2007 Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project Product[1]

Retrospective Analysis of AYK Chinook Salmon Growth

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June 2007

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Summary

Harvests of Yukon and Kuskokwim Chinook salmon declined significantly during 1998-2002 in response to fewer returning salmon. Factors affecting the decline in Chinook salmon abundance are largely unknown. 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 Yukon and Kuskokwim Chinook salmon during each year and life stage in freshwater and the ocean, 1964-2004, using measurements of salmon scale growth. Availability of Yukon scales was greater than that of Kuskokwim scales during 1964-2004.

Harvests of 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 Nino event. Runs of Nushagak District Chinook salmon (Bristol Bay) also appeared to have been affected by these events in addition to the 1989 regime shift. The rapid responses of Chinook salmon abundance to climate change suggest late life stages were primarily affected, at least initially. Therefore, we searched for Chinook salmon growth patterns that might be related to changes in climate.

Comparisons of annual Chinook salmon scale growth patterns with abundance trends and with environmental factors such as the regime shifts were complicated by the high dependency of growth on previous-year growth. Long-term trends in growth were described but further analyses are needed to statistically remove the influence of prior growth before meaningful relationships can be developed between annual growth and abundance.

The unique finding of growth dependency on previous-year growth was consistent among Yukon and Kuskokwim Chinook salmon (ages 1.3 and 1.4) during all life stages except for the homeward migration. For example, growth during the first year at sea was highly correlated with growth in freshwater, and growth during the second year at sea was dependent on growth during the first year at sea. 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 and grow faster. This pattern was not observed in Bristol Bay sockeye salmon and most western Alaska chum salmon.

We tested the hypothesis that Chinook salmon growth was influenced by the strong alternating-year abundances of Asian pink salmon in the Bering Sea. Adult length of Yukon Chinook salmon tended to alternate from year-to-year, especially age-1.3 salmon that were larger during odd-numbered years. Chinook salmon growth during the second year at sea (SW2) was consistently greater during odd-numbered years for both age-1.3 and age-1.4 Chinook salmon returning to the Yukon and Kuskokwim rivers. This finding is opposite of the expected finding if pink salmon, which are less abundant in even years and more abundant in odd years, were directly competing with Chinook salmon. Chum salmon are known to be much more abundant in the Bering Sea during even-numbered years, but their diet overlap with Chinook salmon is approximately 30% and competition with Chinook salmon is less likely. We do not yet know what factors are driving the

alternating-year pattern in Chinook salmon growth but it is conceivable that pink salmon consumed prey that were one year younger than the same prey species consumed by Chinook salmon.

Adult female Chinook salmon (age-1.3 and age-1.4) were significantly longer than male salmon. Greater growth of age-1.3 female Chinook salmon began in freshwater (Yukon) or during the second year at sea (Kuskokwim), then continued during each remaining life stage. In contrast, growth of age-1.4 female Chinook salmon did not become significantly greater until the last year at sea (SW4) and during the homeward migration. The finding of greater female growth is opposite of that for sockeye and chum salmon in which male salmon are longer than female salmon at a given age. This finding suggests that growth may be especially important to the reproductive potential of female Chinook salmon because larger fish tend to produce larger and more numerous eggs.

Growth of age-1.3 Chinook salmon began to exceed that of age-1.4 salmon during freshwater (Yukon) or during the first year at sea (Kuskokwim). Growth of age-1.3 Chinook salmon was significantly greater than that of age-1.4 Chinook salmon during each subsequent life stage except for spring plus growth (FWPL). On average, growth of age-1.3 salmon was 11% (Kuskokwim) to 17% (Yukon) greater than that of age-1.4 salmon growth. These data highlight the complexity when examining growth of salmon at sea.

The unique findings of this investigation (prior year growth dependency, alternating-year growth during SW2, sexual dimorphism during early life, and differential growth of age-1.3 versus age-1.4 salmon early in life) provide new information about Arctic-Yukon-Kuskokwim (AYK) Chinook salmon and the life history strategy of Chinook salmon in general. Additional effort is needed to explore relationships between Chinook salmon growth and abundance and environmental conditions while accounting for strong dependency of growth on previous-year growth.

Introduction

The Yukon and Kuskokwim rivers encompass nearly 40% of Alaska and both rivers support relatively large runs of Chinook salmon. People living within these river basins depend on salmon for subsistence, commercial fishing, culture, and sportfishing. However, poor returns of chinook salmon to the Yukon and Kuskokwim rivers led to severe restrictions on salmon harvests from approximately 1998 to 2002 (Fig. 1; Bue and Hayes 2006, Whitmore et al. 2005). Chinook salmon runs to the nearby Nushagak District (Bristol Bay) also declined beginning in 1999. Factors causing the poor salmon returns are largely unknown (AYK SSI 2006).

Salmon growth is believed to be an important factor influencing survival in both freshwater and marine environments (Juanes 1994, Beamish and Mahnken 2001, Ruggerone et al. 2007). In this investigation, we created a time series of Yukon and Kuskokwim Chinook salmon growth indices, based on scale growth from the early 1960s through 2004. We examined the following hypotheses:

1) The decline of Yukon and Kuskokwim Chinook salmon abundance was associated with less growth in freshwater and/or in the ocean,

2) Growth of Chinook salmon was associated with major ocean-climate events such as the 1976/77 and 1989 regime shifts and the 1997 El Nino event,

3) Growth of Chinook salmon at sea exhibited an alternating-year pattern that was inversely related to Asian pink salmon abundance,

4) Growth of Yukon and Kuskokwim Chinook salmon was correlated,

5) Growth during each life stage was independent of previous growth, and

6) Length-at-age of male and female salmon was similar.

The investigation relied upon measurements of Chinook salmon scales collected by Alaska Department of Fish and Game (ADFG). Scale radii are known to be correlated with salmon body size (Clutter and Whitesel 1956, Henderson and Cass 1991, Fukuwaka and Kaeriyama 1997).

Methods

Scale Collection and Measurements

Adult Chinook salmon scales from the Yukon and Kuskokwim rivers were obtained from the Alaska Department of Fish and Game (ADFG) archive in Anchorage, Alaska. Scales have been collected annually for quantifying age composition since 1965 (Yukon River) or 1964 (Kuskokwim River). 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 are within a relatively small area of the lower river. Fewer scales were available in the Kuskokwim River and we could not be highly selective when choosing scales for measurement. In most years, Kuskokwim Chinook salmon scales were selected from Chinook salmon captured in commercial and/or test fisheries near Bethel. Mesh size was either 5.5-6 inch or 8-8.5 inch mesh. In some years, the Kuskokwim fishery was greatly reduced, therefore scales were also selected from fish sampled at weirs located on the tributaries. Analyses were conducted to determine whether a correction factor was needed to standardize measurements collected from scales using different mesh size and/or location (see below). In both rivers, scales were primarily collected from early June to early July in an attempt to consistently select fish from the same stocks.

The goal was to measure 50 scales from each of the two dominant age groups (ages 1.3 and 1.4)[2] of both the Yukon and Kuskokwim Chinook salmon stocks. Scales were selected for measurement only when: 1) we agreed with the age determination previously made by ADFG, 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 Davis et al. (1990) and 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 (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 Optimas 6.5 image processing software to collect measurement data using a customized program. The scale image was displayed on a digital LCD flat panel tablet and the scale measurement axis was defined as the longest axis extending from the scale focus. 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)). Data associated with the scale such as date of collection, location, sex, fish length, and capture method were included in the dataset.

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 salmon, whereas 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

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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.

growth indices were developed that equally weighted male and female scale growth during each year while utilizing all available scale measurement data:

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 above or below the long-term mean.

Yukon Chinook salmon scales (1,990 digitized scales) were consistently sampled in the same location and with the same gear type, therefore no further adjustments were necessary. However, digitized Kuskokwim Chinook salmon scales were selected from fisheries near Bethel (91% of total scales) using two mesh sizes (5.5-6.0 inch and 8.0-8.5 inch mesh). Approximately 35% of these fish were collected 5.5-6.0 inch mesh, 29% with 8.0-8.5 inch mesh, and 36% with unknown mesh size. During 1986, 1993, 1997 and 2001, additional scales were selected from Chinook salmon sampled at weirs located on four Kuskokwim tributaries (Kwethluk R., Kogrukluk R., George R., Tuluksak R.), representing 9% of the 2,329 digitized scales from the Kuskokwim River (Tables 1 and 2).

ANOVA tests were conducted to determine if mesh size and/or weir samples influenced adult Kuskokwim Chinook salmon length and/or scale annuli measurements. If significant differences occurred, then a correction factor could be applied in order to standardize scale measurements. Two tests were conducted to evaluate the effect of mesh size on scale measurements: 1) all years when one or more mesh sizes were known, and 2) only years when both mesh sizes were available (much smaller sample sizes). Age-1.3 and age-1.4 scales were analyzed separately. ANOVAs indicated adult Chinook salmon length-at-age was significantly greater when sampled by 8.0-8.5 inch mesh gillnets, as expected ($P < 0.05$). Significant differences were also detected for SW3, SW2 (age-1.3 only), and FW1 (age-1.3 only) life stages. Significant growth differences were not detected for FWPL, SW1, SW4 and SWPL life stages of age-1.3 and age-1.4 Chinook salmon. Adjustments were applied to life stage scale measurements of Kuskokwim Chinook salmon when tests indicated consistent statistical differences, as shown in Table 3.

ANOVA tests did not detect significant differences between scale measurements and lengths of Chinook salmon captured with 8-8.5 inch mesh versus gillnets of unknown mesh size ($P > 0.05$), except adult length was significantly greater among fish collected with 8-8.5 inch mesh ($P < 0.05$). A correction factor of 1.057 was applied to lengths of age-1.3 Chinook salmon captured with unknown mesh sizes.

ANOVA tests did not detect significant differences between Kuskokwim Chinook salmon scale measurements sampled at weirs versus 8-8.5 mesh gillnets ($P > 0.05$) when fish from both gears were available in the same year. However, tests were primarily conducted on male salmon (sample size limitations) and relatively few samples were available for these tests (weak statistical power). Thus, no adjustments were made to fish sampled at weirs. These ANOVAs relied upon George River and Kogrukluk weirs because sufficient paired samples were not available for other weirs.

Some Yukon and Kuskokwim 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 not significantly different from normal scale growth in Kuskokwim Chinook salmon (df = 1, 213; F = 2.835; P = 0.094), but it was slightly greater in Yukon Chinook salmon (df = 1, 1588; F = 4.049; P = 0.044). Slightly greater freshwater growth of Yukon abnormal focus scales was opposite the trend of Kuskokwim scales. No effect was observed in adjacent life stages. Fish having an abnormal focus were excluded from statistical analyses.

Results and Discussion

Annual Growth Trends by Life Stage

Freshwater scale growth (FW1 and FWPL) of age-1.3 and age-1.4 Yukon Chinook salmon tended to be relatively high from the 1960s through early 1970s, intermediate from the mid 1970s through early 1980s, then typically below average after 1984 until rebounding in 1999 or 2000 (Figs. 2, 3, 4, 5). Mean annual growth was typically within two standard deviations of the long-term mean. During the first year at sea (SW1), Yukon Chinook salmon growth was variable but tended to be intermediate prior to the mid-1970s, high during and immediately after the 1976/77 regime shift, and below average after the 1989 regime shift. Growth during the second, third, and fourth year at sea tended to be below average from the mid-1980s through the 1990s, then scale growth increased during the early 2000s. In contrast, scale growth during the homeward migration, which can be influenced by scale resorption, tended to be below average prior the mid-1970s and variable thereafter. Adult length of measured age-1.3 Chinook salmon did not show a long-term pattern, whereas length of age-1.4 Chinook salmon tended to reflect growth during each year at sea (Figs. 4 and 5).

The ability to detect trends in Kuskokwim Chinook salmon scale growth was influenced by the lack of scales during the late 1960s and early 1970s (Table 1) and possibly by adjustments made to standardize life-stage growth associated with Chinook salmon captured with small versus large mesh gillnets (Table 3). Growth of age-1.3 and age-1.4 Chinook salmon during freshwater and each year at sea tended to be below average from the mid-1970s to the late 1980s, then above average in the 1990s (Figs. 6 and 7). These patterns shifted to earlier years when growth was examined by brood year (Figs. 8 and 9). Freshwater growth was exceptionally high during the late 1990s. Scale growth during the homeward migration, which is influenced by scale resorption, tended to be average to below average after the mid-1970s to early 1990s, above average until 2001, then markedly below average in 2002-2004. Adult length of age-1.3 salmon was variable throughout the series but tended to be somewhat above average during return years 1995 to 1999 (i.e., brood years 1990 to 1994), then low in more recent years (Fig. 8). Adult length of age-1.4 salmon was variable but tended to be below average after return year 1990 (Fig. 9).

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

Growth of age-1.3 and age-1.4 Chinook salmon during each life stage were compared using correlation analysis. Among Yukon Chinook salmon originating from the same cohort, significant positive correlations were observed during FW1, FWPL, SW2, and SW3 life stages, although some correlations were not high (Table 4). Among Kuskokwim Chinook salmon, significant positive correlations were observed during FW1, FWPL, SW3, SWPL, and adult length. SW1 growth was least correlated among both Yukon and Kuskokwim Chinook salmon. Growth of younger life stages of age-1.3 Chinook salmon tended to be more correlated with growth of older age-1.4 life stages during the same year of rearing in the ocean than with growth of younger age-1.4 life stages.

Comparison of Yukon and Kuskokwim Chinook Salmon Growth

Growth of Yukon versus Kuskokwim Chinook salmon were compared using correlation analysis. Most correlations in freshwater were non-significant (Table 5). All three significant correlations were negative, suggesting that a region-wide factor did not influence freshwater growth of both stocks. In marine waters, growth of Yukon Chinook salmon was not significantly correlated with growth of Kuskokwim Chinook salmon of the same life stage (e.g., SW1) and year at sea (Table 5). Growth of most life stages at sea were not significantly correlated with different life stages co-occurring in the ocean during the same year. However, significant correlations between different life stages of the two stocks were all negative. These data suggest that either Yukon and Kuskokwim Chinook salmon did not experience similar growing conditions in the ocean or that differential growth in freshwater confounded growth correlations in the ocean (see growth dependency below).

Comparison of Adult Length and Scale Growth

Adult size of salmon is primarily established during the last several months at sea (Brett 1995), but resorption of Chinook salmon scales during this period may confound a relationship between adult size and scale growth measurements. Nevertheless, mean annual adult length of Yukon and Kuskokwim Chinook salmon was typically correlated with scale growth.

Length of Yukon age-1.4 Chinook salmon was correlated with total marine scale growth, which explained 38% of the variability in mean length, 1966-2004 (Fig. 10). Approximately 28% of the annual variability in mean length of Yukon age-1.3 Chinook salmon was explained by the combined effects of scale growth during the homeward migration and scale growth during the second year at sea. Length of Yukon age-1.3 Chinook salmon was also positively correlated with total marine scale growth ($R^2 = 0.21$, $P < 0.05$).

Adult length of age-1.3 Chinook salmon returning to the Kuskokwim River was positively correlated with scale growth during the homeward migration. Scale growth explained 30% of the annual variability in adult length from 1975 to 2004. In contrast, adult length of age-1.4 Chinook salmon returning to the Kuskokwim River was negatively correlated with scale growth during SW3, SW4, and homeward migration ($R^2 = 0.23 - 0.31$, $P < 0.05$).

Climate Shift, Chinook Salmon Abundance and Growth

Yukon, Kuskokwim and Nushagak Chinook salmon abundance indices shown in Fig. 1 tend to reflect the 1976/77 ocean regime shift (abundance increase) and the 1997/98 El Nino event (abundance decrease). Both of these broad-scale climate events had a significant impact on the Southeastern Bering Sea and on salmon production (Rogers 1984; Kruse 1998; Peterman et al. 2003; Hunt et al. 2002). In contrast, the 1989 regime shift (Hare and Mantua 2000), which was associated with a significant decline in adult size and abundance of Bristol Bay sockeye salmon (Ruggerone and Link 2006; Ruggerone et al. 2007), did not have an immediate effect on Yukon and Kuskokwim Chinook salmon abundance (Fig. 1). It is noteworthy that adult abundance of Chinook salmon changed rapidly in response to the 1976/77 and 1997/98 climate events, suggesting abundance and survival were largely influenced during late marine life rather than early life.

We did not find statistically significant and meaningful relationships between the Chinook salmon abundance indices and Chinook salmon scale growth during each life stage. The lack of significant relationships probably reflects the strong dependence of scale growth on growth that occurred during the previous year, as noted below. Removal of this dependence through additional statistical analyses is necessary before hypotheses about western Alaska Chinook salmon growth and abundance and survival can be tested. We have initiated analyses to remove previous-year effects on Chinook salmon growth, but we are unable to complete this unexpected analysis given the short time frame of this project.

Annual and seasonal scale growth was compared with the Chinook salmon abundance indices shown in Fig. 1. Abundance of Yukon Chinook salmon was negatively correlated with spring plus growth during the smolt migration ($r = -0.41$; $n = 32$, $P < 0.05$) and positively correlated with scale growth during the homeward migration ($r = 0.38$; $n = 32$, $P < 0.05$). No other variables were correlated with the Yukon abundance index. Abundance of Kuskokwim Chinook salmon was negatively correlated with scale growth during each life stage ($n = 28$, $P < 0.05$). The negative correlations between Kuskokwim Chinook salmon abundance and scale growth were influenced by low scale growth after the 1976/77 regime shift when Chinook salmon abundance was high, followed by relatively high scale growth beginning in the early to mid-1990s.

Scale growth patterns were compared with the 1976/77, 1989, and 1997/98 climate events. Distinct shifts in scale growth during each life stage were not associated with these climate events. The most noticeable pattern occurred among Yukon Chinook salmon during the first year at sea (SW1). Yukon SW1 scale growth tended to be intermediate prior to the mid-1970s, high immediately after the 1976/77 regime shift, and below average after the 1989 regime shift (Figs. 2 and 3). Yukon scale growth during subsequent life stages tended to follow this pattern although the pattern was less defined. Growth of Kuskokwim Chinook salmon during the first year at sea (SW1) tended to be high after the 1989 regime shift compared with growth during the late 1970s and early 1980s (Figs. 6 and 7). Thus, early marine scale growth of Yukon Chinook salmon tended to decrease after the 1989 shift, whereas growth of Kuskokwim Chinook salmon tended to increase. As noted above, growth of Yukon and Kuskokwim Chinook salmon tended to be negatively correlated during each life stage, although correlations were weak and typically non-significant (Table 5).

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). We tested the hypothesis that 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 was 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 AYK Chinook salmon and western Alaska pink salmon, which are much less abundant and are primarily present during even-numbered years. It is possible, however, that pink salmon fry contributed to the diet and growth of yearling Chinook salmon, therefore we also examined growth in freshwater.

In order to remove the effects of time trends and to highlight differences in growth between even- and odd-numbered years, we calculated the first difference of each Chinook salmon scale growth variable, i.e., differenced growth (DG_i) = $G_i - G_{i-1}$, where G is scale growth in year i. Adult length of age-1.3 Chinook salmon was significantly longer when returning in odd-numbered versus even-numbered years (large mesh nets only: df = 1, 35; F = 21.181; $P < 0.001$). The alternating-year pattern was consistent throughout all years, 1968-2004, although it was less apparent during the mid to late 1990s. In contrast, the alternating-year pattern of age-1.4 Chinook salmon length switched in the early 1990s, based on the significant interaction variable that split the dataset into two periods: 1968-1991 and 1992-2004 (df = 1, 33; F = 11.770; P = 0.0016). During odd-numbered return years, Chinook salmon tended to be smaller prior to 1992 and larger during 1992-2004. However, length was not significantly different within each period ($P > 0.05$).

Using differenced values, we examined annual scale growth patterns to determine the life stage in which growth might vary between odd- and even-numbered years. Among age-

1.3 Chinook salmon, annual scale growth did not show an alternating-year pattern, except during SW2 when differenced growth tended to be greater during odd-numbered years at sea (Figs. 11 and 12; df = 1, 36; F = 3.165; P = 0.084). Among age-1.4 Chinook salmon, SW2 scale growth was significantly greater during odd-numbered years at sea (Figs. 11 and 12; df = 1, 36; F = 33.869; P < 0.001), whereas SW3 growth was significantly greater during even-numbered years (df = 1, 36; F = 23.715; P < 0.001). No differences in growth were detected during other life stages of age-1.4 Chinook salmon. As noted below, growth tended to depend on previous-year growth, therefore the significant effect shown during SW3 may reflect SW2 growth. Thus, greater odd-year SW2 growth of both age-1.3 and age-1.4 Yukon Chinook salmon was associated with greater adult length, especially prior to 1992[3].

Kuskokwim scale growth during odd- versus even-years at sea followed the same pattern as Yukon Chinook salmon. Among age-1.3 Chinook salmon, SW2 growth (differenced values) during odd-numbered years at sea tended to be greater than growth during even-numbered years(Figs. 11 and 12; df = 1, 24; F = 2.764; P = 0.109). Likewise, SW2 growth of age-1.4 Chinook salmon was significantly greater during odd-numbered years at sea (Figs. 11 and 12; df = 1, 24; F = 4.437; P = 0.046). Too few Kuskokwim Chinook salmon were consistently sampled near Bethel each year to test whether adult length exhibited an odd/even-year pattern.

Additional statistical analyses confirmed that SW2 growth of Yukon and Kuskokwim Chinook salmon (age-1.3 and age-1.4) was significantly greater during odd-numbered years. A three factor ANOVA (odd/even, age, stock) indicated significant interaction between odd/even years and age (df = 1, 1, 124; F = 4.434; P = 0.037), indicating the strength of the odd/even-year effect was not consistent among age-1.3 and age-1.4 salmon; no difference was detected between stocks. Based on the significant interaction between age and odd/even year, a two factor ANOVA (odd/even, age) was conducted. The ANOVA indicated significantly greater SW2 growth of both age-1.3 (df = 1, 62; F = 5.374; P = 0.022) and age-1.4 (df = 1, 62; F = 26.313; P < 0.001) during odd-numbered years at sea.

Greater SW2 growth of Chinook salmon during odd-numbered years was unexpected. Initially, we expected early marine growth of Chinook salmon might be reduced during odd-numbered years at sea because pink salmon are highly abundant. However, chum salmon were 134% more abundant during even-numbered years, 1991-2000 (Davis et al. 2005). Both Chinook salmon and chum salmon overwinter together in the Bering Sea, as indicated by incidental catches of both species in the pollock fishery. However, diet overlap between Chinook salmon and Chum salmon tends to be relatively small (avg. 30% in odd and even years) and chum eat relatively little fish and squid compared with Chinook salmon (Davis et al. 2005). We do not know which prey species might contribute to this alternating-year pattern of growth, but it is likely a species that is consumed primarily during their second year at sea.

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[3] SW2 growth during odd-numbered years was associated with age-1.3 adults returning in odd-numbered years, whereas it was associated with age-1.4 adults returning in even-numbered years.

Growth Dependence on Earlier Growth

Life stage growth of both Yukon (Fig. 13 and 14) and Kuskokwim (Fig. 15 and 16) Chinook salmon was significantly and positively correlated with growth during the previous year ($P < 0.05$), excluding growth during homeward migration. On average, 60% and 76% of the variability in Yukon and Kuskokwim scale growth, respectively, was explained by growth during the previous year. These relationships were consistent for both age-1.3 and age-1.4 Chinook salmon. Spring growth during the smolt migration period (FWPL) was correlated with total freshwater growth. Growth during the first year at sea was correlated with freshwater growth, but was most highly correlated with growth during early life in freshwater (i.e., circuli 1-4). Growth during each subsequent year was correlated with previous year growth, but growth was most highly correlated with maximum scale growth, as defined as the spacing among the five widest circuli. Regression slopes were consistently below 1.0, indicating scale growth of older life stages grew at a slower rate compared with younger stages.

The only exception to the pattern of growth dependency was during the homeward migration (SWPL). Kuskokwim SWPL growth tended to be positively correlated with growth during the third year at sea (Fig. 15 and 16), whereas Yukon SWPL growth was negatively correlated with growth during the third year and fourth years at sea (Fig. 13 and 14).

Autocorrelation was present in most scale growth time series. However, autocorrelation was nonsignificant in the residuals of the growth regressions described above, indicating the regression models were not significantly influenced by time (L. Conquest, University of Washington, pers. comm.). Furthermore, statistical significance of the regressions was tested by reducing the degrees of freedom to account for autocorrelation within the variables (Pyper and Peterman 1998) and all regressions were statistically significant.

The dependence of growth on prior growth is an unusual finding compared with analyses of 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 growth in the second year versus first year at sea. They suggested the negative relationship might reflect the need to grow fast in the second year if growth in the first year was below average.

Sexual Dimorphism

Two factor ANOVA (sex, mesh size) applied to both Yukon and Kuskokwim salmon indicated adult female Chinook salmon returning at age-1.3 and age-1.4 were significantly longer than male salmon (Fig. 17; Table 6). This pattern was consistent for both small mesh and large mesh gillnets and for both Yukon and Kuskokwim stocks. On average, age-1.3 female Chinook salmon were 59 mm longer than male salmon, whereas age-1.4 salmon were 14 mm longer[4].

In contrast to age-1.3 and age-1.4 salmon, male age-1.5 Yukon Chinook salmon were significantly longer (d = 34 mm) than female salmon (Fig. 17; Table 7). Length of male age-1.5 Kuskokwim salmon was not different from female salmon.

ANOVA was used to identify the life stage(s) at which female Chinook salmon became longer than male salmon. Among age-1.3 Chinook salmon, Yukon female scale radii exceeded that of male salmon beginning in freshwater (FW1; Fig. 18), whereas Kuskokwim female salmon began to exceed growth of male salmon during the second year at sea (Table 7; Fig. 19). Growth of female age-1.3 salmon during all late life stages were consistently greater than male salmon, leading to greater female adult length, as noted above.

In contrast, among age-1.4 salmon, male salmon tended to be larger than female salmon from freshwater residence through the second or third year in the ocean (Table 7; Fig. 19). Growth of age-1.4 female salmon exceeded that of male salmon only during late life stages, including SW4 and the homeward migration. Relatively great growth of female salmon during late marine life led to greater adult length of female compared with male salmon, as discussed above.

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. We hope to provide a more in depth discussion about sexual dimorphism, age structure, and life history strategy in subsequent publications.

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

Faster growing salmon tend to mature at an earlier age. Therefore, scale measurements were used to determine the life stage at which growth of age-1.3 Yukon and Kuskokwim 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 freshwater (Yukon) or during the first year at sea (Kuskokwim; Table 8). Growth of age-1.3 Chinook salmon was significantly greater, on average, during each subsequent life stage except for spring plus growth (FWPL). On average, growth of age-1.3 salmon was 11% (Kuskokwim) to 17% greater (Yukon) than that of age-1.4 salmon growth.

During FWPL, growth of age-1.4 salmon (both stocks) significantly exceeded that of age-1.3 salmon (Table 8). Growth of age-1.3 salmon was 7.7% (Kuskokwim) to 11% less (Yukon) than that of age-1.4 salmon growth. Slower FWPL growth of age-1.3 Chinook salmon might reflect a tendency for larger smolts to migrate earlier in the season, thereby allowing less spring plus growth (FWPL) but greater growth during the first year in the

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[4] Values are unweighted means from fish captured by small and large mesh gillnets.

ocean (SW1). These data highlight the complexity when examining growth of salmon at sea.

Effect of Gillnet Mesh Size on Chinook Salmon Size

The ANOVA to test the effect of sex on adult size of Chinook salmon was also used to examine the effect of mesh size on Chinook salmon size. Large-mesh gillnets (8.0-8.5 inch) captured larger salmon compared with small mesh nets (5.5-6.0 inch), but this effect varied with age of Chinook salmon (Table 6). Large mesh gillnets captured Chinook salmon that were 56 mm (age-1.3), 20 mm (age-1.4), and 30 mm (age-1.5) longer depending on age. Selectivity for female salmon was similar: large mesh gillnets captured Chinook salmon that were 58 mm (age-1.3), 16 mm (age-1.4), and 23 mm (age-1.5) longer than those in small mesh nets, depending on age.

Conclusions

Harvests of Yukon and Kuskokwim Chinook salmon appeared to rapidly increase in response to the 1976/77 ocean regime shift, then rapidly decline in response to the 1997/98 El Nino event. These rapid responses of Chinook salmon abundance to climate change suggest late life stages were primarily affected, at least initially. Comparisons of annual Chinook salmon scale growth patterns with abundance trends and with environmental factors such as the regime shifts were complicated by the high dependency of growth on previous-year growth. Some long-term trends in growth were discussed but further analyses are needed to statistically remove the influence of prior growth before meaningful relationships can be developed between annual growth and abundance.

Growth of Chinook salmon in a given year was highly dependent on growth during the previous year. This unique finding was consistent among Yukon and Kuskokwim Chinook salmon (ages 1.3 and 1.4) during all life stages except for the homeward migration. For example, great growth in freshwater led to great growth during the first year at sea. 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 and grow faster. This pattern was not observed in Bristol Bay sockeye salmon and most western Alaska chum salmon.

We tested the hypothesis that Chinook salmon growth was influenced by the strong alternating-year abundances of Asian pink salmon in the Bering Sea. Diet overlap between pink and Chinook salmon in the Bering Sea is approximately 55% (Davis et al. 2005). Adult length of Yukon Chinook salmon tended to alternate from year-to-year, especially age-1.3 salmon that were longer during odd-numbered years (too few Kuskokwim adult data available for test). Analyses of annual scale growth patterns indicated that SW2 growth was consistently greater during odd-numbered years at sea for both age-1.3 and age-1.4 Chinook salmon returning to the Yukon and Kuskokwim rivers. Interestingly, this finding is opposite the expected finding if pink salmon were directly competing with Chinook salmon. Chum salmon are known to be much more abundant in the Bering Sea during even-numbered years, but their diet overlap with Chinook salmon is approximately 30% (Davis et al. 2005) and competition with Chinook salmon is less likely. We do not yet know what factors are driving the alternating-year pattern in Chinook salmon growth but it is conceivable that it could be caused by pink salmon if pink salmon consumed shared prey that were one year younger than the same prey consumed by Chinook salmon during their second year at sea.

Adult female Chinook salmon (age-1.3 and age-1.4) were significantly longer than male salmon. Scale increments of age-1.3 female Chinook salmon were significantly greater than that of male salmon during each life stage beginning in freshwater (Yukon) or during the second year at sea (Kuskokwim). In contrast, scale increments of age-1.4 female Chinook salmon did not become significantly greater until the last year at sea (SW4) and during the homeward migration. The finding of large female size-at-age contrasts with greater length of male sockeye and chum salmon at a given age. This finding suggests that growth may be especially important to the reproductive potential of female Chinook salmon because larger fish tend to produce larger and more numerous eggs.

Growth of age-1.3 Chinook salmon began to exceed that of age-1.4 salmon during freshwater (Yukon) or during the first year at sea (Kuskokwim). Growth of age-1.3 Chinook salmon was significantly greater than that of age-1.4 Chinook salmon during each subsequent life stage except for spring plus growth (FWPL). On average, growth of age-1.3 salmon was 11% (Kuskokwim) to 17% greater (Yukon) than that of age-1.4 salmon growth. These data highlight the complexity when examining growth of salmon at sea.

The unique findings of this investigation (growth dependency, alternating-year growth during SW2, sexual dimorphism during early life, and differential growth of age-1.3 versus age-1.4 salmon early in life) provide new information about AYK Chinook salmon and life history strategy of Chinook salmon in general. Additional effort is needed to develop relationships between Chinook growth and abundance and environmental conditions while accounting for strong dependency of growth on previous-year growth.

Acknowledgements

This investigation was funded by the AYK Sustainable Salmon Initiative (Projects 45076, 45077, 45078). We thank ADF&G biologists, especially D. Molyneaux, who provided constructive comments on the study. We also appreciate efforts to gather, measure, and catalog scales by D. Folletti, M. Lovejoy, A. Norman, D. Oxman, W. Rosky, and W. Whelan. Constructive comments on the report were provided by E. Ivaska, S. Goodman, C. Jay, J. June, and C. Zimmerman.

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Table 1. Annual scale sample sizes of age-1.3 and age-1.4 Kuskokwim Chinook salmon selected from the fishery catches near Bethel and weirs on tributaries.

	Commercial & Test Fishery Catch			Weir	Total
Year	Unkn mesh	5.5-6"	8.0-8.5"	samples	scales
Age 1.3					
1964	8	0	37	0	45
1965	20	0	23	0	43
1966	0	0	21	0	21
1975	36	0	0	0	36
1977	0	5	34	0	39
1978	4	0	10	0	14
1979	0	3	21	0	24
1981	17	0	12	0	29
1982	0	15	11	0	26
1983	0	23	28	0	51
1984	36	0	0	0	36
1985	0	37	0	0	37
1986	33	0	0	5	38
1987	38	0	0	0	38
1988	0	43	0	0	43
1989	34	0	0	0	34
1990	36	0	0	0	36
1991	39	0	0	0	39
1992	34	0	0	0	34
1993	15	2	8	13	38
1994	51	0	0	0	51
1995	0	41	0	0	41
1996	0	46	0	0	46
1997	0	16	0	10	26
1998	0	47	0	0	47
1999	0	21	0	8	29
2000	0	0	0	29	29
2001	0	7	5	8	20
2002	0	30	19	1	50
2003	0	47	7	4	58
2004	19	0	6	0	25
Age 1.4					
1964	15	0	30	0	45
1965	10	0	22	0	32
1966	0	0	38	0	38
1975	9	0	0	0	9
1977	0	6	42	0	48
1978	14	0	39	0	53
1979	0	0	28	0	28
1981	8	0	43	0	51
1982	0	12	33	0	45
1983	0	20	26	0	46
1984	51	0	0	0	51
1985	0	45	0	0	45
1986	17	0	0	25	42
1987	37	0	0	0	37
1988	0	39	0	0	39
1989	41	0	0	0	41
1990	37	0	0	0	37
1991	31	0	0	0	31
1992	30	0	0	0	30
1993	6	1	4	24	35
1994	31	0	0	0	31
1995	0	50	0	0	50
1996	0	45	0	0	45
1997	0	22	0	19	41
1998	0	33	0	6	39
1999	0	46	0	5	51
2000	0	0	0	28	28
2001	0	6	6	12	24
2002	0	14	36	11	61
2003	0	14	24	8	46
2004	4	0	3	0	7
Total	761	736	616	216	2329

Table 2. Annual scale sample sizes of age-1.3 and age-1.4 Yukon Chinook salmon selected from the fishery catches in the lower river. All fish were collected with 8.0-8.5 inch mesh.

Year	Age-1.3	Age-1.4
1966	5	50
1967	23	50
1968	40	50
1969	44	50
1970	50	50
1971	50	50
1972	50	51
1973	50	50
1974	50	54
1975	50	50
1976	50	51
1977	46	50
1978	16	57
1979	51	51
1980	52	50
1981	50	50
1982	50	54
1983	50	54
1984	30	54
1985	27	52
1986	50	50
1987	33	57
1988	36	60
1989	22	38
1990	52	56
1991	50	56
1992	52	56
1993	50	52
1994	51	50
1995	20	56
1996	54	25
1997	56	48
1998	52	53
1999	26	52
2000	16	50
2001	23	53
2002	53	50
2003	55	50
2004	35	50
Total	1620	1990

Table 3. Effect of gillnet mesh size on Kuskokwim Chinook salmon growth characteristics. Values are ratio of fish growth measurements when captured by 8-8.5 inch mesh vs. 5.5-6 inch mesh based on two tests: 1) all years of data, 2) years when data available for both mesh sizes. Correction factors were applied to fish caught with 5.5-6 inch mesh when consistent significant differences were observed (*) based on ANOVA. (*) indicates one of two tests were significant ($P < 0.05$) and trends of both tests were consistent. (**) indicates both tests were significant ($P < 0.05$) and trends were consistent. (***) indicates both tests were highly significant ($P < 0.01$) and trends were consistent.

Life stage	Age 1.3		Age 1.4	
Adult length	1.117	***	1.028	***
FW1	0.946	*	0.981	NS
FWPL	0.949	NS	0.972	NS
SW1	0.988	NS	0.99	NS
SW2	1.077	**	0.975	NS
SW3	1.101	**	1.014	*
SW4			0.973	NS
SWPL	1.026	NS	0.993	NS

Table 4. Within growth-year correlations (r) between A) age-1.3 and age-1.4 Kuskokwim Chinook salmon and B) age-1.3 and age-1.4 Yukon Chinook salmon. Values within boxes are from the same cohort. Significant correlations are underlined ($P < 0.05$) or shown in bold ($P < 0.01$).

A.

	Kuskokwim age 1.4							
Kuskokwim age 1.3	FW1	FWPL	SW1	SW2	SW3	SW4	SWPL	Length
FW1	0.41	**0.69**	0.28	0.22	0.30	0.41	0.39	
FWPL	0.35	**0.71**	0.14	0.05	0.41	0.21	0.33	
SW1	0.28	0.24	0.21	0.20	**0.49**	0.36	0.47	
SW2	0.28	0.29	0.14	0.27	**0.46**	**0.51**	0.29	
SW3	0.32	0.21	0.42	0.03	0.39	0.36	0.01	
SWPL	0.32	0.38	0.42	0.18	0.35	-0.19	**0.78**	
Length								0.44

B.

	Yukon age 1.4							
Yukon age 1.3	FW1	FWPL	SW1	SW2	SW3	SW4	SWPL	Length
FW1	0.37	**0.63**	0.40	**0.51**	**0.56**	0.42	-0.18	
FWPL	0.33	**0.49**	0.21	0.33	**0.44**	**0.50**	-0.32	
SW1	0.21	-0.08	0.23	**0.41**	0.34	0.37	-0.01	
SW2	0.40	0.37	0.23	**0.61**	**0.57**	**0.49**	-0.09	
SW3	0.27	0.35	0.32	**0.46**	**0.45**	**0.58**	0.06	
SWPL	-0.32	-0.36	-0.09	-0.21	-0.25	-0.16	0.18	
Length								0.08

Table 5. Within growth year correlations (r) between Kuskokwim Chinook salmon and Yukon Chinook salmon during A) freshwater and B) marine life stages. Correlations at $P < 0.05$ underlined; correlations at $P < 0.01$ are bold.

A.

			Kuskokwim			
			Age 1.3		Age 1.4	
			FW1	FWPL	FW1	FWPL
Yukon	Age 1.3	FW1	-0.07	-0.10	-0.44	0.02
		FWPL	-0.16	-0.11	-0.23	-0.47
	Age 1.4	FW1	0.15	0.27	-0.05	0.12
		FWPL	0.01	0.12	-0.38	-0.16

B.

			Kuskokwim								
			Age 1.3				Age 1.4				
			SW1	SW2	SW3	SWPL	SW1	SW2	SW3	SW4	SWPL
Yukon	Age 1.3	SW1	-0.29	-0.33	-0.13	-0.35	-0.04	-0.11	-0.25	0.01	-0.17
		SW2	-0.41	-0.15	-0.32	**-0.47**	-0.41	0.06	-0.15	-0.13	-0.36
		SW3	-0.40	-0.25	-0.14	-0.36	**-0.67**	-0.20	-0.29	0.05	-0.39
		SWPL	0.11	0.23	0.20	-0.18	0.15	0.04	0.16	0.37	-0.02
	Age 1.4	SW1	-0.08	0.07	0.38	-0.21	-0.07	-0.18	0.14	0.04	0.01
		SW2	-0.34	-0.08	0.04	-0.28	-0.33	0.21	-0.25	-0.08	-0.19
		SW3	-0.44	-0.19	0.16	-0.41	0.34	-0.24	-0.01	-0.07	-0.35
		SW4	-0.34	-0.24	0.10	-0.31	**-0.52**	-0.29	-0.14	0.07	-0.30
		SWPL	-0.45	-0.37	0.09	0.06	0.37	0.02	-0.16	0.00	0.05

Table 6. Two factor ANOVAs to examine whether adult length-at-age was influenced by sex and/or gillnet mesh size (5.5-6.0" vs. 8.0-8.5"). The variable associated with significantly larger Chinook salmon is shown, i.e., male (M) or female (F); small mesh (5) or large mesh (8).

	Yukon River					Kuskokwim River				
Age	Factor	Larger	df	F-value	P-value	Factor	Larger	df	F-value	P-value
1.3	Sex	F	1, 9076	542.88	<0.001	Sex	F	1, 2963	447.73	<0.001
	Mesh Size	8	1, 9076	601.95	<0.001	Mesh Size	8	1, 2963	33.85	<0.001
	Interaction		1, 9076	0.88	0.349	Interaction		1, 2963	3.64	0.056
1.4	Sex	F	1, 25217	29.30	<0.001	Sex	F	1, 4106	70.83	<0.001
	Mesh Size	8	1, 25217	74.89	<0.001	Mesh Size	8	1, 4106	117.14	<0.001
	Interaction		1, 25217	1.86	0.172	Interaction		1, 4106	2.94	0.087
1.5	Sex	M	1, 3405	82.13	<0.001	Sex		1, 565	0.02	0.895
	Mesh Size		1, 3405	1.07	0.302	Mesh Size	8	1, 565	51.82	<0.001
	Interaction		1, 3405	0.50	0.480	Interaction	Mixed	1, 565	4.28	0.039

Table 7. ANOVA test results to determine whether scale growth of Yukon and Kuskokwim Chinook salmon at each life stage was influenced by sex. Tests conducted on both age-1.3 and age-1.4 Chinook salmon. The larger sex is identified. See Fig. 17 and Fig. 18 for associated analyses.

	Age-1.3				Age-1.4			
Stage	Larger Sex	n	F-value	P-value	Larger Sex	n	F-value	P-value
Yukon River								
FW1	F	1526	14.15	<0.001	M	1950	3.89	0.049
FWPL		1526	0.32	0.570	M	1950	11.32	<0.001
SW1	F	1526	5.54	0.019		1950	0.69	0.406
SW2	F	1526	9.92	0.002		1950	3.07	0.080
SW3	F	1526	10.33	0.001	M	1950	4.64	0.031
SW4		NA				1950	3.00	0.084
SWPL	F	1010	3.86	0.050	F	1279	16.33	<0.001
SWPL Max	F	994	11.64	<0.001	F	1270	16.26	<0.001
Kuskokwim River								
FW1		1109	0.01	0.911		1196	0.10	0.747
FWPL		1109	0.23	0.629		1196	2.03	0.154
SW1		1109	0.21	0.649	M	1196	9.50	0.002
SW2	F	1109	18.19	<0.001		1196	0.08	0.775
SW3	F	1109	17.59	<0.001		1196	0.14	0.705
SW4		NA			F	1196	27.26	<0.001
SWPL	F	1083	18.92	<0.001	F	1155	17.05	<0.001
SWPL Max	F	1020	9.96	0.002	F	1166	6.86	0.009

Table 8. Two factor ANOVAs (age, sex) to determine whether scale growth at each life stage varied with adult age of Yukon and Kuskokwim Chinook salmon. Percentage difference is the difference in age-1.3 growth relative to age-1.4 growth. See Table 7, Fig. 17 and Fig. 18 for associated analyses.

	n		%		
Stage	age-1.3	age-1.4	difference	F-value	P-value
Yukon River					
FW1	1526	1950	14.1	118.31	<0.001
FWPL	1526	1950	-12.3	15.389	<0.001
SW1	1526	1950	12.9	302.94	<0.001
SW2	1526	1950	21.8	705.96	<0.001
SW3	1526	1950	13.4	305.92	<0.001
SWPL	1010	1279	25.6	93.78	<0.001
SWPL Max	994	1270	13.7	173.12	<0.001
Kuskokwim River					
FW1	1109	1196	0.7	0.58	0.447
FWPL	1109	1196	-7.7	10.63	0.001
SW1	1109	1196	3.9	15.03	<0.001
SW2	1109	1196	12.6	149.98	<0.001
SW3	1109	1196	7.1	46.58	<0.001
SWPL	1083	1155	17.8	35.14	<0.001
SWPL Max	1020	1166	12.7	73.97	<0.001

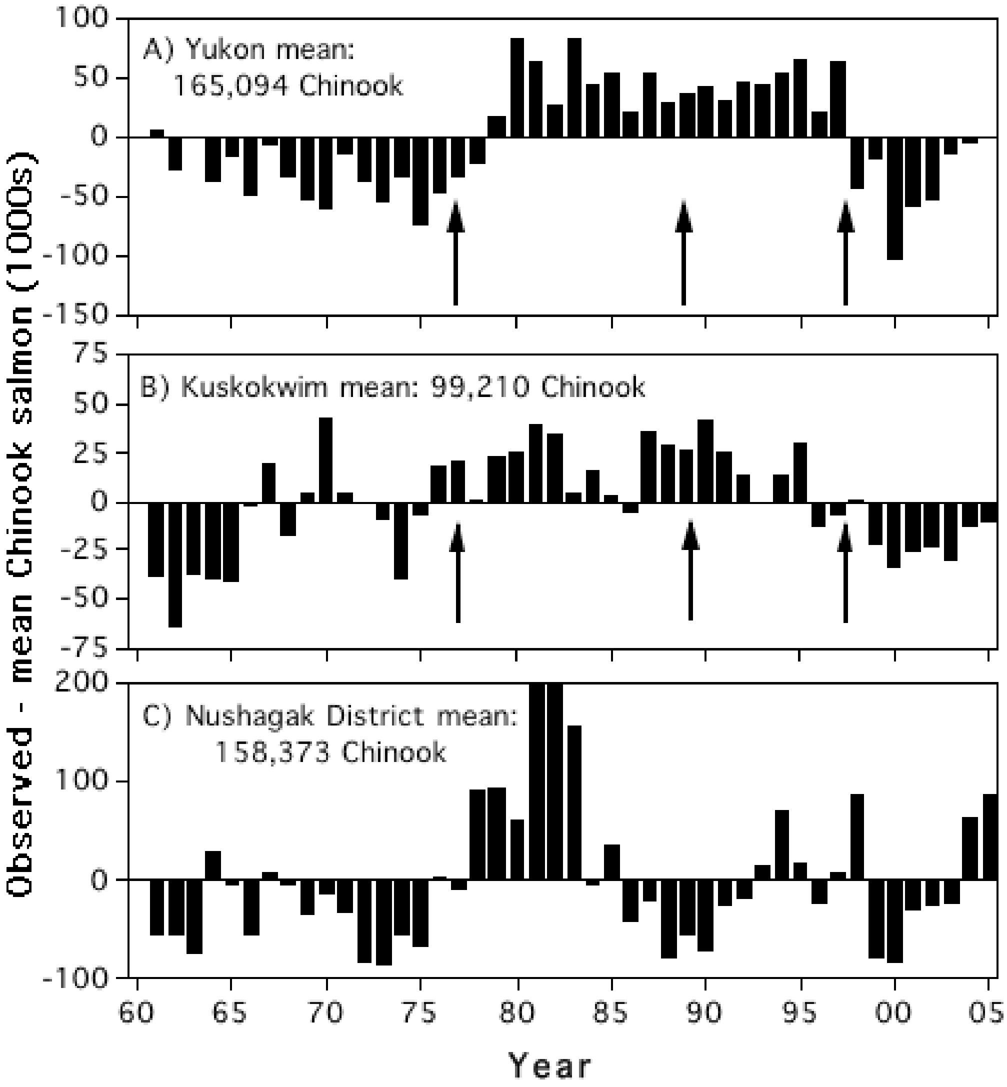

Fig. 1. Catch trends of Yukon and Kuskokwim Chinook salmon and run size trend of Nushagak District Chinook salmon (Bristol Bay), 1961-2005. Yukon values are total catch in Alaska (subsistence, commercial, sport, personal use) and Canadian catch and escapement (escapement prior to 1982 estimated from observed harvest rate during previous five years). Kuskokwim values are total catch (subsistence, commercial, sport, test fish). Subsistence catches prior to 1988 were adjusted by 1.47x based on ratio of 5 years after method change compared with 5 years prior to change. Arrows identify 1976/77 and 1989 climate regime change and 1997/98 El Nino event. Data sources: Bue and Hayes 2006, Whitmore et al. 2005.

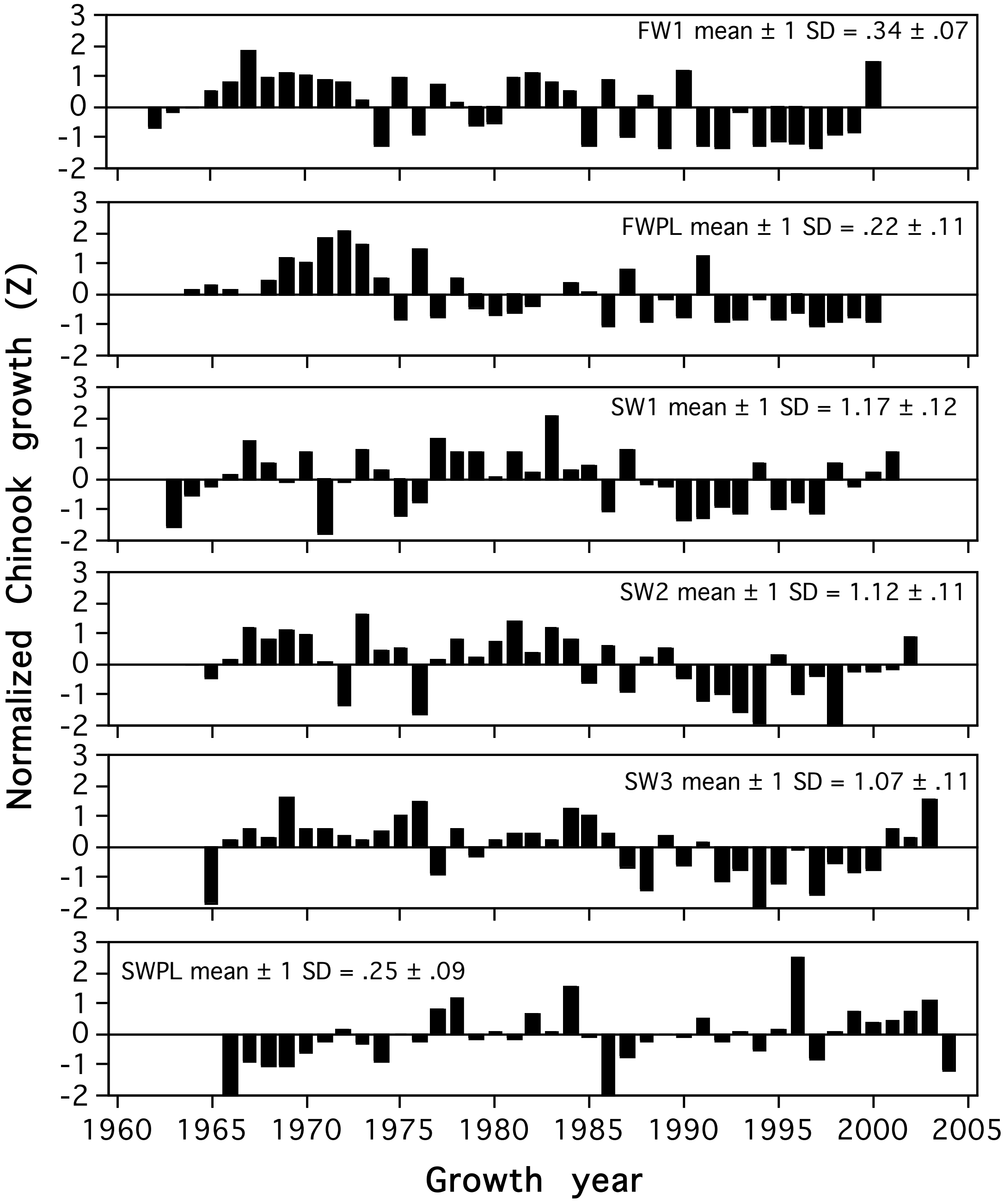

Fig. 2. Mean annual growth of age-1.3 Yukon Chinook salmon during each life stage, growth years 1962-2004. Values are standard deviations above and below the long-term mean. The long-term unweighted mean of male and female scale measurements are shown.

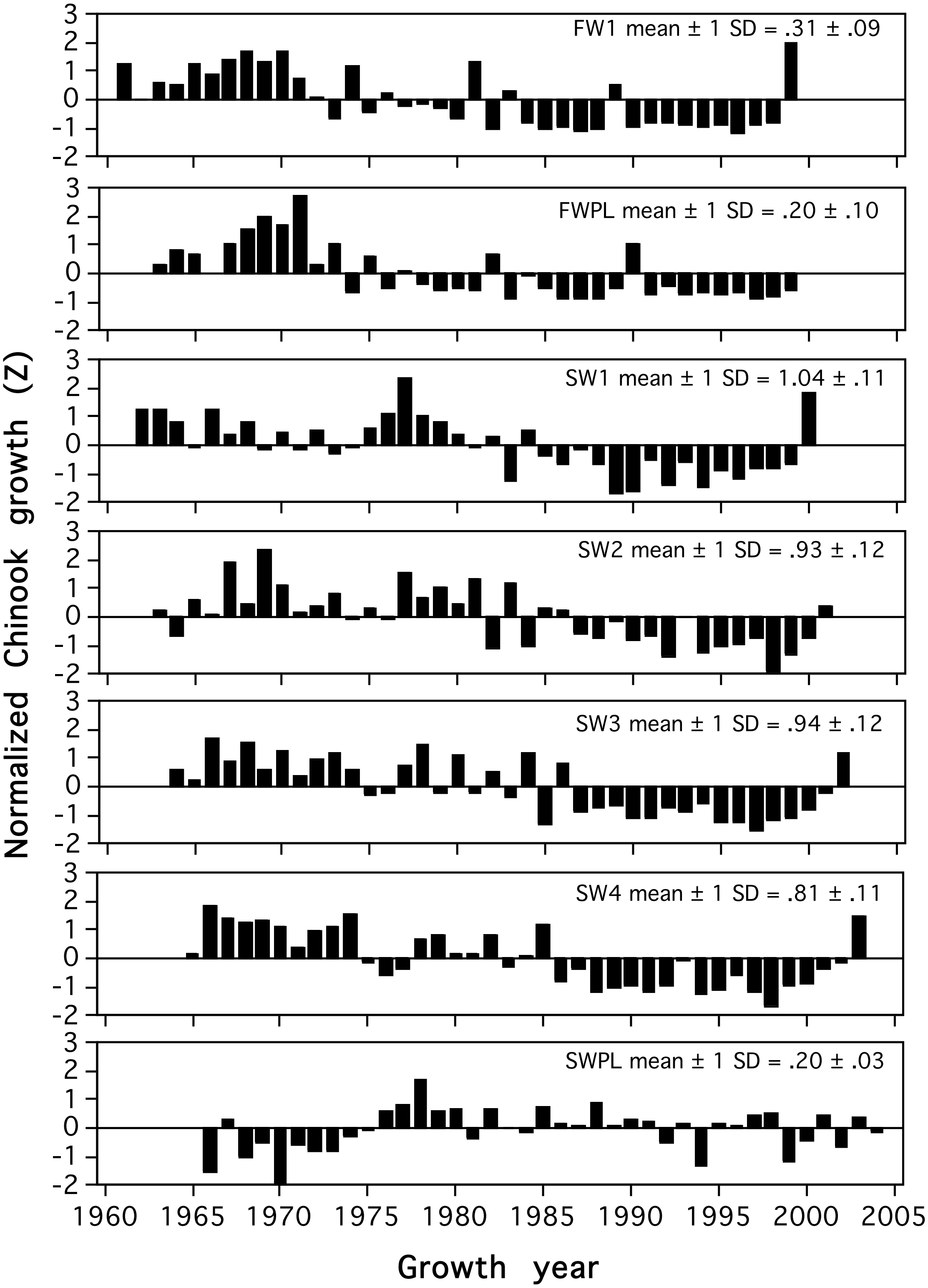

Fig. 3. Mean annual growth of age-1.4 Yukon Chinook salmon during each life stage, growth years 1961-2004. Values are standard deviations above and below the long-term mean.

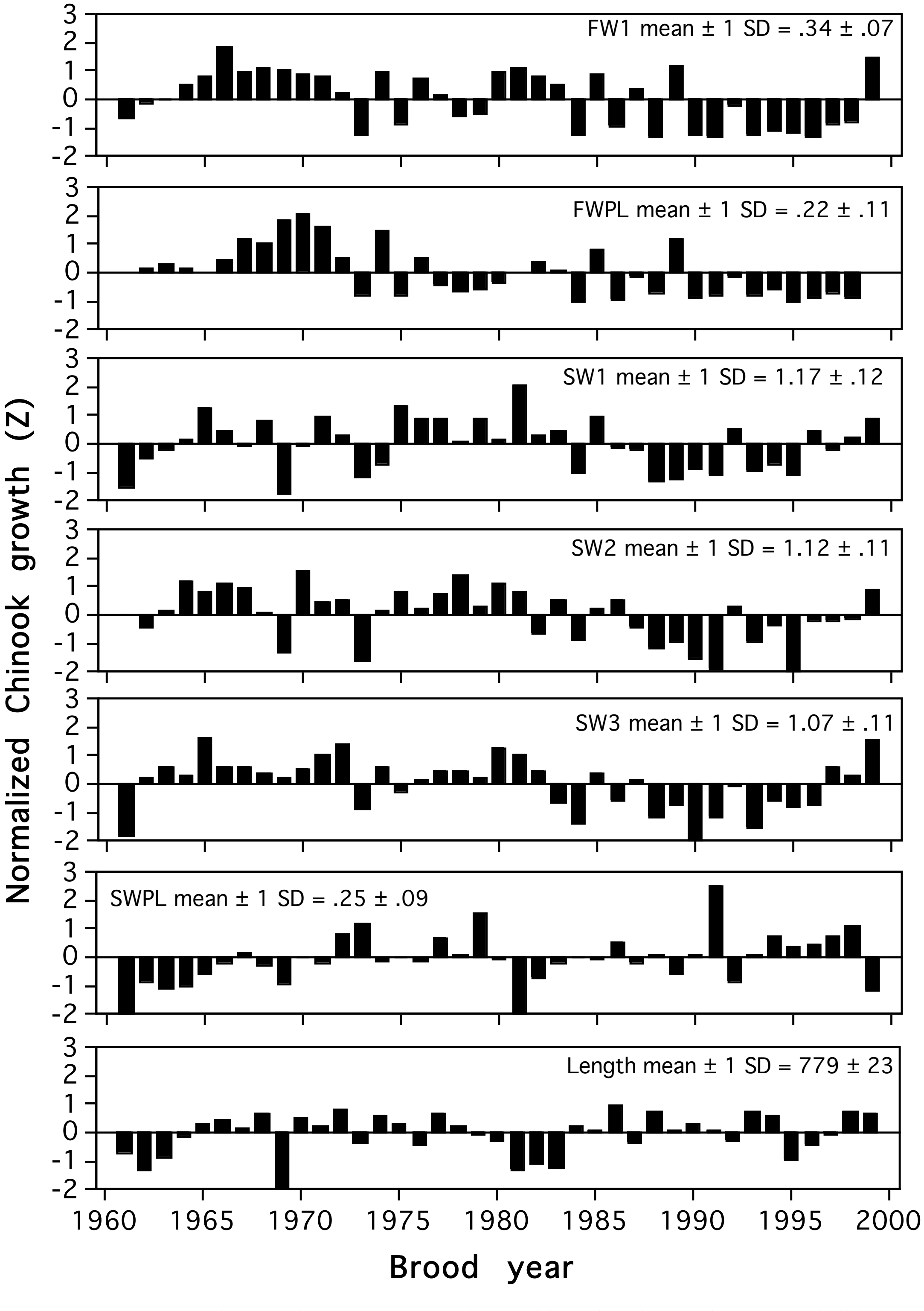

Fig. 4. Mean annual growth of age-1.3 Yukon Chinook salmon during each life stage, brood years 1961-1999. Values are standard deviations above and below the long-term mean.

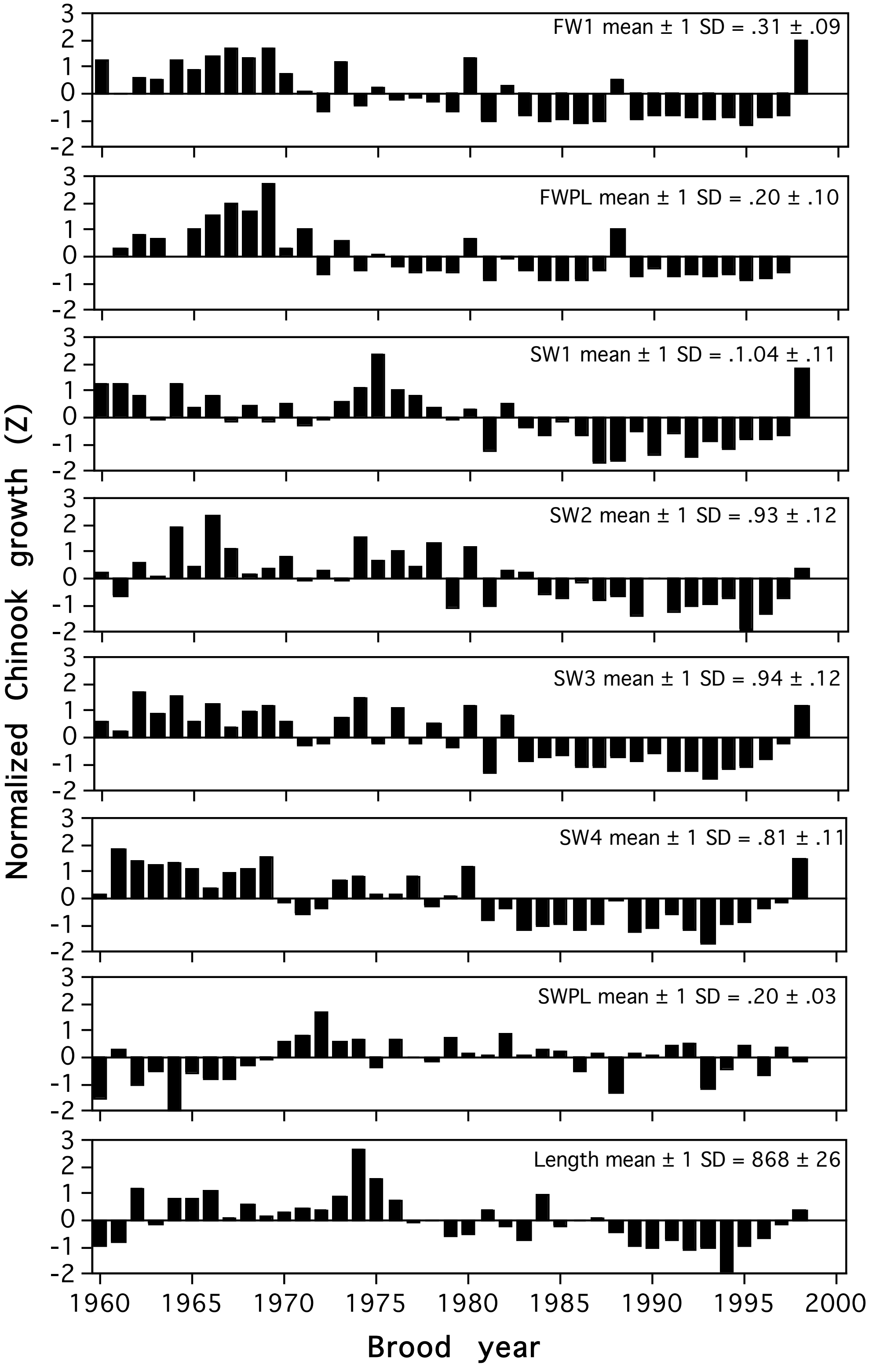

Fig. 5. Mean annual growth of age-1.4 Yukon Chinook salmon during each life stage, brood years 1960-1998. Values are standard deviations above and below the long-term mean.

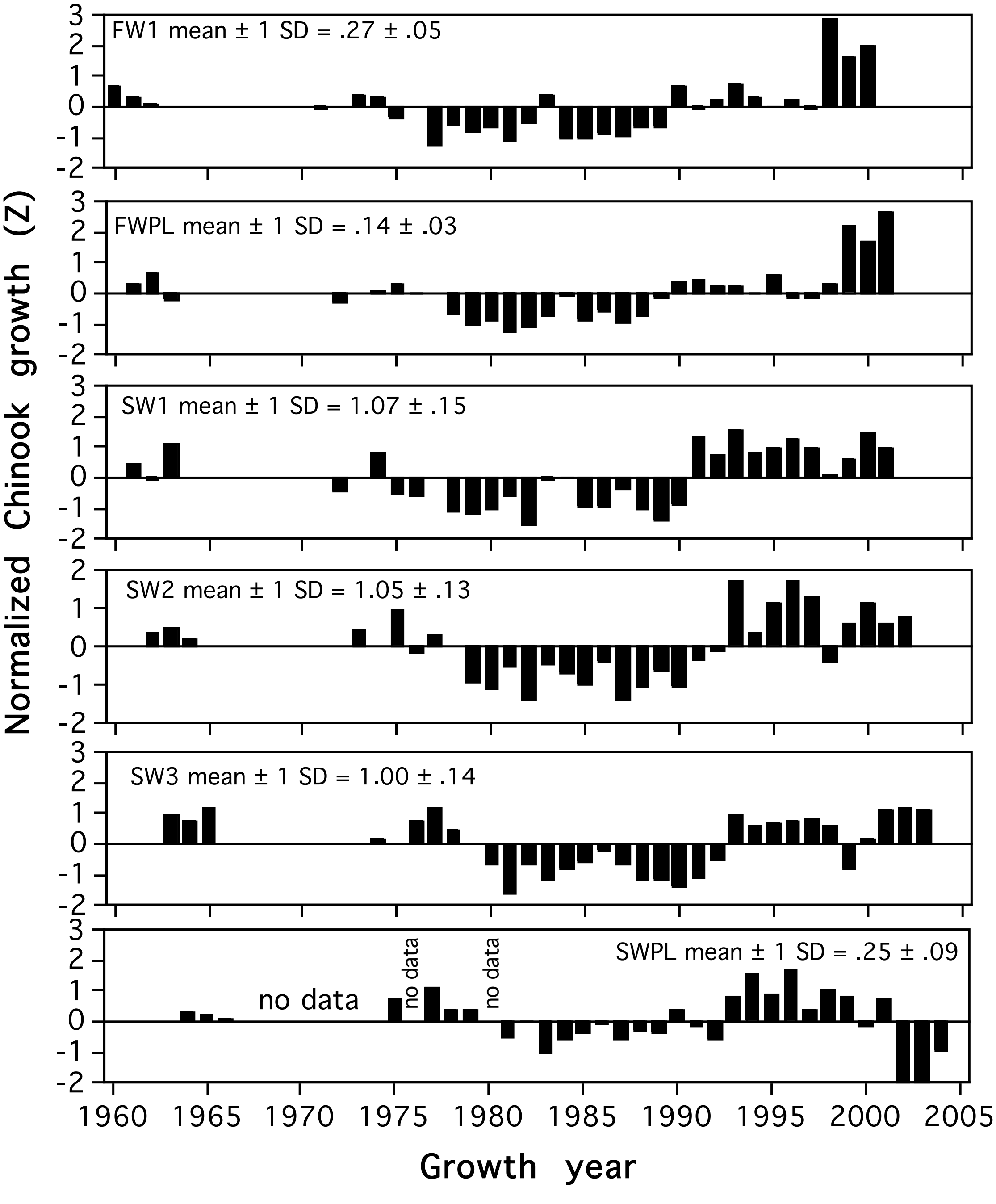

Fig. 6. Mean annual growth of age-1.3 Kuskokwim Chinook salmon during each life stage, growth years 1960-2004. Values are standard deviations above and below the long-term mean.

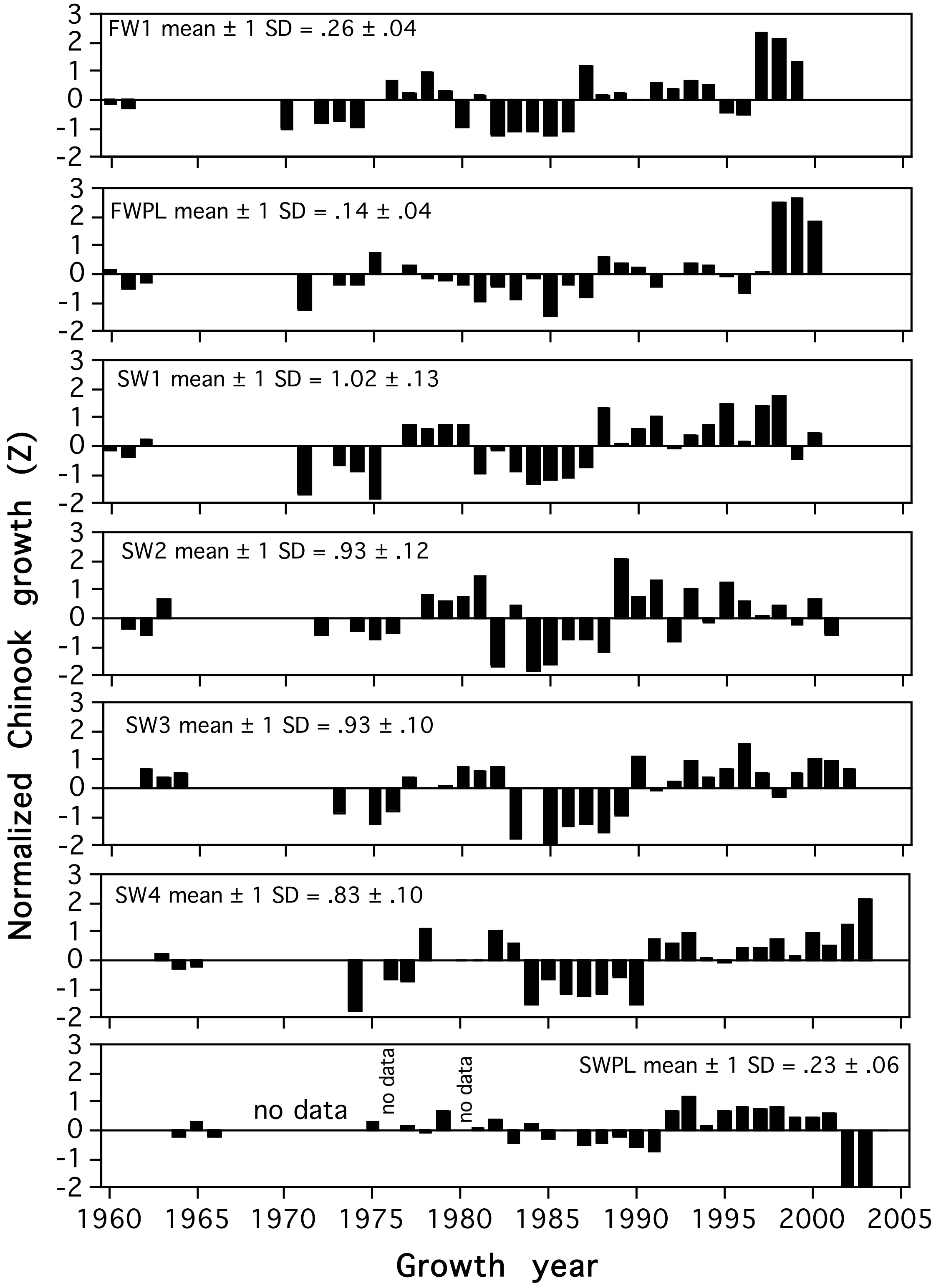

Fig. 7. Mean annual growth of age-1.4 Kuskokwim Chinook salmon during each life stage, growth years 1960-2004. Values are standard deviations above and below the long-term mean.

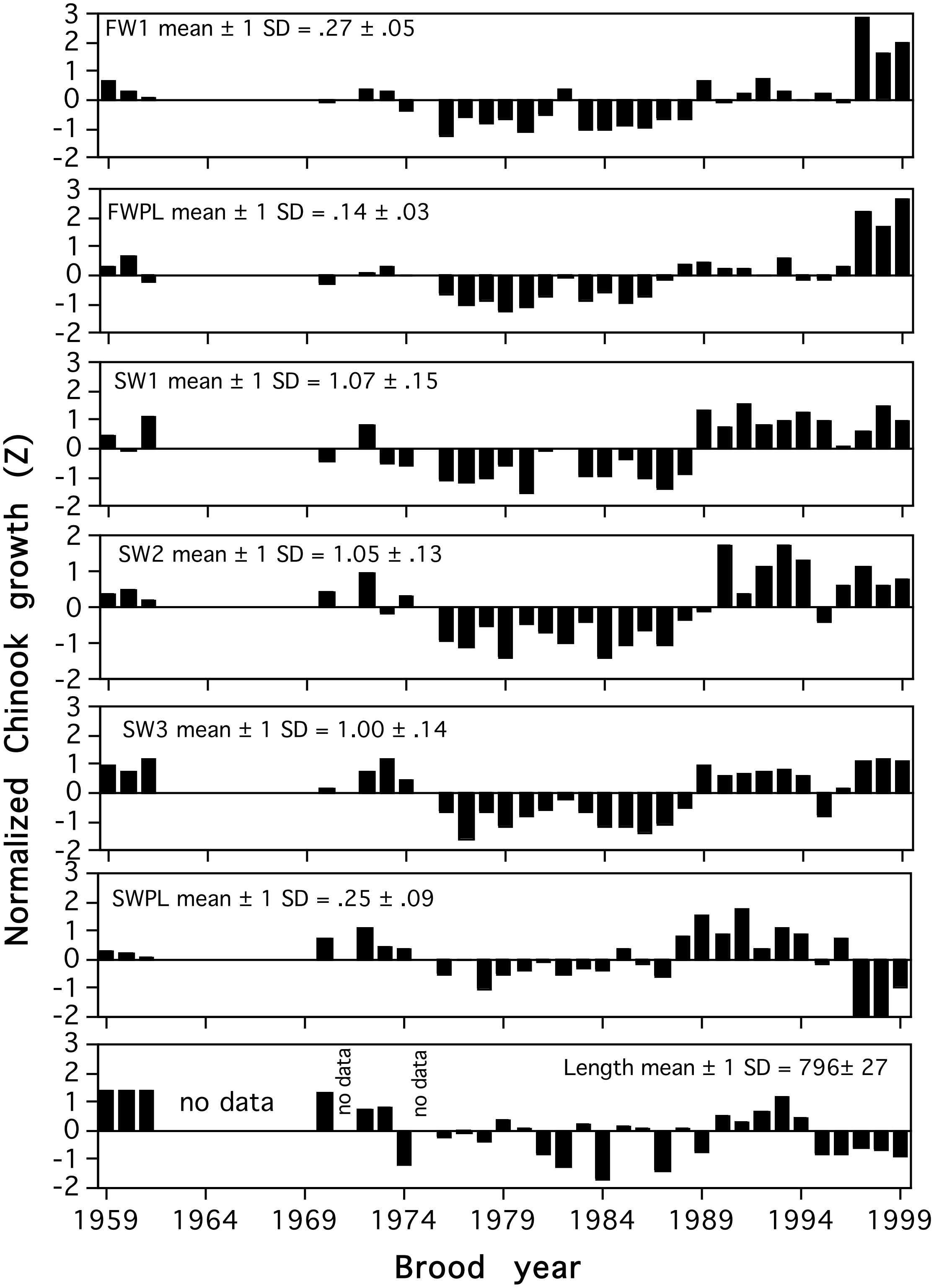

Fig. 8. Mean annual growth of age-1.3 Kuskokwim Chinook salmon during each life stage, brood years 1959-1999. Values are standard deviations above and below the long-term mean.

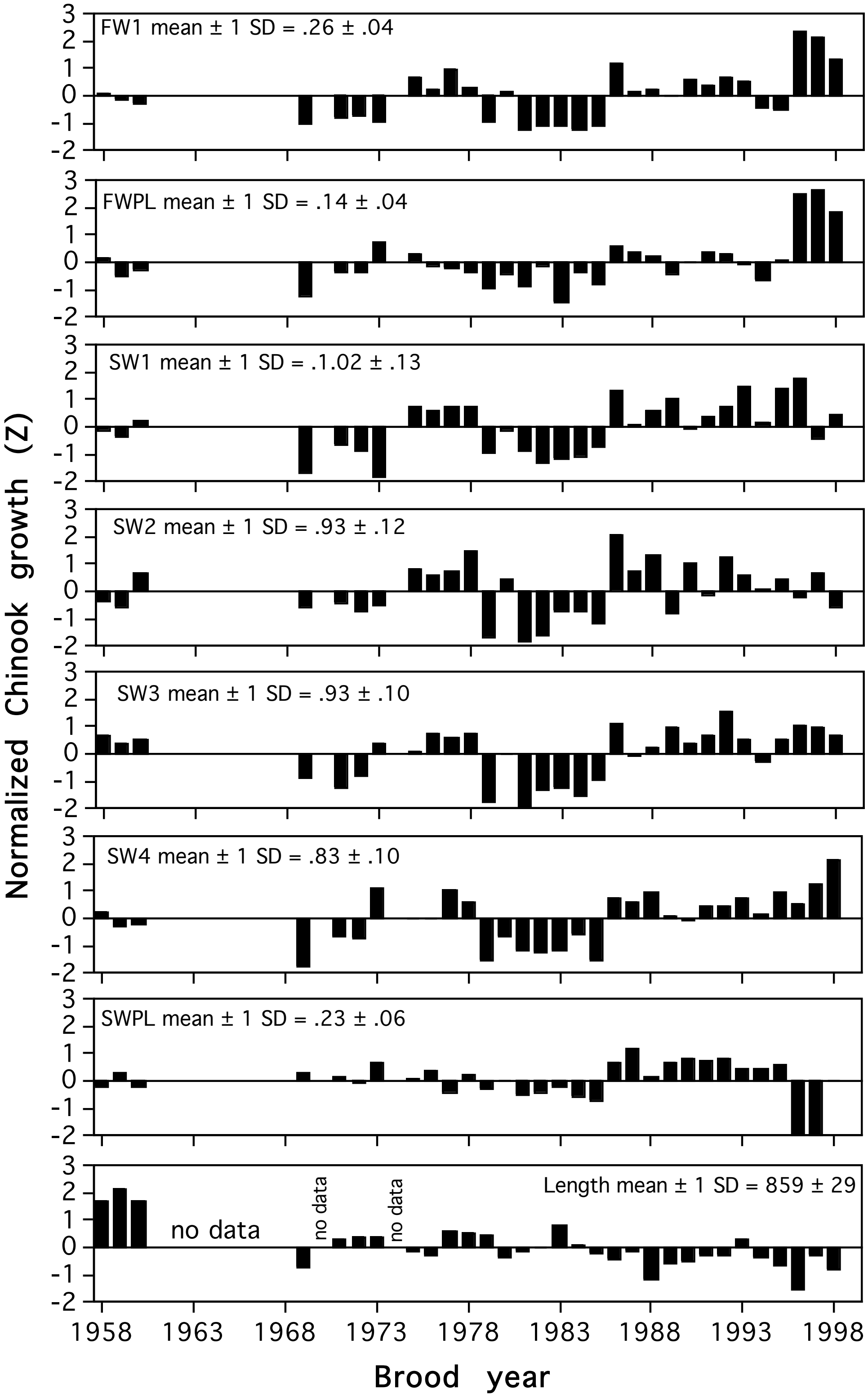

Fig. 9. Mean annual growth of age-1.4 Kuskokwim Chinook salmon during each life stage, brood years 1958-1998. Values are standard deviations above and below the long-term mean.

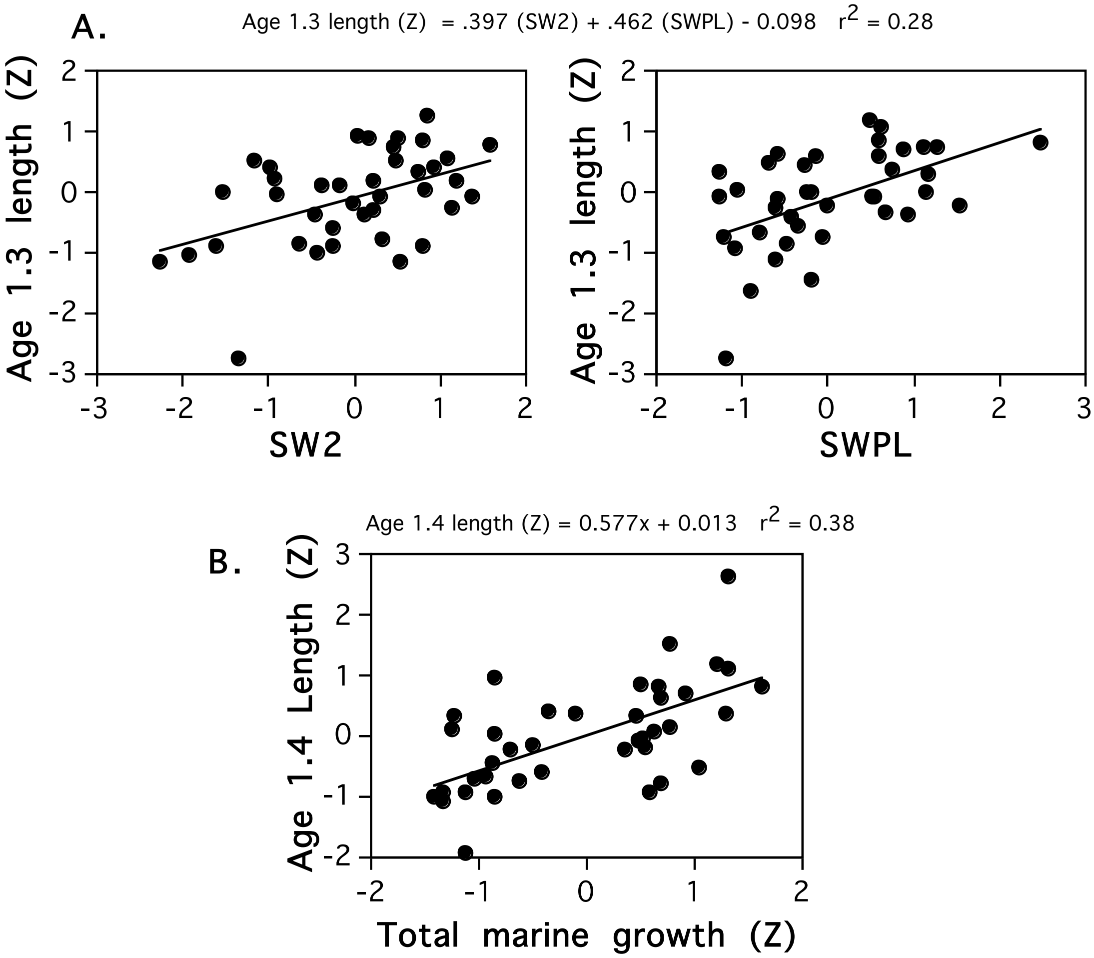

Fig. 10. Relationship between normalized adult length of A) age-1.3 and B) age-1.4 Yukon Chinook salmon and marine scale growth. The age-1.3 length model shows the partial effect of SW2 and SWPL growth on length based on partial residual analysis (Larson and McLeary 1972). Total marine growth (excluding SWPL) was also a significant explanatory variable for age-1.3 length ($P < 0.05$).

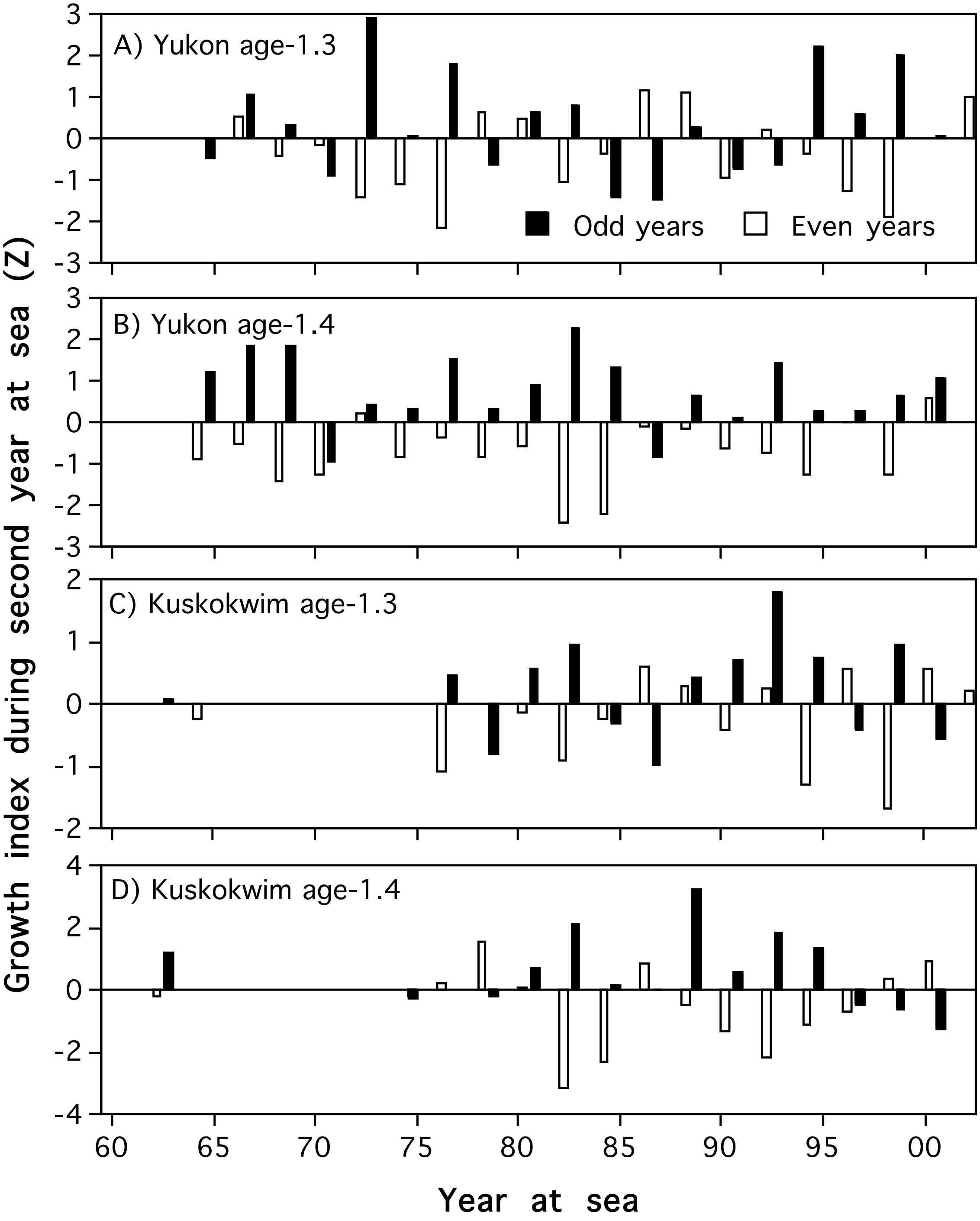

Fig. 11. Index of Yukon and Kuskokwim Chinook salmon growth during the second year at sea (SW2), 1962-2002. Residence during odd-numbered years are black bars, whereas residence during even-numbered years are white bars. Index is the first difference of normalized scale growth. For Kuskokwim fish, difference is based on nearest neighbor (i.e., y-1 or y-3) because data were missing in some years.

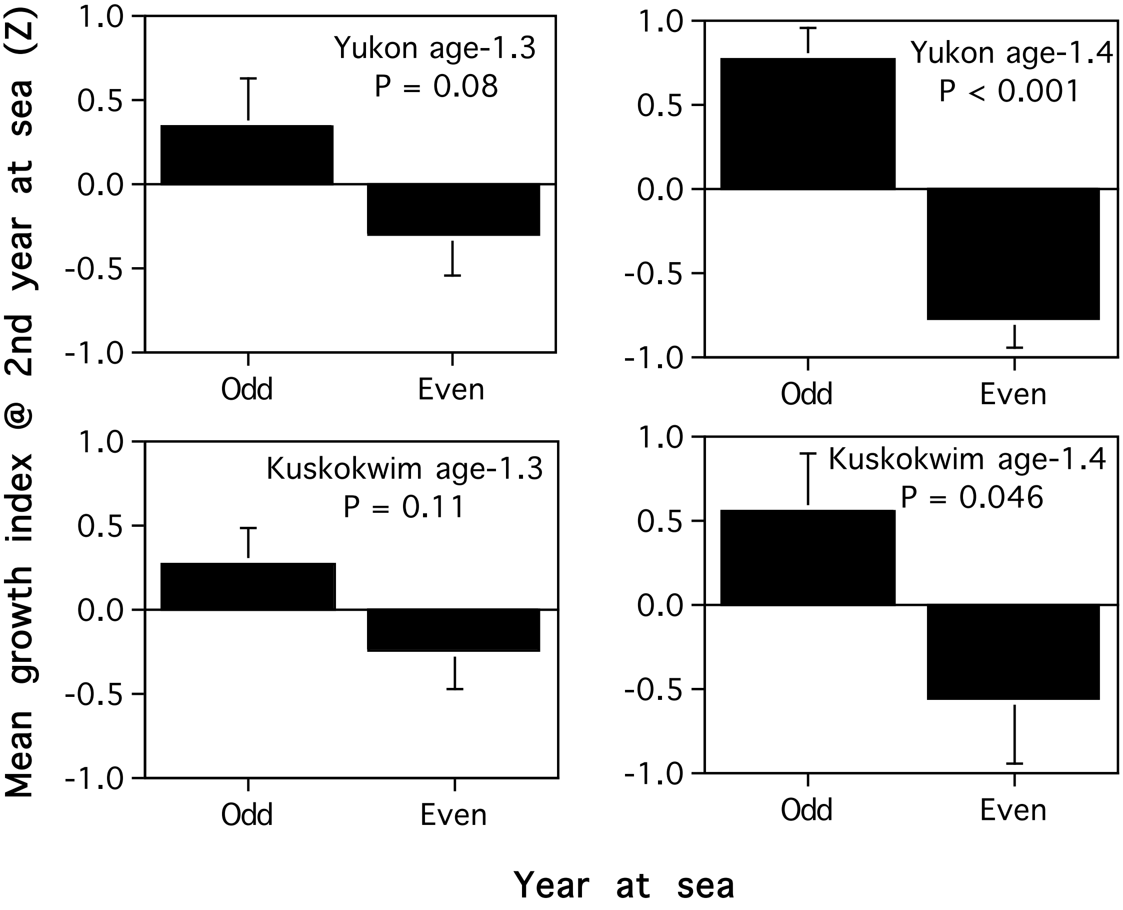

Fig. 12. Mean growth index (± 1 SE) of Yukon and Kuskokwim Chinook salmon during odd- versus even-numbered years of the second year at sea. Index is the first difference of the normalized values. Statistical significance of each ANOVA is shown.

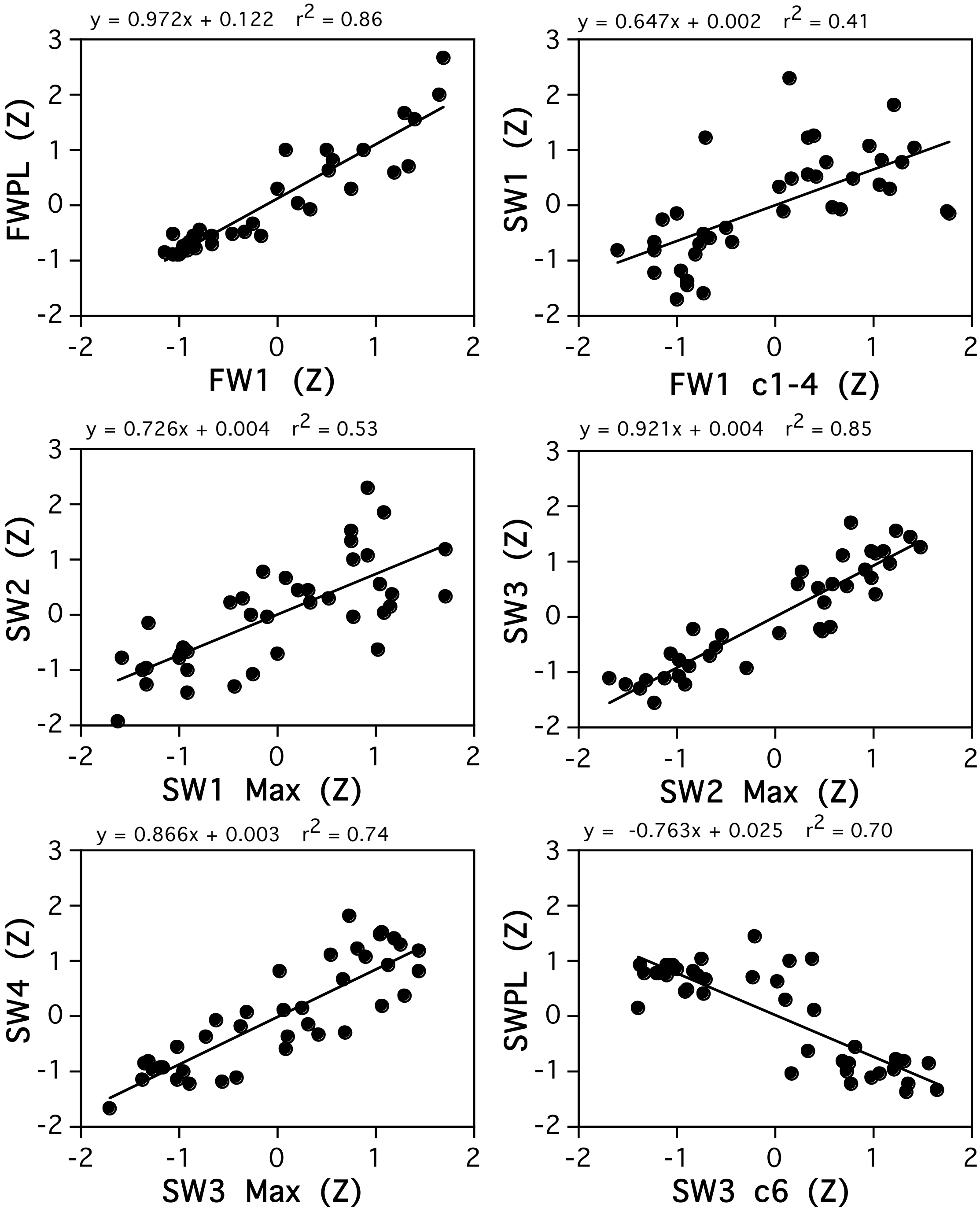

Fig. 13. Relationship between scale growth during each life stage of age-1.4 Yukon Chinook salmon and growth during the previous year. Independent variables include: first four circuli of FW1 excluding focus (FW1 c1-4), width of five maximum circuli during SW1, SW2 and SW3, and width of circuli 1-6 during SW3 (SW3 c6). All values are normalized.

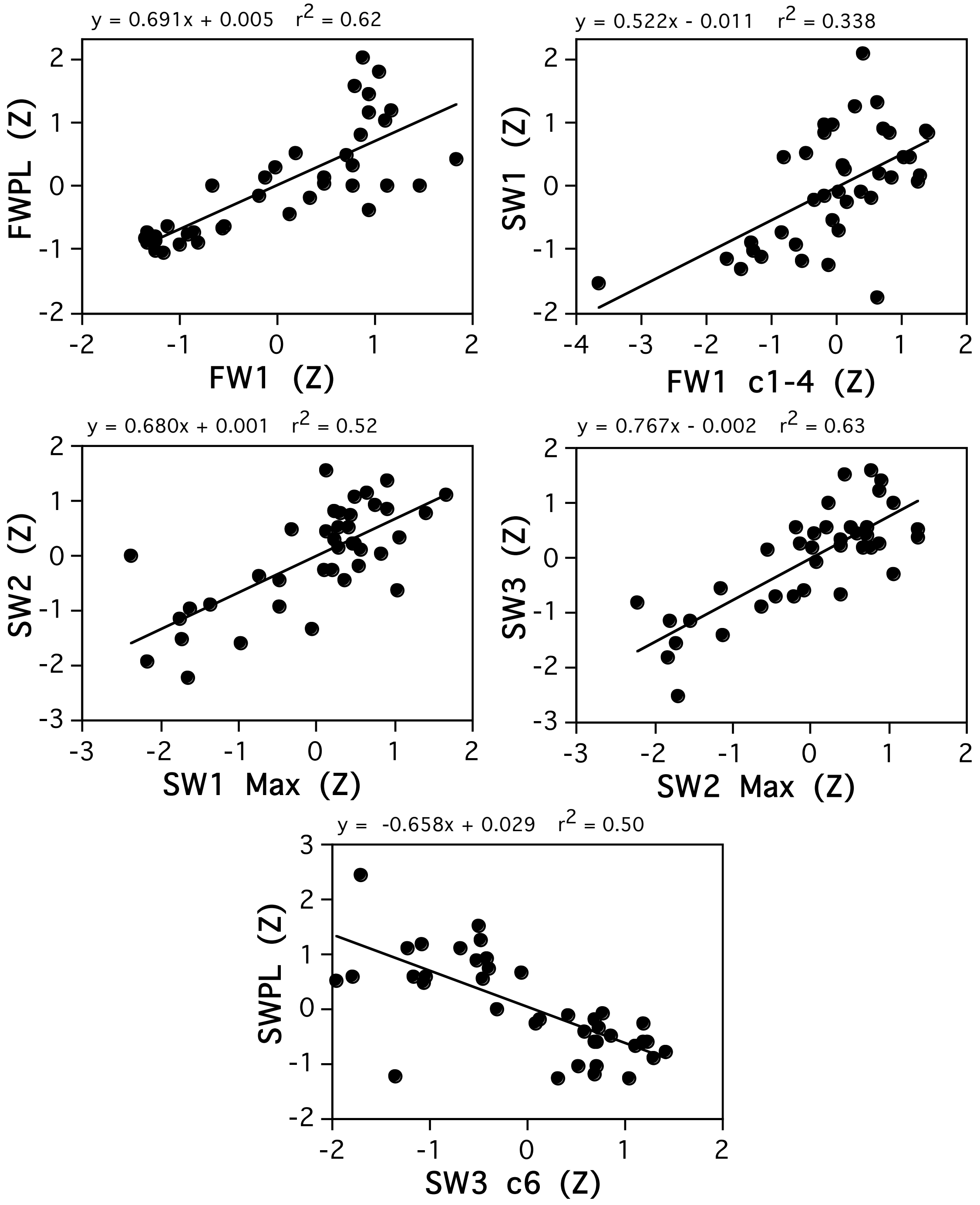

Fig. 14. Relationship between scale growth during each life stage of age-1.3 Yukon Chinook salmon and scale growth during the previous year. Independent variables include: first four circuli of FW1 excluding focus (FW1 c1-4), width of five maximum circuli during SW1, SW2 and SW3, and width of circuli 1-6 during SW3 (SW3 c6). All values are normalized.

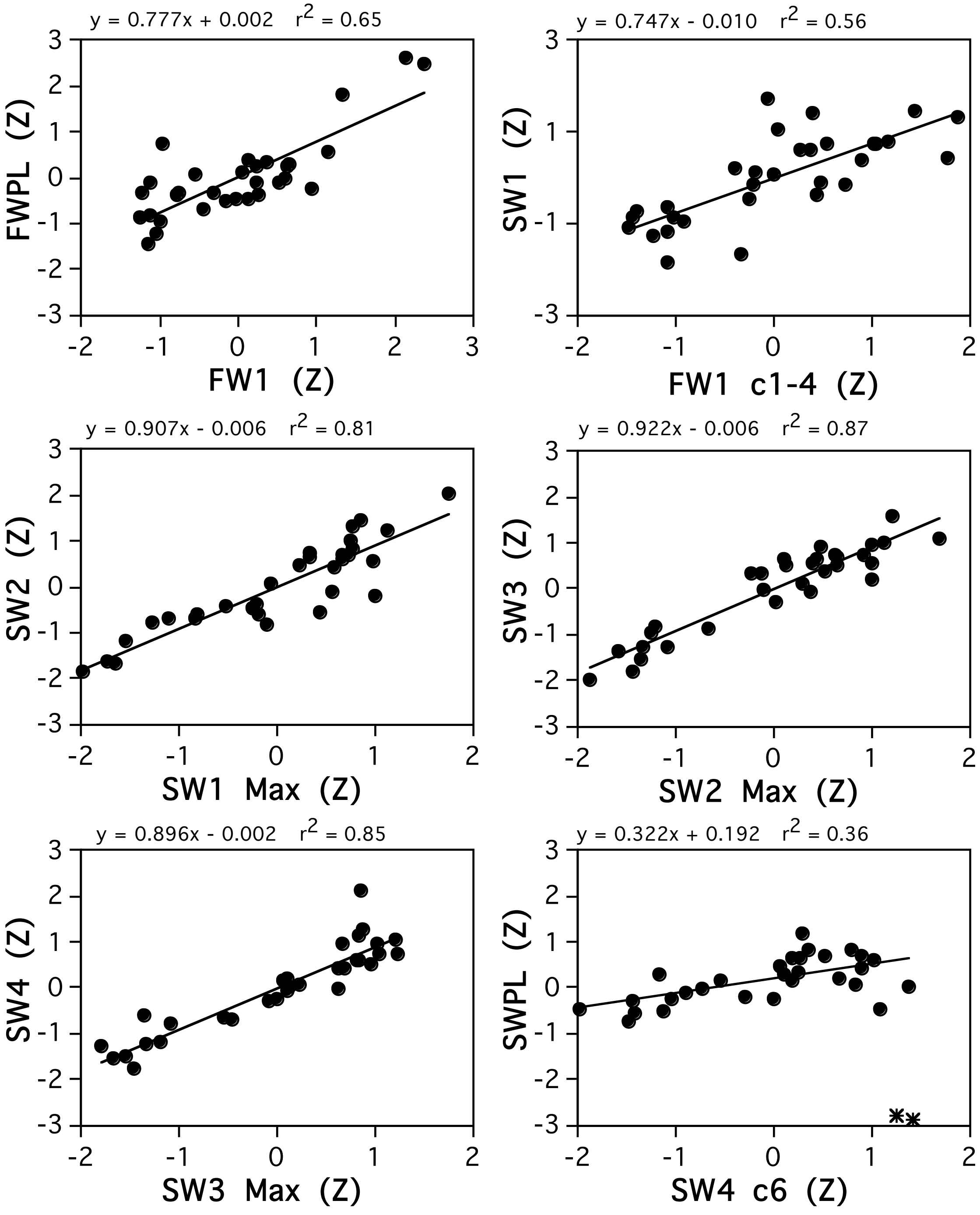

Fig. 15. Relationship between scale growth during each life stage of age-1.4 Kuskokwim Chinook salmon and growth during the previous year. Independent variables include: first four circuli of FW1 excluding focus (FW1 c1-4), width of five maximum circuli during SW1, SW2 and SW3, and width of circuli 1-6 during SW4 (SW4 c6). Two outliers in the SWPL relationship are shown as "*" (return years 2002, 2003). All values are normalized.

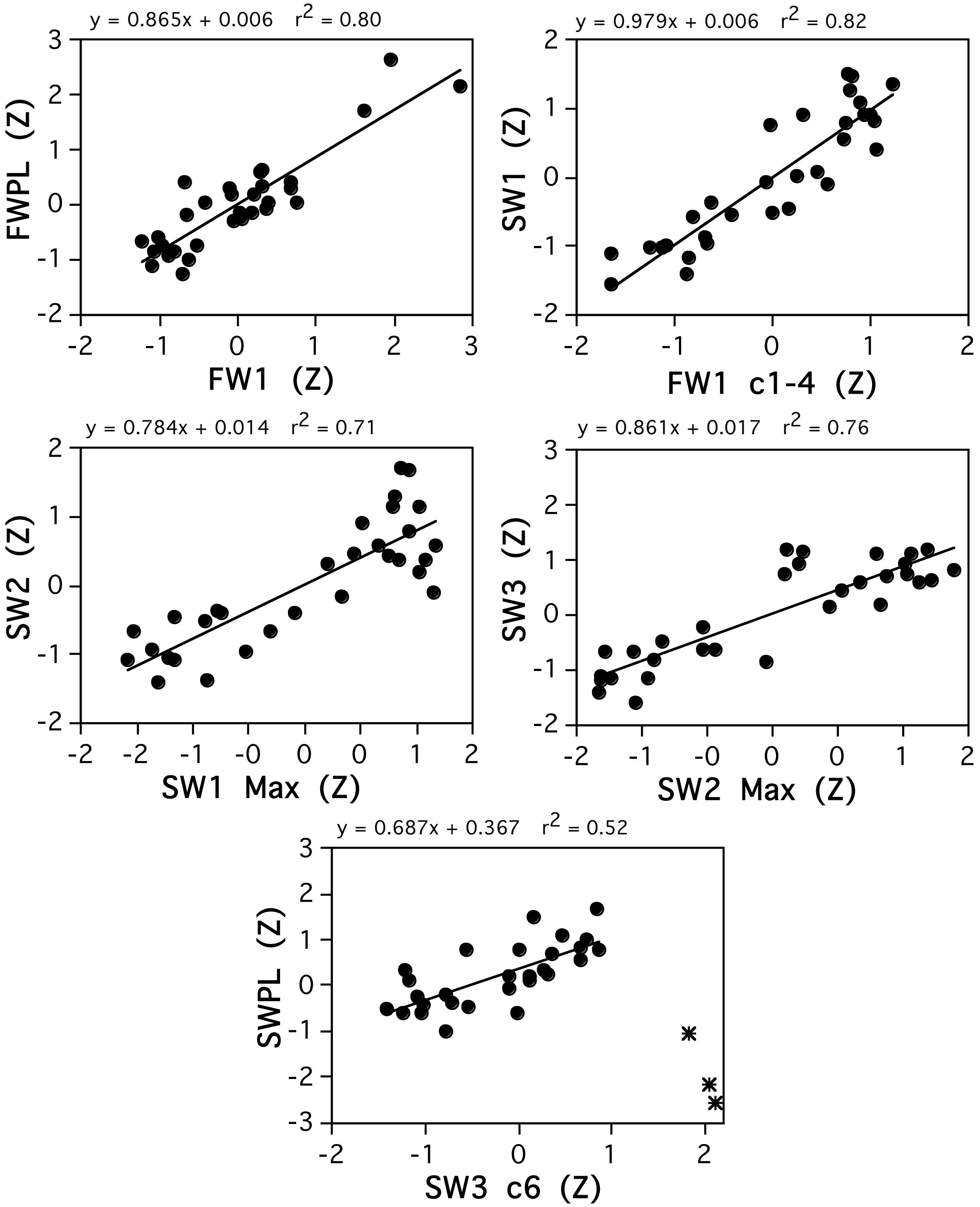

Fig. 16. Relationship between scale growth during each life stage of age-1.3 Kuskokwim Chinook salmon and scale growth during the previous year. Independent variables include: first four circuli of FW1 excluding focus (FW1 c1-4), width of five maximum circuli during SW1, SW2 and SW3, and width of circuli 1-6 during SW3 (SW3 c6). Three outliers in the SWPL relationship are shown as "*" (return yrs 2002, 2003, 2004). All values are normalized.

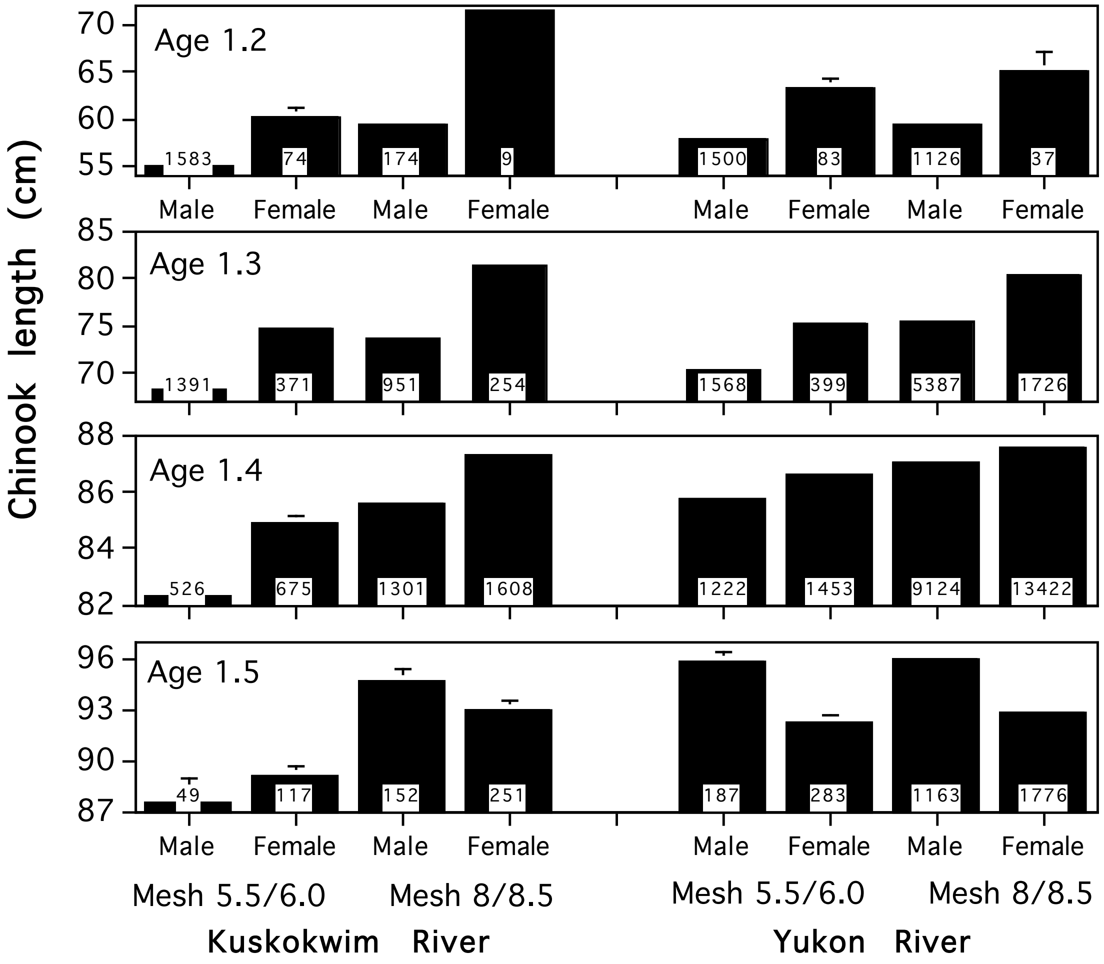

Fig. 17. Mean adult lengths of age-1.3, age-1.4, and age-1.5 male and female Kuskokwim and Yukon Chinook salmon, 1964-2004. Values are mean ± 1 SE. Sample sizes are shown.

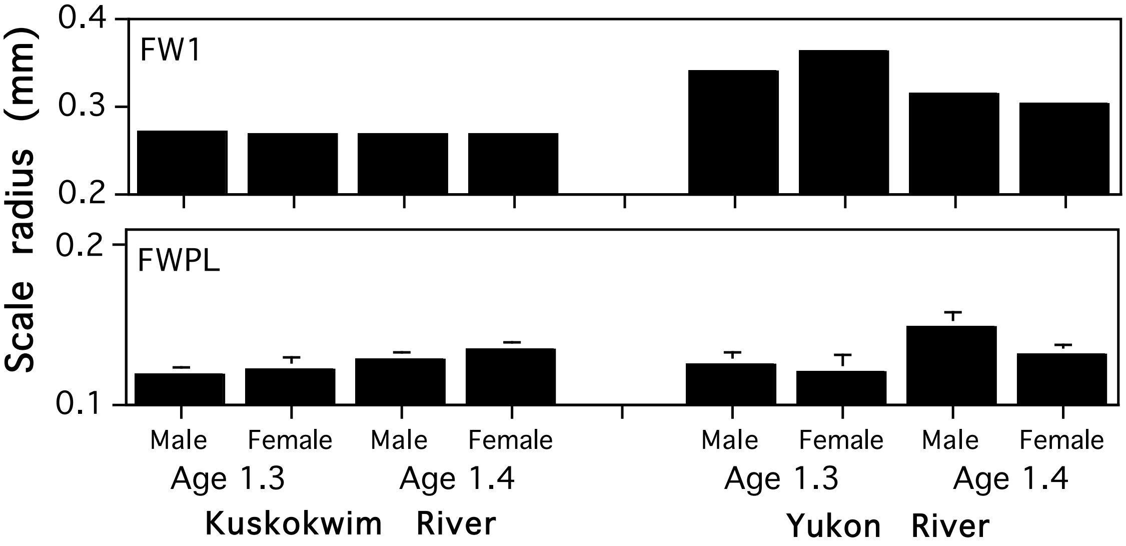

Fig. 18. Scale radius measurements of age-1.3 and age-1.4 male and female Kuskokwim and Yukon Chinook salmon during freshwater residence, 1964-2004. Values are mean ± 95% CI. Sample size of each mean exceeds 320 fish.

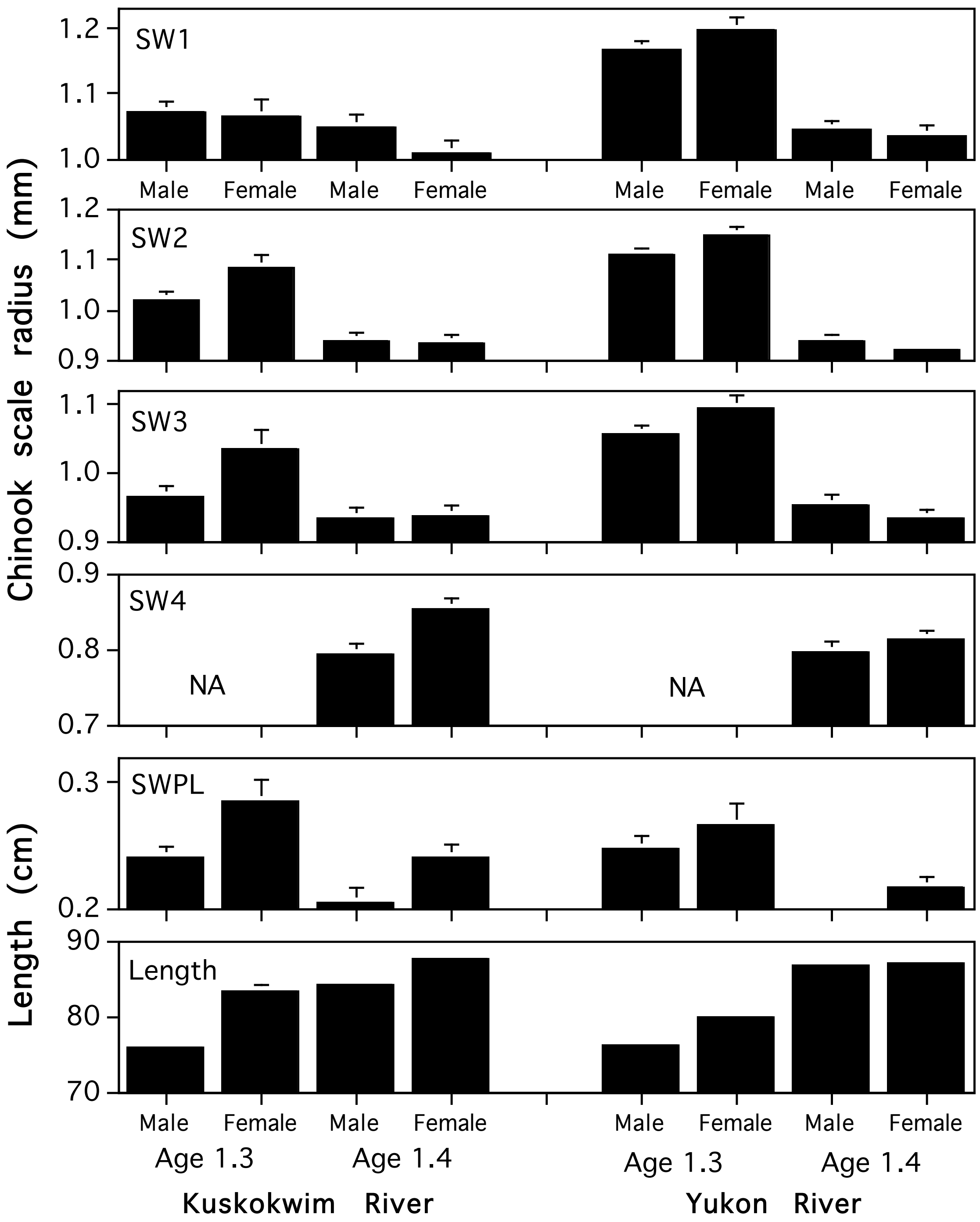

Fig. 19. Scale radius measurements of age-1.3 and age-1.4 male and female Kuskokwim and Yukon Chinook salmon during each year at sea and adult length, 1964-2004. Values are mean ± 95% CI. Sample size of each mean exceeds 320 fish.