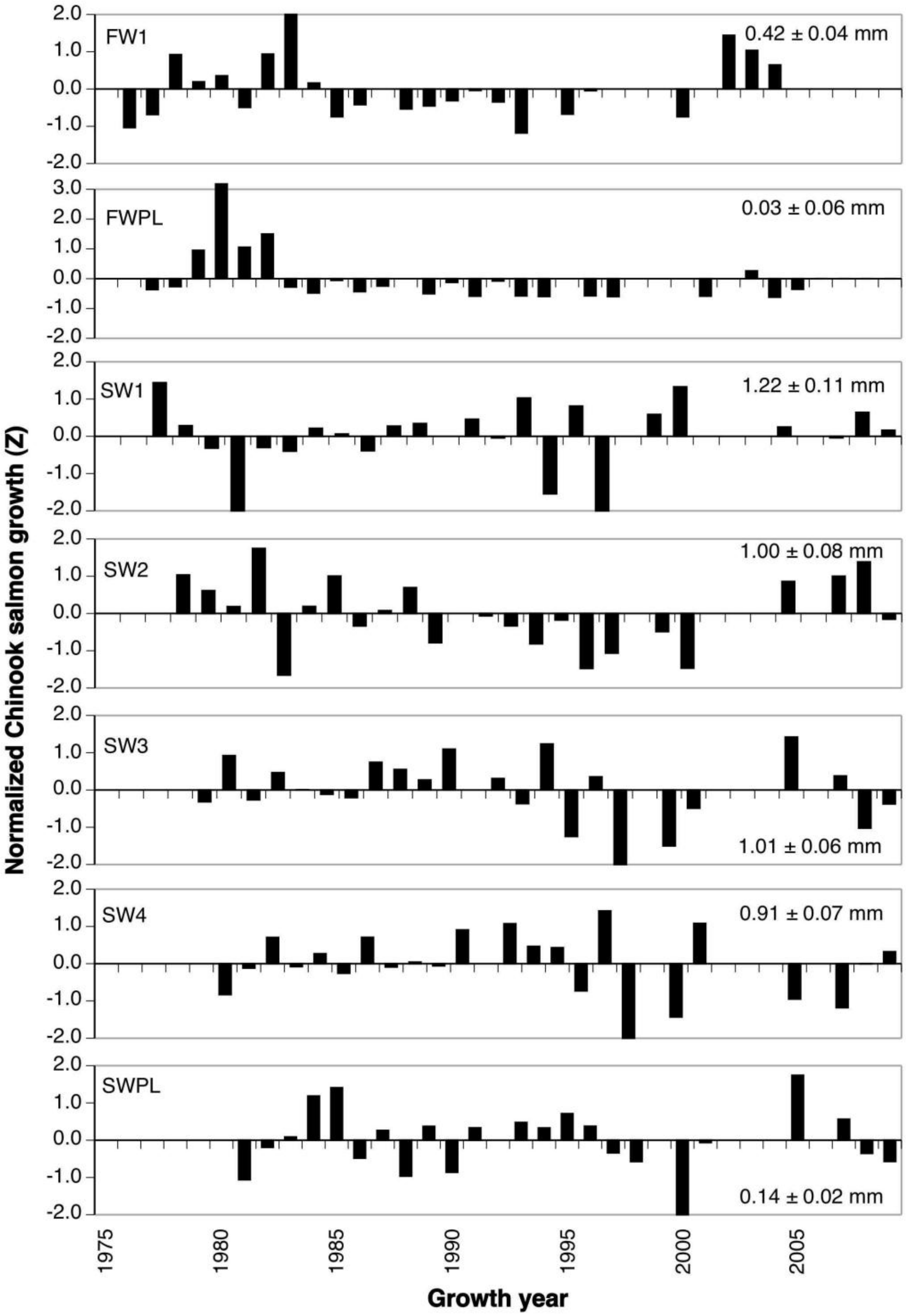

Fig. 5. Mean annual growth of age-1.4 Unalakleet River Chinook salmon during each life stage, growth years 1976-2009. Values are standard deviations above and below the long-term mean. No values for years associated with brood years 1992, 1999, 2002-2004, and 2006.

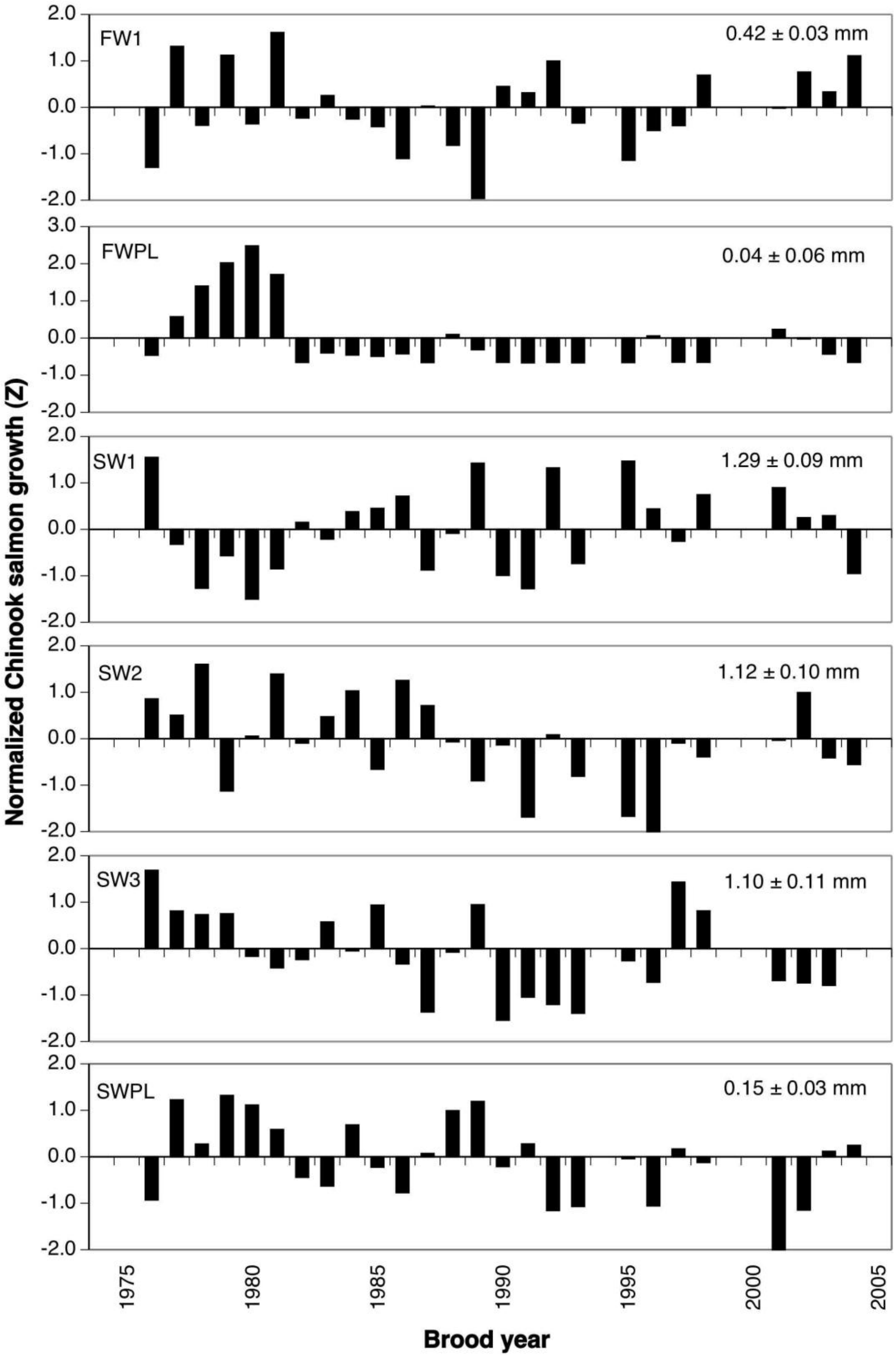

Fig. 6. Mean annual growth of age-1.3 Unalakleet River Chinook salmon during each life stage, brood years 1976-2004. Values are standard deviations above and below the long-term mean. No values for brood years 1999, 2001, 2004, and 2005.

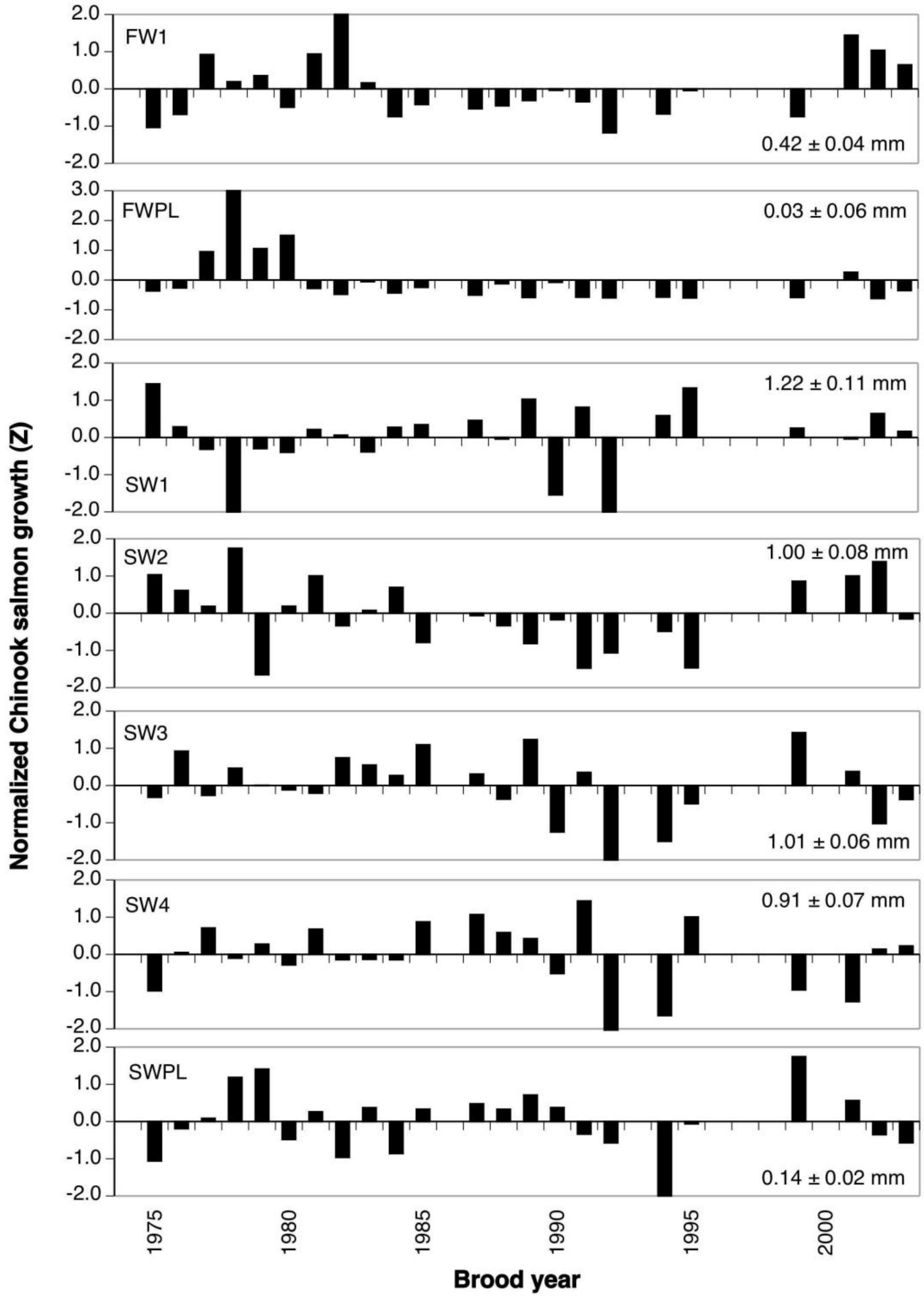

Fig. 7. Mean annual growth of age-1.4 Unalakleet River Chinook salmon during each life stage, brood years 1975-2003. Values are standard deviations above and below the long-term mean. No values for years associated with brood years 1992, 1999, 2002-2004, and 2006.

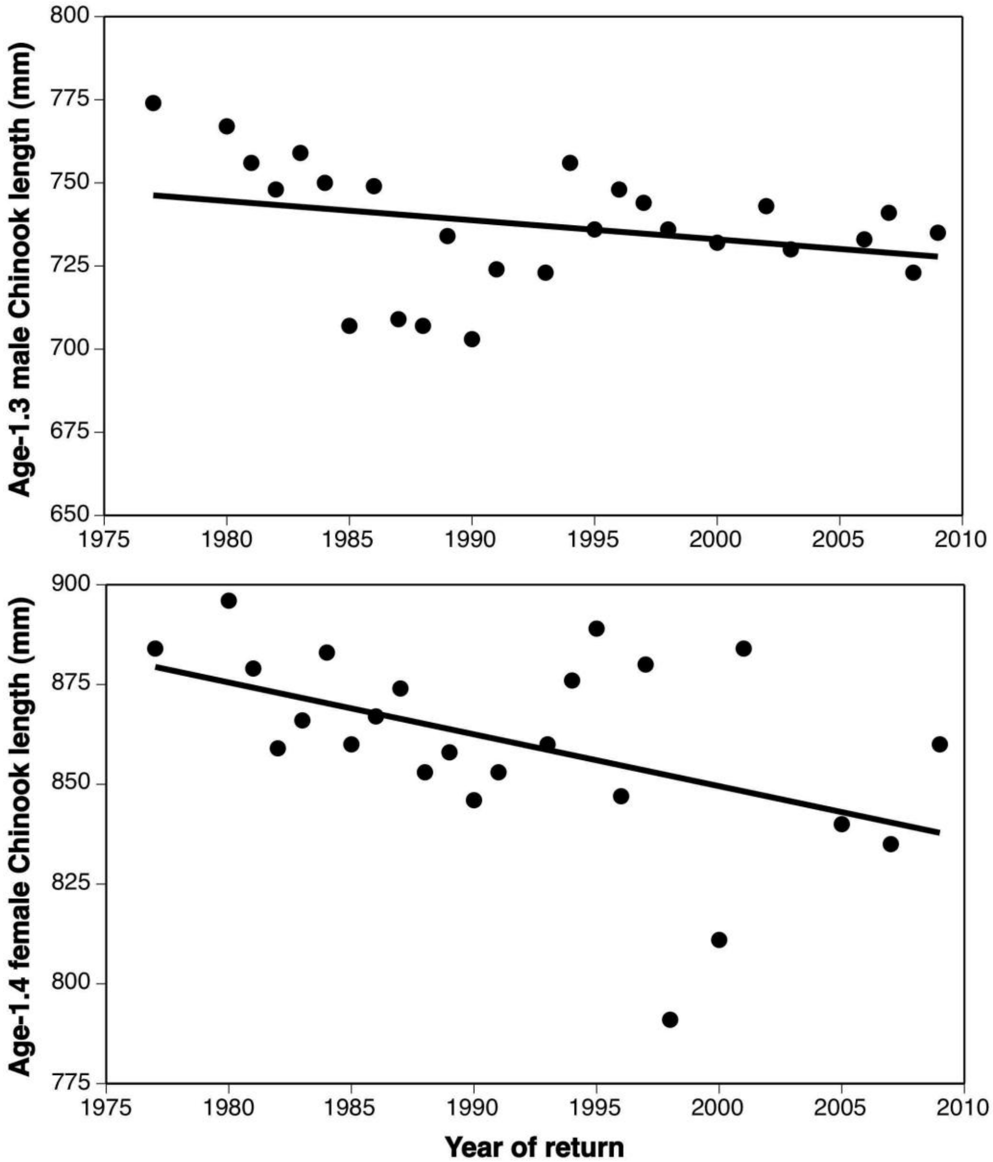

Fig. 8. Decline in length-at-age of age-1.3 and age-1.4 Chinook salmon in the Unalakleet River, 1977-2009. Only commercial catch and test fishery catch fish were used in the analysis. The decline in length of age-1.4 female Chinook salmon was statistically significant ($P = 0.021$). Lengths of male (age-1.3) and female (age-1.4) salmon captured with test fishing gillnets were adjusted by factors of 1.043 and 1.016 to standardize all lengths to commercial catch lengths (based on analysis using years when both gear types were fished). Other age groups did not have sufficient sample size (>10 fish per age and gender).

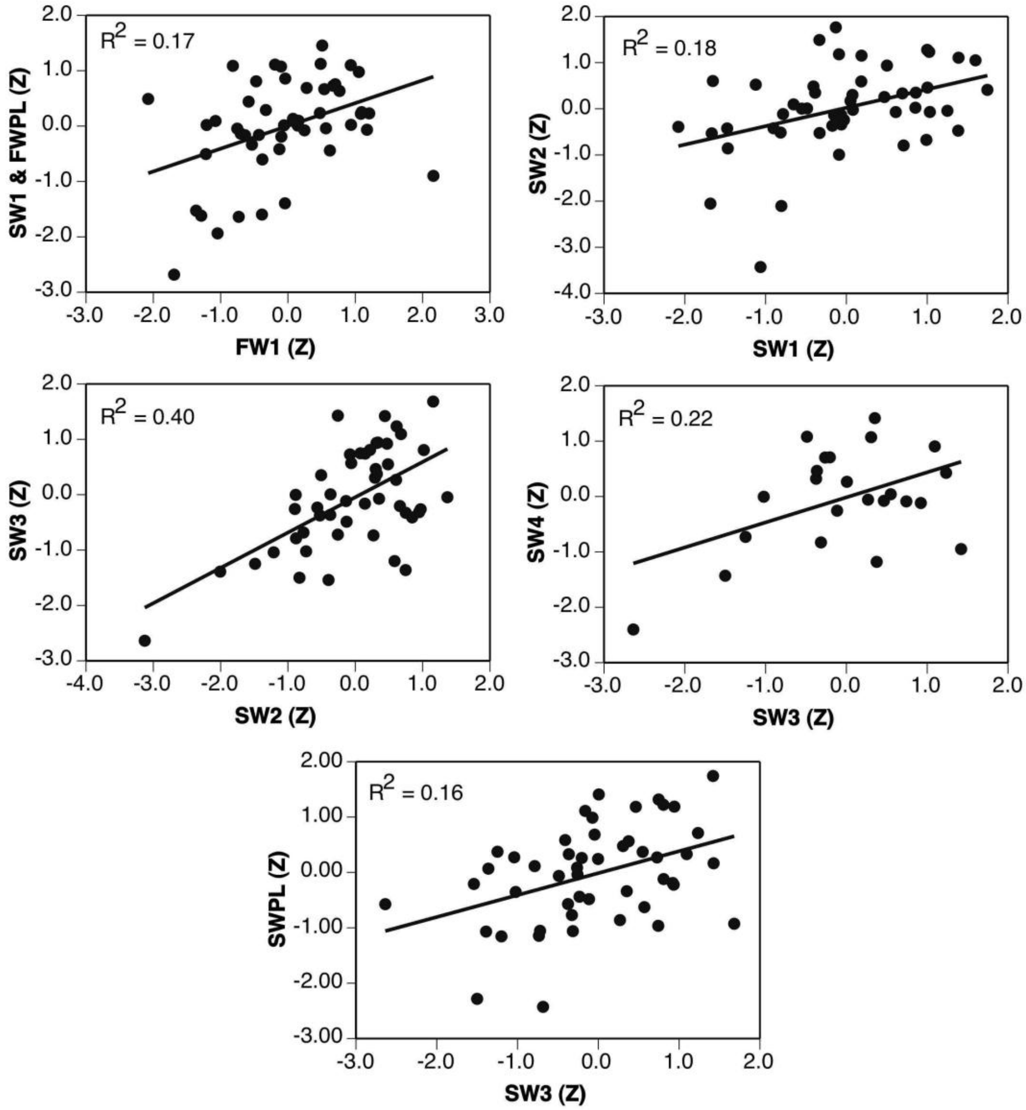

Fig. 9. Relationship between scale growth during each life stage of Unalakleet River Chinook salmon and growth during the previous year. Both age-1.3 and age-1.4 Chinook are included in the graphs. Independent variables include: first four circuli of FW1 excluding focus (FW1 c1-4), width of five maximum circuli during SW1 and SW2, and total SW3 growth. All regressions were statistically significant ($P < 0.05$). All values are normalized.

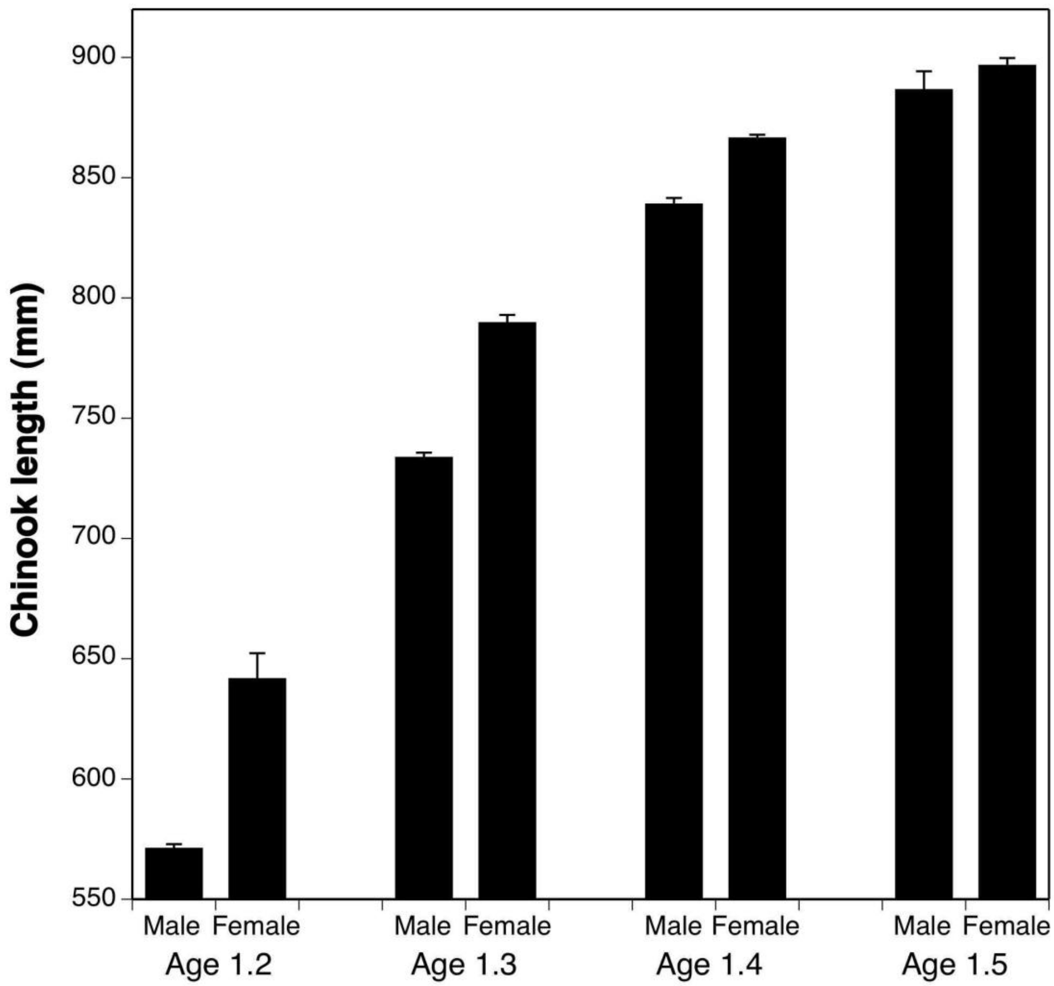

Fig. 10. Mean adult lengths of age-1.3, age-1.3, age-1.4, and age-1.5 male versus female Unalakleet River Chinook salmon, 1969-2009. Values are based on the entire database of 6,553 measured Chinook salmon. Minimum sample size in a category was 90 fish (age-1.2 females). Values are mean ± 1 SE.

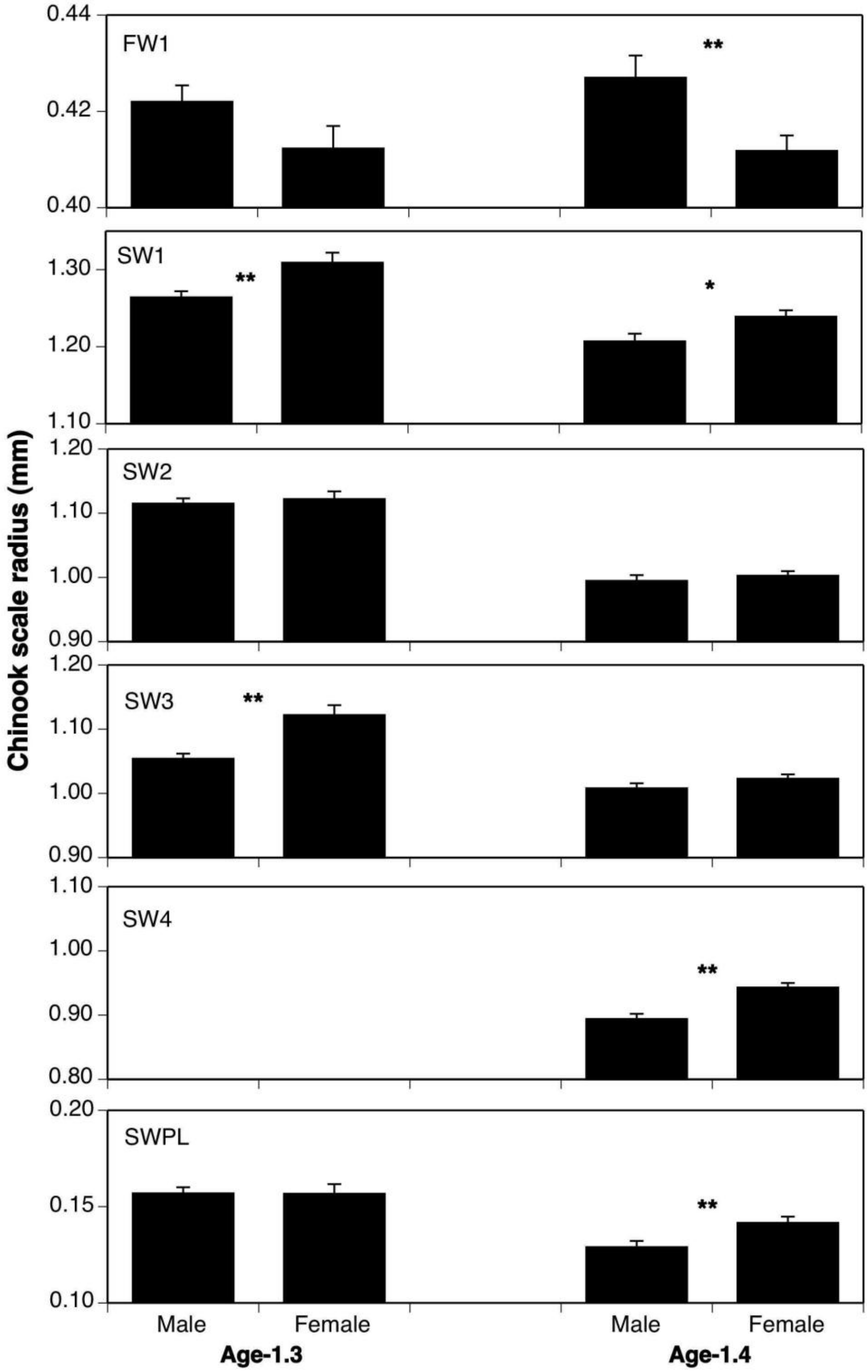

Fig. 11. Scale radius measurements of age-1.3 and age-1.4 male and female Unalakleet River Chinook salmon during each year of life, 1981-2009. Values are mean ± 1 SE. * indicates $P < 0.05$; ** indicates $P < 0.01$. See Tables 4 and 5 for statistical analyses.