North Pacific Anadromous Fish Commission
Bulletin No. 5: 279-285, 2009

Climate, Growth and Population Dynamics of Yukon River Chinook Salmon

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Ruggerone, G.T., J.L. Nielsen, and B.A. Agler 2009. Climate, growth and population dynamics of Yukon River Chinook salmon. N. Pac. Anadr. Fish Comm. Bull. 5: 279–285.

Abstract: Harvests of Yukon Chinook salmon increased in the mid-1970s, then declined during 1998 to 2007 in response to fewer returning salmon. We examined annual growth of age-1.3 and age-1.4 Yukon Chinook salmon scales, 1965–2004, and tested the hypothesis that shifts in Chinook salmon abundance were related to annual growth at sea. Annual scale growth trends were not significantly correlated with salmon abundance indices, sea surface temperature, or climate indices, although growth during the first year at sea appeared to have been affected by the 1977 and 1989 ocean regime shifts. Chinook salmon scale growth was dependent on growth during the previous year, a factor that may have confounded detection of relationships among growth, environmental conditions, and abundance. Scale growth during the second year at sea was greater in odd-numbered years compared with even-numbered years, leading to greater adult length of age-1.3 salmon in odd-numbered years. The alternating-year pattern in Chinook salmon growth was opposite that observed in Bristol Bay sockeye salmon, and it may be related to the higher trophic level of Chinook salmon and indirect competition with pink salmon. This finding highlights the need to investigate alternating-year patterns in salmon growth, prey abundance, and factors that influence these patterns, such as pink salmon.

Keywords: Yukon River, Chinook salmon, growth, abundance, climate, scales

INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) returning to western Alaska represent a major proportion of wild Chinook salmon in North America and Asia. Average harvest (commercial and subsistence) of Chinook salmon in western Alaska, which includes Bristol Bay and the Arctic-Yukon-Kuskokwim (AYK) region, averaged approximately 0.9 ± 0.2 million (SD) salmon per year during 1981–2004 (e.g., Eggers et al. 2005; JTC 2008; Whitmore et al. 2008). However, harvests of Chinook salmon have undergone substantial shifts during the past 40 years. For example, harvests of Yukon and Kuskokwim Chinook salmon (two major stocks) tended to be low during the 1960s through the mid 1970s, high from the late 1970s through the mid 1990s, and low from the late 1990s through the mid 2000s (Fig. 1). These harvest patterns appear to be related to the 1977 ocean regime shift (Hare and Mantua 2000) and the 1997 El Niño (Kruse 1998) that influenced many marine species in the Bering Sea and North Pacific Ocean. Harvests of chum (*O. keta*) and coho salmon (*O. kisutch*) also declined in the late 1990s (AYK SSI (Arctic – Yukon – Kuskokwim Sustainable Salmon Initiative) 2006). The recent decline in harvests triggered multiple "disaster" declarations for this region by state and federal governments because salmon are highly important for subsistence fisheries and the economy of this region (www.aykssi.org/Home.htm).

Growth of salmon is believed to be an important factor influencing survival (Beamish et al. 2004; Farley et al. 2007). Furthermore, annual scale growth measurements of Bristol Bay and Chignik sockeye salmon (*O. nerka*) since the 1950s provided evidence that greater early marine growth was a key mechanism that influenced the doubling of Alaska sockeye salmon abundance after the 1977 ocean regime shift (Ruggerone et al. 2005, 2007a). Survival of Chinook salmon has also been linked to the alternating-year pattern of pink salmon (*O. gorbuscha*) abundance (Grachev 1967; Ruggerone and Goetz 2004; Ruggerone and Nielsen 2004).

In this investigation, we examined trends in annual scale growth of Yukon River Chinook salmon from 1965 to 2004. Salmon scales are known to be correlated with salmon body size (Clutter and Whitesel 1956; Henderson and Cass 1991; Fukuwaka and Kaeriyama 1997; Ruggerone et al. 2009). We tested the following hypotheses:

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1) Harvests of Yukon Chinook salmon were associated with annual growth in fresh water and/or in the ocean;
2) Growth of Chinook salmon was associated with major ocean-climate events, i.e., the 1977 and 1989 ocean regime shifts and the 1997 El Niño event;
3) Growth of Chinook salmon at sea exhibited an alternating-year pattern that may be associated with Asian pink salmon abundance; and
4) Annual growth of Chinook salmon was dependent on the previous year's growth.

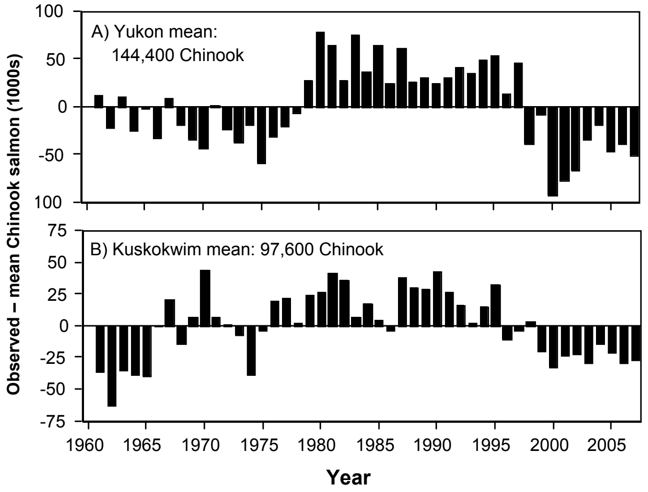

Fig. 1. Catch trends of Yukon and Kuskokwim Chinook salmon, 1961–2007. Values are total catch (subsistence, commercial, sport, personal use). Data sources: Ruggerone et al. 2007b; JTC 2008; Whitmore et al. 2008.

MATERIALS AND METHODS

Scale Collection and Measurements

Scales from adult Chinook salmon from the Yukon River were obtained from the Alaska Department of Fish and Game (ADFG) archive in Anchorage, Alaska. Yukon River scales have been collected annually since 1965 for quantifying age composition. As a means to minimize year-to-year variability in scale growth caused by size-selective gillnets, we selected scales for measurement only when they were from Chinook salmon captured with large mesh (8.5 inch stretched measure) set gillnets (commercial or test fisheries) located in the lower river (river km 20–30). Only scales collected in June and July were measured to ensure fish were from the same stocks.

We measured approximately 50 scales from each of the two dominant Chinook age groups (1.3 and 1.4) or ~100 scales per year. These fish spent one winter in fresh water and three (age-1.3) or four (age-1.4) winters in the ocean. Scales were selected for measurement only when: 1) we agreed with the age determination previously made by ADFG, 2) the scale shape indicated that 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. The high resolution image (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. We used Optimas 6.5 image processing software to collect measurement data using a customized program. The scale image was displayed on an LCD monitor, 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 database.

Standardized Scale Growth

Unequal numbers of male and female Chinook salmon scales were available for measurement in most years for age-1.3 salmon and in one year for age-1.4 salmon. 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 had different growth rates (Ruggerone et al. 2007b). Therefore, scale 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 represent the normalized mean growth of male and female salmon, respectively. Normalized growth is the number of standard deviations above or below the long-term mean.

Environmental Data and Analyses

Seasonal sea surface temperatures (SST) and climate indices that might influence growth of Chinook salmon were obtained from the Bering Climate web page (www.bering-climate.noaa.gov). Climate indices examined included the Pacific Decadal Oscillation index (PDO), Aleutian Low, Arctic Oscillation index, and the North Pacific index. Correlation analyses were conducted to determine whether annual growth of Chinook salmon scales was associated with climate indices and/or seasonal SST. Serial autocorrelation among residuals was examined, and correlation tests were re-examined using differenced values when autocorrelation was significant.

Chinook and Pink Salmon Relationships

Pink salmon in the Bering Sea were highly abundant in odd-numbered years compared with even-numbered years (Davis et al. 2005). In order to remove the effects of time trends and to highlight differences in Chinook salmon scale growth between even- and odd-numbered years, we calculated the first difference of each scale growth variable and adult length-at-age:

Differenced growth (DG_i) = $G_i - G_{i-1}$,

where G is normalized scale growth or adult length in year i.

RESULTS

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 the early 1970s, intermediate from the mid 1970s through the early 1980s, then typically below average after 1984 until rebounding in 1999 or 2000 (Figs. 2, 3). Mean annual growth was typically within two standard deviations of the long-term mean. During the first year at sea (SW1), scale growth was variable but tended to be intermediate prior to the mid 1970s, high during and immediately after the 1977 regime shift, and below average after the 1989 regime shift. Growth during the second, third, and fourth year at sea was typically above average prior to the mid-1980s, below average from the mid-1980s through 1990s, then higher beginning in 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 age-1.3 Chinook salmon did not show a long-term pattern; whereas, the length of age-1.4 Chinook salmon was relatively high during the 1960s through 1982, intermediate through 1993, and typically below average from 1994 through 2002 (Fig. 4).

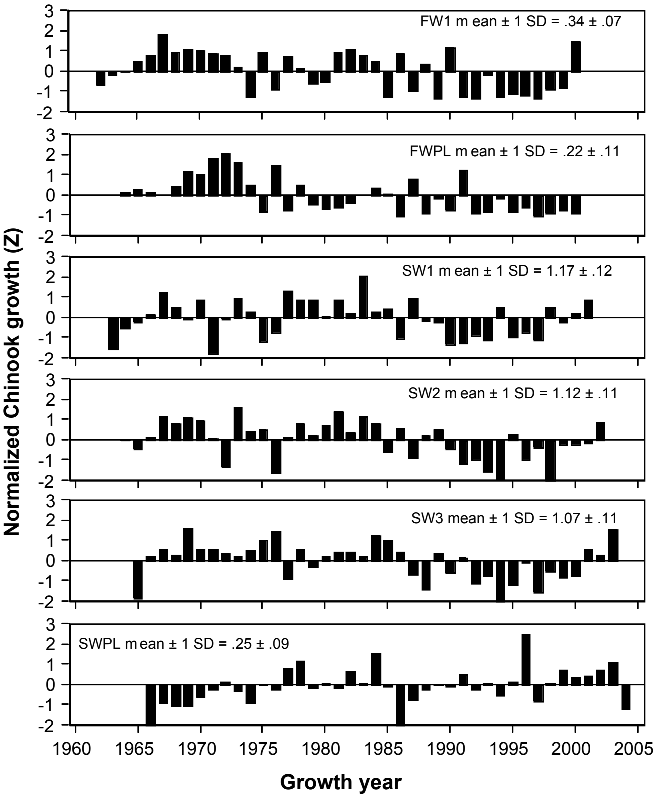

Fig. 2. Mean annual growth of age-1.3 Yukon Chinook salmon during each life stage, growth years 1962–2004. Values are standard deviations above and below the long-term mean. The long-term unweighted mean of male and female scale measurements is shown.

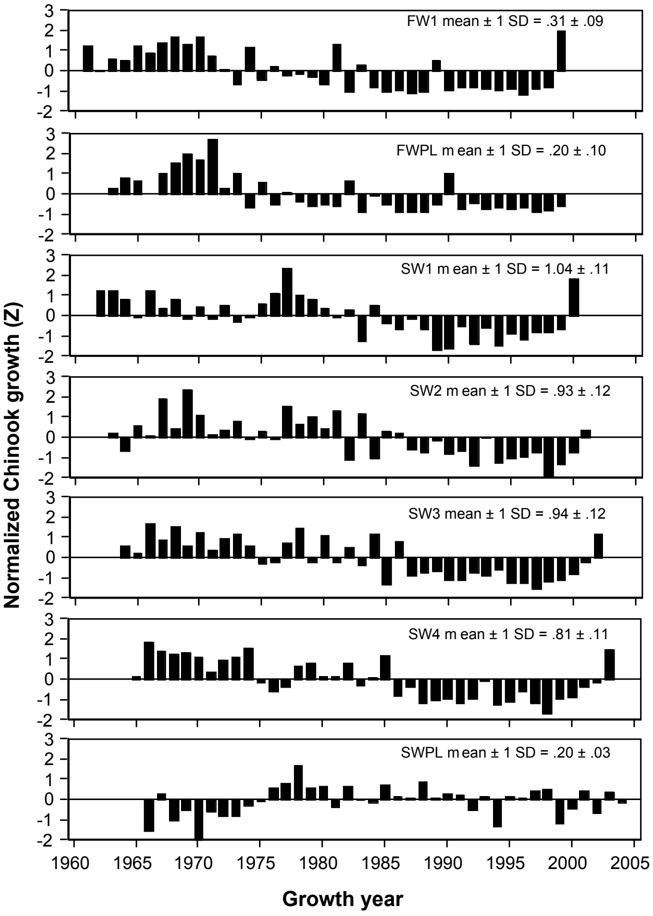

Fig. 3. Mean annual growth of age-1.4 Yukon Chinook salmon during each life stage, growth years 1961–2004. Values are standard deviations above and below the long-term mean. The long-term unweighted mean of male and female scale measurements is shown.

Climate Shift, Chinook Salmon Abundance and Growth

Harvests of Yukon Chinook salmon since 1965 were not correlated with annual marine growth of Chinook salmon scales except for a weak positive correlation with scale growth during the homeward migration ($r = 0.38$; n = 32, $P < 0.05$). Harvests were negatively correlated with spring plus growth during the smolt migration ($r = -0.41$; n = 32, $P < 0.05$).

Scale growth patterns were compared with the 1977, 1989, and 1997/98 climate events. Distinct shifts in scale growth during each life stage were not visibly associated with these climate events. The most noticeable pattern occurred during the first year at sea (SW1) in which scale growth tended to be intermediate (age-1.4 salmon) or variable (age-1.3 salmon) prior to the mid-1970s, high immediately after the 1977 regime shift, and below average after the 1989 regime shift (Figs. 2, 3). Scale growth during subsequent life stages tended to follow this pattern, although the pattern was less defined.

Annual scale growth was compared with SST and climate variables, but statistically significant and meaningful relationships were not detected ($P > 0.05$). Scale growth was sometimes weakly correlated with SST and climate variables, but this correlation was largely caused by autocorrelation even when utilizing the first difference of variables.

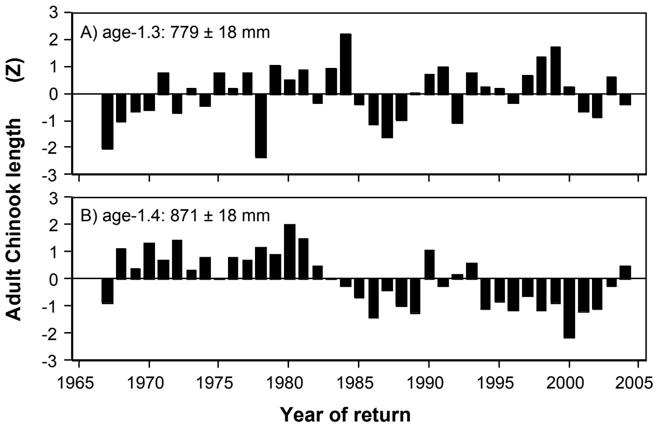

Fig. 4. Normalized length of age-1.3 and age-1.4 adult Yukon Chinook salmon, 1967–2004. Mean length ± 1 SD is shown. Each value is the mean of male and female salmon in the ADFG database for all Chinook salmon sampled with 8.5-inch mesh in the lower Yukon River (n = 30,600 measurements).

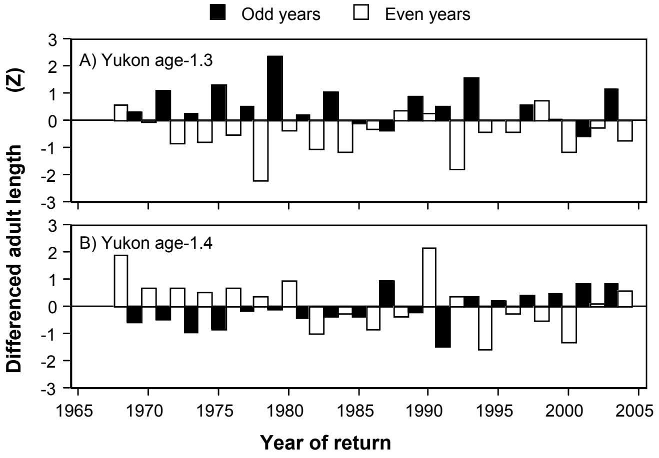

Fig. 5. Differenced length of age-1.3 and age-1.4 adult Yukon Chinook salmon, 1968–2004. Fish returning during odd-numbered years are shown by black bars, and fish returning during even-numbered years are shown by white bars. Values are the first difference of normalized adult length. Values are based on the ADFG database for all salmon sampled with 8.5-inch mesh in the lower Yukon River (30,600 measurements).

Growth in Relation to Asian Pink Salmon

Adult length of age-1.3 Chinook salmon (differenced values to remove long-term trend) was significantly longer when returning in odd-numbered versus even-numbered years (ANOVA: $df = 1, 35$; $F = 21.181$; $P < 0.001$). The alternating-year pattern was consistent throughout all years, 1968–2004, although it was less apparent during the mid to late 1990s (Fig. 5A). In contrast, the alternating-year pattern of age-1.4 Chinook salmon length switched in the early 1990s (Fig. 5B). Age-1.4 Chinook salmon tended to be smaller during odd-numbered years prior to 1992, while they tended to be larger in odd-numbered years during 1992–2004. Length of age-1.4 salmon was not significantly different between even and odd years within each period ($P > 0.05$), owing to the small number of years within each period.

We examined annual scale growth patterns (differenced) to determine the life stage in which growth varied between odd- and even-numbered years. Among age-1.4 Chinook salmon, SW2 scale growth was significantly greater during odd-numbered years at sea (Fig. 6B; $df = 1, 36$; $F = 33.869$; $P < 0.001$), whereas SW3 growth was significantly greater during even-numbered years (Fig. 6C; $df = 1, 36$; $F = 23.715$; $P < 0.001$). No differences in growth were detected during other life stages of age-1.4 Chinook salmon. Age-1.4 Chinook salmon experienced relatively high growth in odd-numbered years of their second year at sea followed by relatively high growth during the third year at sea. These fish returned to the Yukon River during even-numbered years in which length-at-age was relatively high prior to the early 1990s (Fig. 5B).

Age-1.3 Chinook salmon also exhibited an alternating-year pattern during SW2 where differenced growth was greater during odd-numbered years at sea (Fig. 6A; $df = 1, 36$; $F = 3.165$; $P = 0.084$). Greater SW2 growth during odd-numbered years of age-1.3 was associated with greater adult length among fish that returned in odd-numbered years (Fig. 5A). An alternating-year pattern was not detected among other life stages of age-1.3 Chinook salmon.

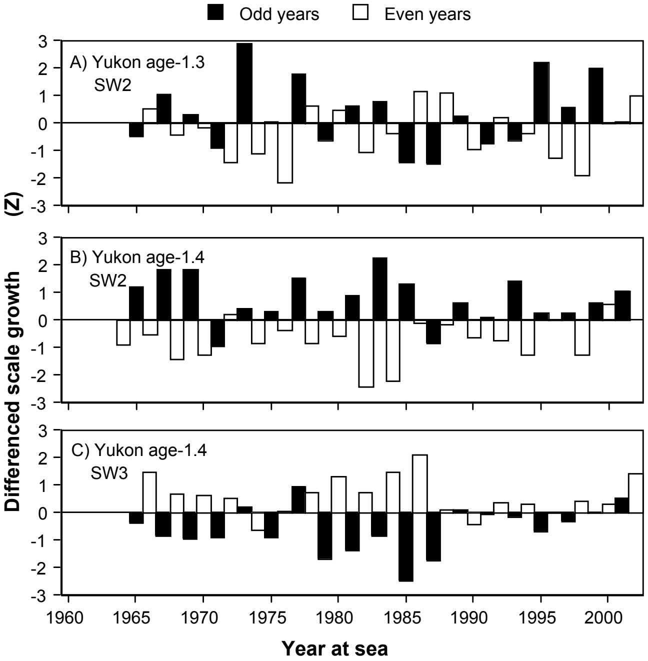

Fig. 6. Index of Yukon Chinook salmon growth during the second (A, B) and third (C) years at sea, 1964–2002. Odd-numbered years are represented by black bars, and even-numbered years are shown by white bars. Index is the first difference of normalized scale growth.

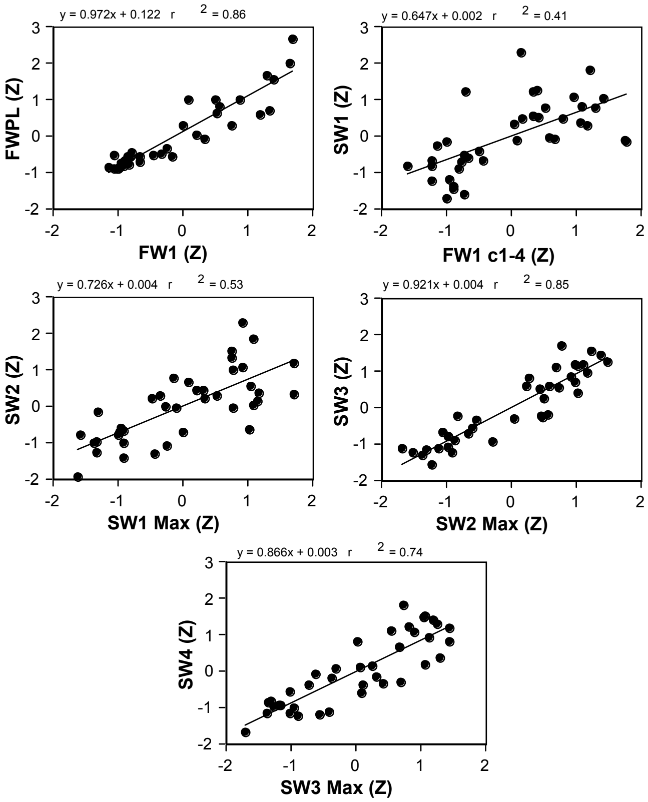

Fig. 7. Relationship between average scale growth during each life stage of age-1.4 Yukon Chinook salmon and average scale growth during the previous year. Independent variables include: total growth in fresh water (FW1), the first four circuli of freshwater growth excluding the scale focus (FW1 c1-4) and width of five maximum circuli during each year in the ocean (SW1, SW2 and SW3). All values are normalized. Relationships for age-1.3 Chinook salmon were similar, and are not shown here (Ruggerone et al. 2007b).

Growth in Relation to Prior Growth

Scale growth of Yukon Chinook salmon during each life stage in fresh water (FWPL) and the ocean (SW1, SW2, SW3, SW4) was significantly and positively correlated with growth during the previous life stage ($P < 0.05$; Fig. 7). On average, 60% of the variability in annual Yukon scale growth was explained by growth during the previous life stage. 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 total freshwater growth, but it was most highly correlated with growth during early life in fresh water (i.e., circuli 1–4). Growth during each subsequent year in the ocean was correlated with the previous year's growth, but growth was most highly correlated with maximum scale growth, as defined as the spacing among the five widest circuli.

Autocorrelation was present in the scale growth time series. However, autocorrelation was non-significant in the residuals of the scale growth regressions described above, indicating the regression models were not significantly influenced by time (L. Conquest, University of Washington, pers. comm.). 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.

DISCUSSION

Yukon and other Chinook salmon harvests in western Alaska tended to reflect the 1977 ocean regime shift (abundance increase) and the 1997/98 El Niño 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; Hunt et al. 2002; Peterman et al. 2003). 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 et al. 2007a), did not have an apparent effect on Chinook salmon abundance in western Alaska.

Harvests of western Alaska Chinook salmon changed relatively rapidly in response to the 1977 and 1997/98 climate events, and these abundance levels persisted for a number of years. The rapid decline in the late 1990s suggests that Chinook salmon abundance and survival may have been initially influenced during late marine life. The persistence of relatively low harvests after the 1997/1998 El Niño suggests that the El Niño event may have affected multiple year-classes that occupied the ocean during this period. Additionally, the El Niño event may have altered the abundances and/or distributions of other marine species, leading to a prolonged influence on Chinook salmon abundance.

Adult length and annual scale growth at sea of Yukon Chinook salmon did not appear to be closely linked to shifts in abundance of Chinook salmon. Furthermore, no positive correlation existed between scale growth during each life stage and ocean conditions such as sea surface temperature. Scale growth during the first year at sea appeared to have been affected by the 1977 (growth increase) and 1989 (growth decrease) ocean regime shifts.

Mean scale growth of Chinook salmon at sea was dependent on the previous year's growth, and this dependency may have confounded potential relationships between growth and abundance or environmental conditions. Additional research indicated that scale growth of individual Yukon and Kuskokwim Chinook salmon was dependent on scale growth during the previous life stage (Ruggerone et al. 2009). Adult length of individual Chinook salmon tended to be positively correlated with scale growth in fresh water, indicating an important link between growth at sea and growth and habitat quality in fresh water. Adult length of individual Chinook salmon was also correlated with marine scale growth, especially cumulative scale growth after the first year at sea.

The dependence of growth on prior growth of Chinook salmon 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). Instead, Bristol Bay sockeye salmon exhibited a significant negative correlation between scale growth in the second year versus first year at sea, possibly reflecting the need to grow fast in the second year if growth in the first year was below average (Ruggerone et al. 2005). The dependency of Chinook salmon growth on prior growth may reflect the tendency of Chinook salmon to consume relatively large, mobile prey such as fishes and squid (Davis et al. 2005) and the greater ability of larger Chinook salmon to capture these prey.

Previous studies indicated that Chinook salmon growth and survival was influenced by competition with pink salmon, especially when Chinook salmon initially entered marine waters (Grachev 1967; Ruggerone and Goetz 2004; Ruggerone and Nielsen 2004). Pink salmon are exceptionally abundant in the central Bering Sea during odd- versus even-numbered years (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, we did not detect direct competition between pink salmon and Chinook salmon, possibly because Yukon Chinook salmon do not overlap with Asian pink salmon until the second year at sea and because pink salmon from western Alaska are not abundant (JTC 2008; Whitmore et al. 2008).

Instead, growth of age-1.3 and age-1.4 Chinook salmon during the second year at sea (SW2) was greater during odd-numbered years, i.e., years when pink salmon were highly abundant. Growth of age-1.4 Chinook salmon during the third year at sea (SW3) was lower during odd-numbered years, but this pattern may reflect the dependency of growth on previous year's growth, as discussed previously. The alternating-year pattern in scale growth led to greater adult length-at-age in odd-numbered years, especially among age-1.3 Chinook salmon. These growth patterns were also detected in Kuskokwim Chinook salmon (Ruggerone et al. 2007b).

The alternating-year pattern of Yukon Chinook salmon was opposite to that observed among Bristol Bay sockeye salmon, which experienced lower growth during odd-numbered years (Ruggerone et al. 2003, 2005). Diet overlap is much greater between pink and sockeye salmon versus pink and Chinook salmon. Chinook salmon also feed on higher trophic level prey (Davis et al. 2005). The cause of the alternating-year pattern of Chinook salmon growth is unknown, but it may be related to a cascading effect of pink salmon on the epipelagic food web. If so, this finding would indicate indirect competition between pink and Chinook salmon in offshore areas. Future studies of salmon diets on the high seas should attempt to identify prey species that contribute to these alternating-year patterns in salmon growth and to identify the extent to which prey life history contributes to this pattern.

ACKNOWLEDGEMENTS

This investigation was funded by the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative (AYK SSI Projects 45076, 45077, 45078) and the U.S. Geological Survey's Global Change Program, USGS Alaska Science Center. Mention of trade names does not imply endorsement by the U.S. Government. We appreciate constructive comments by D. Molyneaux, S. Goodman, C. Jay, J. June, C. Zimmerman, and two anonymous reviewers. We also appreciate efforts to gather, measure, and catalog scales by D. Folletti, M. Lovejoy, A. Norman, D. Oxman, W. Rosky, and W. Whelan.

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