

2008 Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project Product¹

Retrospective Analyses of AYK Chum & Coho Salmon

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SUMMARY

Most salmon populations in the Arctic-Yukon-Kuskokwim (AYK) region of Alaska declined unexpectedly in the late 1990s and early 2000s. In this investigation, we tested the hypotheses that growth and/or abundance of Norton Sound chum salmon (Kwiniuk stock), Norton Sound coho salmon (Unalakleet stock) and Kuskokwim coho salmon were influenced by climate change and/or by interactions with pink salmon and/or Asian hatchery salmon. Based on previous studies, we anticipated that competitive interactions with pink salmon would adversely affect growth and/or productivity of Norton Sound chum salmon, whereas pink salmon would provide prey for piscivorous coho salmon. We also anticipated that coho salmon growth and abundance might benefit from larval pollock, which are known to be important prey. We tested these hypotheses through retrospective analyses of seasonal and annual growth and abundance of AYK chum and coho salmon stocks in relation to abundances of pink salmon and/or Asian chum salmon, pollock spawning biomass, and climate-related variables. Salmon scale growth is known to be correlated with salmon length, consequently salmon growth estimates were based on scale measurements of adult salmon and adult salmon length-at-age during the past several decades.

Kwiniuk Chum Salmon

Kwiniuk chum salmon scale growth during early marine life (first 10 scale circuli of first year at sea) was less among fry that migrated to sea in odd-numbered years (odd-year migrants), 1979 to 2003, a pattern that was consistent for both age-0.3¹ and age-0.4 chum salmon. Reduced early marine growth of odd-year chum salmon migrants corresponded with relatively high abundances of juvenile pink salmon emigrating from Norton Sound during odd-numbered years. Early marine growth of Kwiniuk chum salmon (avg. age-0.3 and 0.4) was negatively correlated with adult Kwiniuk pink salmon abundance during the previous year, suggesting that greater juvenile pink salmon abundance led to reduced early marine growth of chum salmon. Approximately 22% of the annual variation in early marine growth was explained by adult pink salmon abundance during the 32-year period. The possible effect of competition on incremental scale growth declined after circuli number 10, apparently reflecting dispersion of both chum and pink salmon into offshore areas of the Bering Sea. Date of ice-out in Norton Sound, Nome spring air temperature, and sea surface temperature (SST) in the North Pacific Ocean during winter and spring were not correlated with early marine growth of chum salmon.

Odd- and even-year scale growth patterns of age-0.3 and age-0.4 chum salmon differed during the second (SW2)² year at sea. Growth of age-0.3 chum salmon scales tended to be greater during odd-numbered years ($P = 0.13$), whereas growth of age-0.4 chum salmon was significantly less during odd-numbered years at sea. During the third year at sea, growth of age-0.3 salmon (not statistically significant) and age-0.4 chum salmon (statistically significant) tended to be greater during odd-numbered years at sea. Scale growth during the fourth year at

¹ Age designations identify the number of winters in freshwater after emergence (e.g., 1.x) followed by winters in the ocean (e.g., x.3).

² Annual and seasonal growth zones of salmon scales were identified by several acronyms: FW1 is scale growth during the first year in freshwater, FW2 is growth during the second year in freshwater, and FWPL is spring plus growth that occurs during smoltification. SW1, SW2, SW3, and SW4 identify annual growth at sea, and SWPL identifies growth of maturing salmon during the homeward migration.

sea, during homeward migration, and adult length-at-age did not significantly vary by odd- and even-numbered years at sea. Annual trends in chum salmon scale growth indicated that odd-year migrants that matured as age-0.4 salmon exhibited reduced growth during early marine life (possible pink salmon effect) then experienced above average growth during each subsequent year relative to even-year migrants. Except for early marine growth, scale growth of age-0.3 chum salmon tended to be lower during even-numbered years at sea. The inconsistent marine growth patterns of age-0.3 and age-0.4 chum salmon may reflect different migration patterns and/or different diet of faster growing age-0.3 versus slower growing age-0.4 chum salmon (see below).

Scale growth of age-0.3 chum salmon was significantly greater than that of age-0.4 chum salmon during each year at sea, including the homeward migration. Growth of male age-0.3 and male age-0.4 salmon became significantly greater than that of female salmon during the third year at sea (SW3) and continued during all subsequent life stages, including adult length. However, examination of scale circuli widths indicated greater growth of age-0.3 male chum salmon may begin immediately after entry to the ocean, whereas age-0.4 male chum salmon grew relatively slowly during early marine life. The percentage of age-0.3 chum returning from the brood year (i.e., progeny returning from year when parents spawned) was positively correlated with scale growth of age-0.3 salmon during the third year at sea (SW3). These findings are consistent with other studies indicating that faster growth leads to earlier maturation of chum salmon, but our study suggests the relationship between growth and maturation may begin soon after emergence and migration into the ocean.

Length-at-age of adult Kwiniuk chum salmon (mean of age-0.3 and age-0.4 salmon) was negatively correlated with abundance of Asian hatchery chum salmon ($r = -0.60$) and total Asian chum salmon ($r = -0.60$) that returned to their natal stream during the same year, 1974-2005. Scale growth of age-0.3 and age-0.4 Kwiniuk chum salmon during the second year at sea (SW2) was negatively correlated with total Asian chum salmon abundance maturing in the same year as Kwiniuk chum salmon. Approximately 12% and 24%, respectively, of the variability in SW2 scale growth was explained by Asian chum salmon during the 32-year period. Other variables, including Eastern Kamchatka pink salmon and SST, did not explain as much variability in Kwiniuk chum salmon growth as did Asian chum salmon abundance, although scale growth during SW2 and SW3 tended to be negatively correlated with Kamchatka pink salmon abundance.

Productivity of Kwiniuk chum salmon (return per spawner; R/S) could be explained by the following multivariate model:

$$1) \text{ Log}_e \text{ chum R/S} = 12.97 - 1.118 (\text{Asian chum}) + 0.35 (\text{Marine productivity}) \\ - 0.74 (\text{Escapement}) - 0.207 (\text{Pink salmon}).$$

Kwiniuk chum salmon productivity decreased with greater spawners (i.e., parents), decreased with greater adult abundance of Asian chum salmon two to four years after the Kwiniuk chum salmon brood year (i.e., salmon that coexisted at sea), decreased with greater adult abundance of Eastern Kamchatka pink salmon two years after the Kwiniuk chum salmon brood year, and increased with an index of early marine productivity. These four variables explained 68% of the variability in Kwiniuk chum salmon productivity during the 37-year period.

Norton Sound Chum Salmon

Adult chum salmon recruits from parent spawners were estimated for chum salmon throughout Norton Sound (1970-2001 brood years) except for Norton Bay and Shaktoolik subdistricts. Productivity of Norton Sound chum salmon (R/S) was highly correlated with productivity of Kwiniuk chum salmon ($r = 0.76$) suggesting that common factors affect chum salmon productivity throughout Norton Sound. Variables used to explain productivity of Kwiniuk chum salmon (see model above) explained 71% of Norton Sound chum salmon productivity during the 32-year period. Productivity of Norton Sound chum salmon decreased with greater spawners (i.e., parents), decreased with greater adult abundance of Asian chum salmon two to four years after the Kwiniuk chum salmon brood year, decreased with greater adult abundance of Eastern Kamchatka pink salmon two years after the Kwiniuk chum salmon brood year, and increased with an index of early marine productivity.

Kuskokwim and Unalakleet Coho Salmon

Commercial catch of Kuskokwim and Unalakleet coho salmon was 49% and 33% greater during even- versus odd-numbered years, 1965-2007, providing evidence for interaction with alternating-year abundances of pink salmon. Approximately 82% (Unalakleet) and 90% (Kuskokwim) of these adults returned after two winters in freshwater and one winter at sea, i.e., age-2.1. Scale growth of age-2.1 coho salmon Kuskokwim and Unalakleet rivers was estimated from adult scales collected during 1965-2006 and 1980-2006, respectively.

Scale growth of juvenile Kuskokwim and Unalakleet coho salmon produced by the less numerous odd-year parents was significantly greater during the first (FW1) of two years in freshwater. Coho fry produced by odd-year spawners would have been too small to consume pink salmon fry, but they may have benefited from food provided by pink salmon carcasses during late summer of even-numbered years and by reduced density of juvenile coho salmon resulting from fewer adults returning in odd-numbered years. Growth of juvenile Kuskokwim coho salmon produced by odd-year broods continued to exceed that of even-year broods during the second year in freshwater (odd-numbered growth year), suggesting they may have benefited from numerous pink salmon fry produced by the dominant even-year adult pink salmon spawners. Alternating-year growth of Unalakleet coho salmon was not apparent during FW2.

In contrast to growth in freshwater, progeny of even-year brood coho salmon in the Kuskokwim River experienced significantly greater growth during the first year at sea (SW1), a pattern that was not apparent among Unalakleet coho salmon (shorter time series). These coho entered the Bering Sea in odd-numbered years and may have consumed numerous pink salmon fry produced by the dominant even-year broods in western Alaska. However, examination of scale circuli growth trends indicated that differential growth occurred during late SW1 growth (i.e., circuli 21-43) indicating Kuskokwim pink salmon fry were not likely a key factor affecting SW1 growth. Both coho stocks exhibited a marked shift in the alternating-year growth pattern during the latter portion of SW1 (increased late season growth of odd-years). The ocean location in which this shift in growth occurs is unknown, but tagging data show maturing coho salmon from western Alaska to be distributed south to 47°N and east to 145°W (tagged May to July), i.e., an area that includes the Gulf of Alaska. Therefore, AYK coho salmon likely cross multiple ocean

habitats during their first growing season at sea. Adult Kuskokwim coho returning in even-numbered years experienced significantly greater growth during SW1, and these fish were significantly more abundant than those returning in odd-numbered years. This relationship was less obvious for Unalakleet coho salmon in which the growth time series was much shorter.

Most coho salmon return to the AYK region in August, and scale growth and circuli counts during the homeward migration (SWPL) are approximately 60% less than that during SW1. Kuskokwim and Unalakleet coho salmon scale growth during the homeward migration was greater during odd-numbered years, corresponding with fewer adult coho salmon. Adult length of Kuskokwim and Unalakleet coho salmon (scale data and the entire age-sex-length (ASL) database) did not significantly differ between even- and odd-years of return, probably reflecting tradeoffs in growth during SW1 and SWPL.

In contrast with chum salmon, length of age-2.1 male coho salmon was not significantly different from female coho salmon. Size of male versus female Kuskokwim coho salmon significantly declined beginning with the 1997 El Niño and continued through 2006, suggesting this climate event had a differential effect on male versus female coho salmon.

Catch per unit effort (CPUE) of Kuskokwim coho salmon in the commercial fishery was positively correlated with scale growth during the first year at sea (SW1; $r = 0.55$), 1965 to 2006. Residuals from the linear regression of CPUE on SW1 were typically low from 1965-1977, moderate from 1978-1988, high from 1989-1996, and low to average from 1997-2006, corresponding with ocean regime shifts in 1977 and 1989 and the 1997/98 El Niño. CPUE of Kuskokwim coho salmon was explained by the following multivariate relationship:

$$2) \text{ CPUE} = -15.43 + 12.192 (\text{SW1}) + 5.076 (\text{period } 1977\text{-}1988) + 8.345 (\text{period } 1989\text{-}1996),$$

where “dummy” variables (value was “1” within the shift period, or “0” otherwise) were used to test for effects of climate shifts. These variables explained 67% of coho CPUE variability during the past 41 years. The model indicates that coho CPUE increased with greater growth during the first year at sea, and that CPUE also increased during 1977-1988 and further increased in 1989-1996, then declined to pre-1977 values beginning with the 1997 El Niño. Other scale growth variables, seasonal SST, Bering Sea ice cover index, and climate indices (Aleutian Low, PDO) did not add significant information to the model.

Coho salmon growth during the first year at sea (SW1) was positively correlated with the spawning biomass of pollock in the Bering Sea and with pink salmon abundance in Eastern Kamchatka. The multivariate model was:

$$3) \text{ SW1 (mm)} = 1.527 + 0.104 (\text{pollock}) + 0.00172 (\text{pink salmon}).$$

Pollock spawning biomass (millions mt) and Eastern Kamchatka pink salmon abundance (millions of adults) explained 60% of the variability in coho scale growth during the first year at sea. Standardized partial regression coefficients indicated pollock explained much more of the variability in SW1 than pink salmon.

Models 2 and 3 suggest coho CPUE was linked to pollock spawning biomass, ocean regime shifts in 1977 and 1989, and with pink salmon abundance. The effect of these variables on Kuskokwim coho CPUE is shown in the following multivariate equation:

$$4) \text{ CPUE} = 0.643 + 2.4 (\text{Pollock}) + 3.6 (\text{period 1977-1988}) + 6.7 (\text{period 1989-1996}) + 0.29 (\text{pink salmon}).$$

This model explained 80% of Kuskokwim coho CPUE variability during the past 41 years. Standardized partial regression coefficients indicated pollock and the 1989 regime shift explained most of the variability in CPUE followed by the 1977 regime shift and pink salmon. The significant decline and low coho CPUE after the 1997 El Niño was essentially equivalent to that prior to the 1977 regime shift. Seasonal SST did not add significant information to the model.

These models suggest coho salmon, which are highly piscivorous, grow faster during their first year at sea when pollock spawning biomass is high and many larval pollock are available. Ocean regime shifts in 1977 and in 1989 led to progressively greater coho CPUE followed by exceptionally low CPUE during and after the 1997 El Niño. The positive correlation of coho CPUE with Eastern Kamchatka pink salmon abundance was opposite of that observed in Bristol Bay sockeye salmon but consistent with alternating-year growth of AYK Chinook salmon. Presumably, the positive correlation of coho CPUE and Asian pink salmon abundance reflects the higher trophic level of coho salmon versus pink and sockeye salmon and a cascading trophic effect caused by numerous Asian pink salmon.

Commercial catch of Unalakleet coho salmon (1980-2006) was not correlated with scale growth during each life stage or with adult length-at-age. Catch of Unalakleet coho salmon during a 41-year period (1965-2006) was positively correlated with catch of Kuskokwim coho salmon ($r = 0.52$), Dec-Mar SST ($r = 0.41$) and June SST ($r = 0.48$) in the North Pacific Ocean, annual PDO index ($r = 0.34$), and North Pacific Index (April-July; $r = 0.32$). These variables explained less than 27% of the variability in Unalakleet coho catch during the past 41 years. CPUE of Unalakleet coho salmon in the test fishery (1985-2007) was not correlated with scale growth or other environmental variables unless the exceptionally high CPUE values during 2005-2007 were excluded.

Conclusions

This retrospective analysis of AYK chum salmon and coho salmon indicated that growth was important to productivity of these salmon stocks. Salmon growth was influenced by climate related factors or to density-dependent interactions with other species. Evidence suggested that Norton Sound chum salmon may compete with Asian chum salmon, Kamchatka pink salmon, and with Norton Sound pink salmon during early marine life. In contrast, juvenile Kuskokwim coho salmon may benefit from pink salmon in freshwater habitats and from larval pollock in the Bering Sea. The complexity of species interactions in the ocean was highlighted by the alternating year pattern of coho salmon growth and abundance. Research is needed to identify prey and their life history patterns that may contribute to alternating-years patterns of AYK salmon.

INTRODUCTION

As a keystone species, Pacific salmon (*Oncorhynchus* spp.) are considered to be a critical component of a watershed. Yet in a relatively pristine region of Alaska, exceptionally low numbers of chum, Chinook and coho salmon returned to Norton Sound and the Yukon and Kuskokwim rivers in the late 1990s and early 2000s. Low returns and harvests prompted 15 disaster declarations for the Arctic-Yukon-Kuskokwim (AYK) region by the Governor of Alaska and federal agencies (AYK SSI 2006). Some salmon stocks have been in decline for more than 15 years, leading to severe restrictions on commercial and subsistence fisheries and significant hardships for people that depend on salmon (AYK SSI 2006, Brannian et al. 2006, Menard and Bergstrom 2006, Banducci et al. 2007, Whitmore et al. 2008).

Significant advances have been made during the past two decades in unraveling the effects of climate change and species interaction impacts on growth, survival, and abundance of Pacific salmon. Large scale climate patterns have resulted in so-called ocean regime shifts during the mid-1970s and again in 1989, leading to significant shifts in abundances of salmon and other species in the North Pacific Ocean and Bering Sea (e.g., Rogers 1984, Alverson 1992, Mantua et al. 1997, Anderson and Piatt 1999, Hare and Mantua 2000). The 1989 regime shift was not a reversal back to previous conditions, but rather a new state of conditions. The 1997/1998 El Niño event also had a dramatic effect on the eastern Bering Sea ecosystem, including Chinook (Ruggerone et al. 2007a) and sockeye salmon (Kruse 1998) returning to western Alaska. Although large-scale shifts in ocean productivity can affect salmon across broad regions, recent research indicates productivity of salmon within a region is more correlated than somewhat distant stocks, indicating the importance of understanding regional oceanic conditions (Pyper et al. 2005).

In the Bering Sea, the timing of sea ice break-up is important to the development of the pelagic food web each spring (Hunt et al. 2004). Sea ice has melted relatively early since the mid-1970s and exceptionally early during 2000-2004 (Overland and Stabeno 2004). The unusual climatic events in the Bering Sea in recent years led Overland and Stabeno (2004) to conclude that significant changes in the composition of marine species could occur if the warming trend continues. It is not known how the early breakup of sea ice has affected growth and/or survival of juvenile chum salmon, such as those in Norton Sound, but it has been hypothesized by local biologists that timing of ice break-up is important to chum salmon survival (C. Lean, former Alaska Department of Fish and Game (ADFG) management biologist, pers. comm.). For example, ice cover in Norton Sound may protect small salmon from piscivorous birds while promoting food production for salmon.

Salmon growth appears to be a key mechanism linking salmon survival and abundance to climate change. For example, the doubling in abundance of Bristol Bay sockeye salmon after the mid-1970s regime shift was associated with a significant increase in their growth during the first and second years at sea, as determined by measurements of scale increments (Ruggerone et al. 2005, 2007b). Examination of seasonal scale growth indicated sockeye growth immediately after entry into the Bering Sea was greater after the mid-1970s (Ruggerone et al. 2005). Growth during the third year at sea and during the adult return to Bristol Bay was inversely related to high sockeye salmon and Asian pink salmon abundance. Recent evidence suggests the 1989 regime shift had a

significant effect on Bristol Bay salmon. Size at age of adult Bristol Bay sockeye immediately following the 1989 regime shift and during subsequent years was consistently low, suggesting a possible link between the 1989 regime shift and the significant decline in some Bristol Bay stocks such as the Kvichak River stock (Ruggerone and Link 2006). During 1977-1988, a period of high sockeye salmon abundance, size-at-age of Bristol Bay sockeye salmon was exceptionally great after accounting for abundance and competitive effects of sockeye salmon and Asian pink salmon in the Bering Sea.

Pink salmon often express significant alternating years of abundance, a trait that has been used to examine their interactions with other salmon species. In a review of pink salmon interactions with other salmon, Ruggerone and Nielsen (2004) suggested that pink salmon may be competitively dominant over other salmon species in the North Pacific Ocean and Bering Sea because they are highly abundant, grow rapidly, and consume prey that might otherwise be consumed by other salmon species. For example, in the Pacific Northwest, abundance of chum salmon is inversely related to abundance of pink salmon because pink and chum fry compete for similar prey in the marine waters and because chum salmon may have a genetic trait that influences age composition and reduces competition (Smoker 1984, Salo 1991). Pink salmon have been shown to affect feeding and distribution of chum salmon on the high seas. When interacting with abundant odd-year Asian pink salmon on the high seas, Bristol Bay sockeye salmon experienced significantly lower growth at sea (scale and adult length-at-age data), leading to a 26% to 45% reduction in smolt to adult survival (depending on smolt age), and 92 million fewer adult returns during 1977-1997 smolt years (Ruggerone et al. 2003). In the Pacific Northwest, subyearling Chinook salmon experienced a 62% reduction in survival and reduced growth when they entered marine waters in even-numbered years along with numerous juvenile pink salmon, based on the analysis of 53 million coded-wire-tagged Chinook salmon during 1972-1997 (Ruggerone and Goetz 2004). These studies of density-dependent growth and survival among salmon at sea raise the question: how much does large-scale hatchery production affect growth and survival of wild salmon (Holt et al. 2008)? This question is particularly relevant for AYK salmon in response to tremendous production of hatchery chum salmon in Japan, whose ocean distribution and diet overlaps with that of AYK chum salmon (Myers et al. 1996, 2004).

In the AYK region adult pink salmon are relatively abundant in even-numbered years compared with odd-numbered years. For example, in Norton Sound, spawning escapement of pink salmon to six rivers (combined) averaged approximately 3.6 million fish in even-numbered years compared with 0.6 million fish in odd-numbered years, 1995-2007. Pink salmon were exceptionally abundant during 2004-2006, averaging 4.9 million spawners in these six index rivers (S. Kent, ADFG, pers. comm.), possibly reflecting the beneficial effects of warm spring temperatures on pink salmon. Norton Sound biologists have hypothesized that pink salmon may adversely affect Norton Sound chum salmon (G. Todd, ADFG, pers. comm.). Spawning pink and chum salmon overlap in both time and space, and abundant pink salmon may impact chum salmon through superimposition of redds. Both pink and chum fry emerge in spring and enter nearshore marine waters to consume prey and grow rapidly. Studies in other regions indicate pink and chum fry compete for similar prey (Salo 1991). These observations suggest progeny from even-year chum salmon in Norton Sound may be adversely affected by pink salmon.

In contrast, pink salmon may provide food for piscivorous juvenile coho salmon in rivers and nearshore marine areas of Norton Sound and the Kuskokwim area, as they appear to do in other regions (Ruggerone and Nielsen 2004). The Kuskokwim River supports one of the largest runs of coho salmon in Alaska, and commercial harvests of coho were 49% greater in even-numbered versus odd-numbered years during 1965-2007. Likewise, commercial harvests of Unalakleet coho salmon were 33% greater during even-numbered years, 1965-2007. Given the dominance of four-year old coho salmon (age 2.1), these observations are consistent with the hypothesis that juvenile coho salmon benefit from predation on pink salmon fry in fresh and nearshore marine waters.

In this investigation, we tested the following hypotheses:

- Growth and/or abundance of Norton Sound chum salmon has been influenced by climate change and/or reduced by interactions with pink salmon and/or Asian hatchery salmon.
- Growth and/or abundance of Norton Sound and Kuskokwim coho salmon has been influenced by climate change and/or enhanced by interactions with pink salmon.

We tested these hypotheses through retrospective analyses of 1) seasonal and annual growth of Norton Sound chum and coho salmon and Kuskokwim coho salmon, and 2) abundance indices of chum and coho salmon in relation to abundances of pink salmon and/or Asian chum salmon. Seasonal and annual growth of salmon was based on scale increments, which are known to be correlated with salmon body length (Fukuwaka and Kaeriyama 1997, Fisher and Pearcy 2005).

Specific objectives of the project included:

- 1) Reconstruct annual and seasonal growth indices of Kwiniuk River chum salmon (adult return years 1975-2006), Unalakleet coho salmon (1980-2006), and Kuskokwim coho salmon (1965-2006), based on measurements of scale increments.
- 2) Evaluate potential adverse effects of pink salmon, Asian hatchery chum salmon, and climate change on growth and productivity of Kwiniuk River chum salmon.
- 3) Estimate Norton Sound adult chum salmon returns from each parent spawning year (brood year) and examine productivity of Norton Sound chum salmon in relation to Kwiniuk chum salmon scale growth, climate change, and competition at sea with other salmon.
- 4) Evaluate climate change effects and potential beneficial effects of pink salmon abundance and pollock spawning biomass (larval fishes) on growth and abundance of Kuskokwim River and Unalakleet River coho salmon.

METHODS

Study Areas

The Kwiniuk River drains into the north side of Norton Sound just east of Moses Point, approximately 160 km east of Nome (Fig. 1). Kwiniuk and Tubutulik rivers are the primary salmon spawning tributaries supporting the Moses Point fishery (Subdistrict 3). Although commercial fishing at Moses Point began in 1962, significant commercial harvests of chum salmon have not occurred since 1988 (Kent 2007). Subsistence fisheries occur in both drainages and in nearshore marine waters. Tagging studies indicate relatively few Kwiniuk chum salmon are captured in adjacent subdistricts (Gaudet and Schaefer 1982). Chum, pink, and Chinook salmon escapement has been enumerated from a tower on the Kwiniuk River since 1965.

The Unalakleet River enters the eastern portion of Norton Sound (Fig. 1). Chinook, coho, chum and pink salmon have been enumerated from a tower on the North River, a major tributary, since 1972 (Banducci et al. 2007). Additionally, salmon have been enumerated by aerial surveys of the North River during most years since 1962. The Unalakleet River produces the largest run of coho salmon in Norton Sound. Coho salmon have been regularly harvested by commercial and subsistence fishermen in nearshore marine areas and within the lower river.

The Kuskokwim River is the second largest river in Alaska and it produces the largest coho run in Alaska. The Kuskokwim River is located south of Norton Sound and the Yukon River, but north of Bristol Bay. Coho salmon is the major species harvested by commercial fishermen in the Kuskokwim River. Most commercial harvests occur in the lower river near Bethel (Fig. 2). Spawning escapement has been estimated on only a few tributaries of the Kuskokwim River (Whitmore et al. 2008).

Scale Collection and Measurements

Adult chum salmon scales from the Kwiniuk River (Moses Point fishery) and coho salmon scales from the Unalakleet River and the Kuskokwim River were obtained from the ADFG regional archive in Anchorage, Alaska. Scales have been collected annually for quantifying age composition since at least 1975 in the Kwiniuk River, 1980 in the Unalakleet River, and 1965 in the Kuskokwim River. Kwiniuk chum salmon scales were collected from salmon captured by set gillnets (5 7/8" stretched mesh) in the Moses Point fishery and Kwiniuk River from 1975 to 1991 and by beach seine in the river from 1992 to 2006. Chum scales were primarily collected during June 25 to July 14 each year. Unalakleet coho salmon scales were first collected in 1975, but consistent sampling did not begin until 1980. These coho salmon were sampled from the commercial fishery near the river mouth that utilized 5 7/8" stretched mesh set gillnets. Additional samples were obtained in 1981 and 1982 from the variable mesh test fishery gillnets. Most Unalakleet coho salmon scales were collected from late July through late August. Kuskokwim coho salmon scales were collected primarily by drift gillnets (5.5-6.0 stretched mesh) near Bethel from approximately late July through late August.

The goal was to measure 50 scales from each of the two dominant age groups of Kwiniuk chum salmon (ages-0.3 and 0.4)³ and from the dominant age group of Unalakleet and Kuskokwim coho salmon (age-2.1). 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 collected 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 images (3352 x 4425 pixels) permitted the entire scale to be viewed and provided enough pixels between narrow circuli to ensure accurate measurements of circuli spacing. The scale image was displayed on a high resolution digital monitor, and Optimas 6.5 image processing software was used to collect measurement data using a customized interface. The scale measurement axis was defined as the longest axis extending from the scale focus to the outermost edge. Distance (mm) between circuli was measured within each growth zone depending on species, i.e. from the scale focus to the outer edge of the first freshwater annulus (FW1), growth during the second year in freshwater (FW2), 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 Kwiniuk chum salmon scales were available for measurement in some years. Male and female chum salmon grew at different growth rates (see below). Therefore, chum salmon scale growth indices were developed that equally weighted male and female scale growth during each year, allowing utilization of 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 represent the normalized mean growth of male and female salmon, respectively. Normalized growth was the number of standard deviations above or below the long-term mean. This approach was not utilized for Kuskokwim and Unalakleet coho salmon because equal numbers of male and female salmon were measured each year.

Testing for Pink Salmon Effect

Pink salmon have a two-year cycle that contributes to an alternating-year pattern of abundance. In the AYK region, adult pink salmon were relatively abundant in even-numbered years and produced many fry that entered the Bering Sea in odd-numbered years. In contrast, pink salmon

³ 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.

from eastern Kamchatka, the Asian stock that likely had the most overlap with Norton Sound Chum salmon, were dominated by odd-year adult pink salmon. The distribution of Asian and Norton Sound chum salmon probably did not overlap until the second year at sea (SW2). To highlight the potential effect of pink salmon on chum salmon growth, we statistically removed long-term trends in chum scale measurements by calculating the first difference (d) among mean annual (y) growth measurements during each life stage, as demonstrated with the following example for the first year at sea (SW1):

$$SW1_d = SW1_y - SW1_{y-1}$$

Most statistical tests that examined potential effects of pink salmon on chum salmon growth were conducted using differenced values. No statistical adjustments (e.g., degrees of freedom) were necessary for these tests (L. Conquest, Center for Quantitative Sciences, University of Washington, pers. comm.).

Indices of AYK Salmon Abundance

Kwiniuk Chum Salmon

A brood table (adult returns per spawner) for Kwiniuk chum salmon was obtained from T. Hamazaki (ADFG) and updated for 2005 and 2006 using data provided by S. Kent (ADFG). Hilborn et al. (2007) examined productivity of Kwiniuk chum salmon based on the original dataset. Spawning escapement in the Kwiniuk River was estimated each year from a tower. Aerial counts in the Kwiniuk and Tubutulik rivers were used to identify the proportion of Kwiniuk-bound chum salmon in the Moses Point fishery, along with spawning escapement enumerated from the Kwiniuk tower, and age composition from the scales.

Norton Sound Chum Salmon

Except for Moses Point (Kwiniuk stock), brood tables have not been developed for chum salmon in other Norton Sound subdistricts because age composition and spawning escapement data were missing in some years. In order to examine potential effects of pink salmon and Asian chum salmon on returns of Norton Sound chum salmon, we approximated adult salmon returns from each brood year (i.e., parents) for Nome, Golovin, Moses Point, and Unalakleet subdistricts, brood years 1970-2001. Norton Bay and Shaktoolik subdistricts were not included because spawning escapement and age composition were typically not estimated in these areas. Age composition of Moses Point (Kwiniuk) and Unalakleet chum salmon was fairly complete back to 1965 whereas age composition was available for less than 10 years in Nome (9 years) and Golovin (6 years) (www.sf.adfg.state.ak.us/CFPROJECTS/AYKDBMS/DataTypes/ASL.aspx). Available age composition data for each stock was compared with that of Moses Point and Unalakleet chum salmon using regression analysis. These correlations indicated age composition of Golovin salmon was correlated with that of Moses Point salmon (% age 0.3: $r = 0.89$); whereas, age composition of Nome salmon was correlated with that of Unalakleet salmon (% age 0.3: $r = 0.72$; correlation with Moses Point was weak, $r = 0.20$). Therefore, age composition of Unalakleet salmon was applied to Nome salmon data and age composition of Moses Point salmon was applied to Golovin salmon.

Commercial catch of chum salmon in each subdistrict was reported by ADFG each year, although commercial catch has been nil in some recent years (Banducci et al. 2005, S. Kent, ADFG, pers. comm.). Subsistence catch estimates were typically determined by interviews, thus they were less accurate compared with commercial catch estimates. Subsistence catch was not reported in some subdistricts during the 1980s and early 1990s, therefore subsistence catch for these years was approximated from the average of the three previous and three following years when catch was reported.

Spawning escapement of chum salmon in Norton Sound was estimated by aerial surveys during most years and by towers or weirs in recent years. Tower and weir counts were typically considered more accurate and complete than aerial counts, which enumerate only a subset of the spawning population. Spawning escapements were expanded to “tower” count estimates using the following approach. When available, tower counts were regressed on aerial survey counts in a watershed in order to develop a predictive relationship, e.g., Nome, Eldorado, Niukluk, and North rivers. North River counts were expanded by a factor of 7.1 in an attempt to account for chum salmon in the entire Unalakleet watershed. This expansion factor was based on a tagging study during 2004-2006, which indicated approximately 14% of chum spawners in the Unalakleet watershed occurred upstream of the North River tower (range: 10-13.6%, S. Kent, ADFG, pers. comm.). If escapement in a watershed was only enumerated by aerial surveys, then the median ratio of tower counts to aerial counts in the area was applied to the aerial counts, e.g., 4.2-5.1. Missing escapement values in a watershed were estimated from values in adjacent watersheds and the proportion represented by the missing watershed, on average. Linear interpolation was used to estimate escapement when values were not available in adjacent watersheds. On average, spawning escapement was enumerated using aerial counts and/or tower counts during 85% of the years, 1970-2001. Although we attempted to account for all spawners within the monitored watershed, we note that the above approach likely underestimated spawning escapement in the subdistricts to the extent that escapement in some smaller drainages was not counted.

Unalakleet Coho Salmon

In the Unalakleet River, standardized coho salmon catch per unit effort data (CPUE) have been developed from the test fishery since 1985 (S. Kent, pers. comm.). CPUE was based on catch per hour of fishing per 20 fathom (test fish nets). Total coho abundance was estimated during the past few years (Joy and Reed 2007), but the time series was too short to make meaningful comparisons with scale growth.

Kuskokwim Coho salmon

Although coho salmon was the primary commercial salmon species harvested in the Kuskokwim River, harvests since 1965 might not consistently reflect coho salmon abundance. Total coho salmon run size was not available because spawning escapements were not estimated. Therefore, an index of coho abundance was developed from coho salmon commercial catch per fishing permit per day (CPUE) during the month of August. These values were obtained from Ward et al. (2003) for years 1974-1998. CPUE values during 1965-1973 and 1999-2006 were

calculated from a linear regression of CPUE on coho catch per Log_e of unique permits (Catch per Permit) fished during the coho season ($\text{CPUE} = 3.94 + 0.138 \times \text{Catch per Permit}$; $R^2 = 0.72$). Predicted estimates of CPUE were used for recent years in which effort for coho salmon was relatively low (few permits and/or days fished) and fishing was restricted to lower or upper sub-districts. Permits fished exclusively during the coho season were not available prior to 1970, therefore permits fished during the coho season were estimated from mean permits per fishing period throughout the season using a regression developed with data during 1970-1987 ($R^2 = 0.94$). The Kuskokwim coho salmon CPUE Index was highly correlated with observed commercial catch during 1965-2006 ($r = 0.91$).

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 and Bethel were obtained from <http://climate.gi.alaska.edu>. An ice-out date for Norton Sound, based on the date at which ice in Norton Sound reached a 30% concentration, was provided by S. Jewett, University of Alaska, Fairbanks (<http://www.ims.uaf.edu/NS/>). Abundances of Asian chum salmon and Eastern Kamchatka pink salmon were obtained from Ruggerone et al. (2008).

An index of early marine productivity in Norton Sound was developed from residuals (observed – predicted) of the following recruitment curve for Kwiniuk pink salmon, brood years 1965-2002:

$$1) \text{Log}_e R/S = 5.21 - 0.395 (\text{pink escapement}) - 0.018 (\text{Kamchatka pink salmon}),$$

where overall $P = 0.012$, $P (\text{Log}_e \text{pink escapement}; 1000\text{s}) = 0.004$, and $P (\text{Eastern Kamchatka pink abundance}, Y + 2) = 0.040$. The model explained 22% of pink salmon productivity. Inclusion of Kamchatka pink salmon in the model removed its small effect on the productivity index. This index assumed that productivity of pink salmon reflected early marine productivity after density-dependent effects associated with pink salmon were removed. Pink salmon may provide a reasonable index of early marine productivity because juvenile pink salmon migrate to sea immediately after emergence, then spend one winter at sea before returning to spawn.

RESULTS AND DISCUSSION

Kwiniuk Chum Salmon

Scale Growth Trends

Trends in scale growth by life stage of age-0.3 and age-0.4 Kwiniuk chum salmon are shown in Figs. 3-6 with respect to brood year and year of growth⁴. Positive correlation coefficients between age-0.3 and age-0.4 scale growth steadily increased with each successive life stage. Correlations within SW1 ($r = 0.33$) and SW2 ($r = 0.35$) were non-significant, whereas correlations during subsequent stages were statistically significant ($P < 0.05$), and they increased with age: SW3 ($r = 0.47$), SWPL ($r = 0.74$), and adult length ($r = 0.85$).

Adult length of age-0.3 chum salmon was significantly correlated with scale growth during SW2 ($r = 0.43$) and SW3 ($r = 0.50$) but not with SWPL ($r = -0.01$). Adult length of age-0.4 chum salmon was correlated with scale growth during SW3 ($r = 0.53$) and SW4 ($r = 0.50$) but not with SWPL ($r = -0.09$). Thus, adult length was primarily correlated with growth that occurred during the most recent two full-years at sea but not with scale growth during the homeward migration, a period that includes cessation of feeding and a shift in energy allocation from somatic growth to egg production.

Mean scale growth during each life stage of Kwiniuk chum salmon tended to be weakly correlated with scale growth during the previous year. For age-0.3 chum salmon, SW2 was related to SW1 ($r = 0.39$), SW3 was related to SW2 (0.64), and SWPL was related to SW3 (0.39). For age-0.4 chum salmon, SW3 was related to SW2 (0.38), and SW4 was related to SW3 (0.54), but other life stages were not significantly correlated ($P > 0.05$).

SW1 growth of age-0.3 and age-0.4 Kwiniuk chum salmon was variable, and no long-term trend was apparent during the 32-year period (Figs. 3-6). During SW2, scale growth tended to be below average beginning in 1988 (age-0.3) or 1991 (age-0.4) growth year. SW3 growth of both age-groups tended to be below average during 1988-1996. Scale growth during SW4 (age-0.4 salmon) tended to be below average during 1986-1997. SWPL of both ages tended to be below average in 1980 and earlier years. Adult length of both age-0.3 and age-0.4 chum salmon tended to be below average beginning in 1985 and thereafter, except for average to above average length in 2000-2003.

Chum Salmon Growth and Environmental Variables

Scale growth of age-0.3 and age-0.4 Kwiniuk chum salmon during each stage at sea was not correlated with SST in the North Pacific Ocean during winter, spring or summer, except SW1 growth of age-0.4 salmon was correlated with SST during spring and summer ($r = 0.40$). Adult length of age-0.3 and age-0.4 chum salmon was negatively correlated with winter SST (Dec-March) during the year of return ($r = -0.41$ and $r = -0.49$, respectively).

⁴ Brood year is the year in which the parents spawned. Thus, scale growth organized by brood year is based on the same individuals during each life stage of a given brood year. In contrast, scale measurements organized by year of growth reflects growth at each life stage among fish of different ages that occurred in the same calendar year.

Kwiniuk Chum Salmon Growth and Asian Chum Salmon Abundance

Adult chum salmon length-at-age (mean of age-0.3 and age-0.4 male and female salmon from the ASL database) was negatively correlated with Log_e Asian hatchery chum salmon ($r = -0.60$) and Log_e total Asian chum salmon ($r = -0.60$) that returned to their natal stream during the same year, 1974-2005 (Fig. 7). Asian chum salmon abundance (Fig. 8) explained approximately 36% of the variability in length-at-age of Kwiniuk chum salmon. Serial autocorrelation was somewhat high when length was regressed on total chum salmon abundance ($r = 0.31$; Durbin Watson statistic $P < 0.05$) but non-significant when only hatchery salmon were included in the model (DW statistic = 1.45). Other variables, such as Asian pink salmon, Yukon chum salmon catch and SST, did not explain as much variability in adult length. No additional information was added by other variables ($P > 0.05$).

SW2 scale growth of age-0.4 ($r = -0.49$, $P = 0.006$) and age-0.3 ($r = -0.35$, $P = 0.06$) chum salmon was negatively correlated with Log_e total Asian chum salmon abundance maturing in the same year as Kwiniuk chum salmon. Approximately 24% and 12%, respectively, of the variability in SW2 scale growth was explained by total Asian chum salmon during the 32-year period.

Kwiniuk Chum Salmon Interactions with Pink Salmon

Cumulative growth increments of Kwiniuk chum salmon circuli tended to be greater for chum fry entering Norton Sound during even-numbered years when relatively few pink salmon fry were present (Figs. 9 and 10). This effect was most apparent during the first 10 circuli increments, indicating the alternating pattern of chum salmon growth occurred during initial entry and residence in Norton Sound.

Cumulative growth during the first 10 circuli was significantly less for odd-year migrants for both age-0.3 (ANOVA: $df = 1, 17$; $F = 16.03$, $P < 0.001$) and age-0.4 chum salmon ($df = 1, 18$; $F = 4.99$, $P = 0.038$), smolt years 1979 to 2003 (Fig. 11). These years represent the period when pink salmon spawners and presumably their progeny were relatively abundant (Banducci et al. 2007). Growth of odd-year migrants was consistently less for age-0.3 chum salmon when all years of scale growth data were included (migration years 1972 to 2003; $df = 1, 23$, $F = 25.035$, $P < 0.001$) but not different for age-0.4 chum salmon ($df = 1, 23$, $F = 0.60$, $P > 0.05$). Total scale growth of age-0.3 and age-0.4 chum salmon during the first year at sea was not different between odd- and even-year migrants, 1979-2003. The effect of competition on incremental scale growth declined after circuli number 10 (Fig. 10), apparently reflecting dispersion of both chum and pink salmon into offshore areas of the Bering Sea.

The potential effect of competition with pink salmon fry on early marine growth of Kwiniuk chum salmon was further examined by plotting cumulative scale growth of chum salmon during the first 10 circuli pairs against peak aerial survey counts of Kwiniuk adult pink salmon during the parent spawning year. Early marine growth of Kwiniuk chum salmon (avg. age-0.3 and 0.4) was negatively correlated with Log_e of adult pink salmon abundance during the previous year ($n = 32$, $F = 8.33$, $P = 0.007$, serial autocorrelation = 0.021 ($P > 0.05$)). Approximately 22% of the annual variation in early marine growth was explained by adult pink salmon abundance during

the 32-year period (Fig. 12). Date of ice-out in Norton Sound, Nome spring air temperature, and SST in the North Pacific Ocean during winter and spring were not correlated with early marine chum growth ($P > 0.05$).

Odd- and even-year growth patterns of age-0.3 and age-0.4 chum salmon differed during the second (SW2) year at sea, but they were similar during the third year (SW3) and during homeward migration (Figs. 10, 11). During the second year at sea (SW2), growth of age-0.3 chum salmon scales tended to be greater during odd-numbered years ($P = 0.13$), whereas growth of age-0.4 chum salmon was significantly less during odd-numbered years at sea ($df = 1, 23, F = 4.698, P = 0.04$; Fig. 11). During the third year at sea, growth of age-0.3 salmon tended to be greater during odd-numbered years at sea (but not significant), and growth of age-0.4 chum salmon was significantly greater during odd-numbered years at sea ($df = 1, 23, F = 19.946, P < 0.001$). Scale growth of age-0.4 salmon during the fourth year at sea switched and tended to be less during odd-numbered years ($P = 0.24$). During the homeward migration, scale growth of both age groups tended to be greater during odd-numbered years, but the difference was not statistically significant ($P = 0.20, 0.24$, respectively).

Scale growth of Kwiniuk chum salmon was compared with abundance of immature pink salmon (fish maturing in following year) and maturing pink salmon returning to Eastern Kamchatka. Age-0.3 chum salmon scale growth during SW2 tended to be negatively correlated with immature Kamchatka pink salmon ($r = -0.31, P = 0.09$). Age-0.4 chum salmon scale growth during SW2 was negatively correlated with abundance of maturing pink salmon ($r = 0.38, P = 0.035$), and growth during SW3 was negatively correlated with abundance of immature pink salmon ($r = -0.44, P = 0.016$). No significant correlations between pink salmon and scale growth were observed during other life stages.

These data indicate that odd-year migrants that matured as age-4 salmon experienced reduced growth during early marine life but experienced above average growth during each subsequent year compared with even-year migrants (Fig. 10). In contrast, growth of age-0.3 chum salmon tended to be lower during even-numbered years at sea except during SW1. Kwiniuk chum salmon growth during SW2 and/or SW3 tended to be negatively correlated with Eastern Kamchatka pink salmon abundance. However, the scale growth correlation with Kamchatka pink salmon was weak compared with the correlation with Asian chum salmon abundance. Adult length-at-age of chum salmon sampled for scales in this study or extracted from the ADFG ASL database did not vary by odd- and even-numbered years at sea ($P > 0.05$).

Growth and Age at Maturation of Male and Female Salmon

Scale growth of age-0.3 chum salmon was significantly greater than that of age-0.4 chum salmon during each year at sea, including the homeward migration (Fig. 13; two factor ANOVA: age, gender: $df = 1, 108, P < 0.05$). Growth of male age-0.3 and age-0.4 salmon was significantly greater than that of female salmon during the third year at sea (SW3) and continued during all subsequent life stages, including adult length ($df = 1, 108, P < 0.05$).

Scale increments suggest that growth of age-0.3 male chum salmon exceeded that of age-0.4 male salmon immediately after entry to Norton Sound and continued thereafter (Fig. 14a).

Greater growth of age-0.3 versus age-0.4 chum salmon was greater for male versus female salmon, especially during SW1.

Scale growth increments of age-0.3 male chum salmon tended to be greater than that of female salmon beginning immediately after entry to Norton Sound and continuing throughout all life stages (Fig. 14b). In contrast, scale growth increments of male age-0.4 chum salmon tended to be somewhat smaller or similar to that of female salmon until SW3, when growth of male salmon increased significantly.

The percentage of age-0.3 chum returning from a parent spawning year (brood year) was positively correlated with scale growth of age-0.3 salmon during the third year at sea (SW3; $n = 30$, $F = 5.361$, $P = 0.028$). The amount of variability in age composition explained by scale growth was 16%.

These data show that sexual dimorphism in chum salmon began during early marine life, but greater growth of male salmon was most apparent among age-0.3 versus age-0.4 chum salmon. Faster growing chum salmon matured at an earlier age. The growth differential of earlier maturing chum salmon was detected soon after entry to Norton Sound and it continued throughout life.

Kwiniuk Chum Salmon Productivity

Productivity of Kwiniuk chum salmon averaged 1.8 adult salmon per spawner (R/S) since 1965, indicating productivity of the stock is relatively low (Table 2). A statistical model was developed to explain Log_e R/S of Kwiniuk chum salmon during brood years 1965-2001, as shown in the following equation (Fig. 15):

$$2) \text{Log}_e \text{R/S} = 12.97 - 1.118 (\text{Asian chum}) + 0.35 (\text{Marine productivity}) - 0.74 (\text{Escapement}) - 0.207 (\text{Pink salmon}).$$

Log_e R/S decreased with greater parent spawners (Log_e 1,000s; partial $P < 0.001$), decreased with greater mean adult abundance of Asian chum salmon two to four years after the Kwiniuk chum salmon brood year (Log_e millions; $P < 0.001$), decreased with greater adult abundance of Eastern Kamchatka pink salmon two years after the Kwiniuk chum salmon brood year (Log_e millions; $P = 0.019$), and increased with the aforementioned early marine productivity index ($P < 0.001$). These four variables explained 68% of the variability in Log_e R/S during the 37 year period (adjusted R^2 ; overall $P < 0.001$). Autocorrelation among residuals at lags of one to six years was non-significant ($P > 0.05$). Collinearity among the independent variables was negligible, as indicated by Variance Inflation Factor (VIF) values of 1.1-1.2. Regression corrected plots show that the relationships were linear and did not have outliers (Fig. 15). Standardized regression coefficients indicated that Asian chum salmon, chum spawning escapement, and marine productivity index had equal weight in explaining productivity of Kwiniuk chum salmon, whereas the effect of Kamchatka pink salmon was less.

Scale growth of age-0.3 chum salmon added significant new information to the aforementioned model of Kwiniuk chum salmon productivity (partial $P = 0.045$). Variability explained by this

model increased to 73% during the 33-year period when scale data were available (two years predicted from age-0.4 SW1 growth). However, autocorrelation among residuals was significant at a lag of six years ($P < 0.05$). Collinearity among independent variables remained low ($VIF = 1.1-1.4$). No new significant information was added to the model by other variables (e.g., SST, ice cover, Nome air temperature, Pribilof Island air temperature).

As noted in the Introduction, ice is believed to be an important factor contributing to the survival of Norton Sound chum salmon. Ice cover may protect migrating salmon fry from piscivorous birds, and it may stimulate zooplankton productivity in Norton Sound. A multivariate model was developed that incorporated available ice data:

$$3) \text{ Log}_e R/S = 4.01 + 0.49 (\text{Marine productivity}) - 0.57 (\text{Escapement}) \\ + 0.013 (\text{Ice-out date}),$$

where overall $P < 0.001$, $P (\text{Ice-out date}) = 0.026$, $P (\text{Marine productivity}) < 0.001$, and $P (\text{Log}_e 1,000s \text{ Escapement}) = 0.020$; serial autocorrelation $P > 0.05$. The model explained 57% of chum salmon variability during the 27-year period. Asian chum salmon abundance could be included in this model, however the P-value for ice-out date increased to 0.08 and that of Asian chum salmon was 0.07. In other words, Asian chum salmon explained slightly more variability than ice-out date within the 27-year period but neither variable was statistically significant at the $P = 0.05$ level when both were forced into the model. This model suggests that the presence of ice in Norton Sound had a positive effect on the productivity of Kwiniuk chum salmon. However, the previous model, which utilized Asian chum salmon, explained more variability in chum salmon productivity over a longer period of time (37 years).

Norton Sound Chum Salmon

A brood table that included most chum salmon in Norton Sound is shown in Table 3. Chum salmon Log_e recruits from parents ($r = 0.85$) and $\text{Log}_e R/S$ ($r = 0.76$) were highly correlated with that of Kwiniuk chum salmon (Fig. 16) even though Kwiniuk chum salmon represented only 10.7% of the total return of Norton Sound chum salmon, on average. Productivity (R/S) of Norton Sound chum salmon has been low since 1970 (avg. 1.4 R/S).

R/S of Norton Sound stocks produced by even-year broods was significantly higher than that from odd-year broods, 1970-2001 (differenced normalized values: $df = 1, 120$; $F = 7.085$, $P = 0.009$). This pattern was consistent among the subdistricts as indicated by the non-significant ANOVA interaction term ($P > 0.05$) when incorporating stock as an independent variable during preliminary analyses. The percentage of age-0.4 versus age-0.3 chum salmon produced by even-year broods was greater than that produced by odd-year broods ($df = 1, 120$; $F = 5.60$, $P = 0.020$). As described above, scale growth of age-0.4 chum salmon produced by even-year broods was greater than that of odd-year broods during each year at sea except for the first year when competition with Norton Sound pink salmon may have reduced scale growth of both age-0.4 and age-0.3 chum salmon (Fig. 11). The greater growth of age-0.4 salmon produced by even-year broods might have contributed to greater R/S from even-year broods.

Productivity of Norton Sound chum salmon was compared with the same variables that explained 68% of the variability of Kwiniuk chum salmon productivity during 1965-2001 brood years (Fig. 17):

$$4) \text{ Log}_e \text{ R/S} = 4.15 - 0.75 (\text{Asian chum}) + 0.29 (\text{Marine productivity}) - 0.003 (\text{Escapement}) - 0.004 (\text{Pink salmon}).$$

$\text{Log}_e \text{ R/S}$ decreased with greater parent spawners (1,000s; partial $P < 0.001$), decreased with greater mean adult abundance of Asian chum salmon two to four years after the Kwiniuk chum salmon brood year (Log_e millions; $P = 0.001$), decreased with greater adult abundance of Eastern Kamchatka pink salmon two years after the Kwiniuk chum salmon brood year (millions; $P = 0.029$), and increased with the aforementioned early marine productivity index ($P < 0.001$). These four variables explained 71% of the variability in $\text{Log}_e \text{ R/S}$ during the 32-year period (adjusted R^2 ; overall $P < 0.001$). Autocorrelation among residuals at lags of one to six years was non-significant ($P > 0.05$). Collinearity among the independent variables was negligible (VIF 1.1-1.3). Regression corrected plots show that the relationships were linear and the model did not have outliers (Fig. 17). Standardized regression coefficients indicated that the marine productivity index explained slightly more variability in chum salmon productivity, followed by spawning escapement, Asian chum salmon, and Eastern Kamchatka pink salmon. Other variables, including SST and Kwiniuk salmon scale growth, did not add significant new information to the model.

Kuskokwim and Unalakleet Coho Salmon

Scale Growth Trends

Trends in scale growth by life stage and adult length of Kuskokwim coho salmon are shown in Fig. 18 (by brood year) and Fig. 19 (by year of growth). FW1 and SW1 scale growth tended to be below average during brood years 1961-1974. FW1 scale growth tended to be above average from 1977 through the 1990 brood year and was variable thereafter. SW1 scale growth tended to be above average from late 1978 through the 2000 brood year. Long-term trends were not apparent among FW2 and SWPL life stages and adult length. SWPL was inversely correlated with SW1 ($r = -0.57$), suggesting the possibility of compensatory or “catch-up” growth. Adult length was positively correlated with SW1 ($r = 0.33$).

Scale growth measurements of Unalakleet coho salmon were available for a shorter period of time, i.e., beginning with the 1976 brood year (Figs. 20 and 21). FW1 scale growth tended to be above average during brood years 1976-1984 then below average from 1985-2000. Scale growth during the second year in freshwater was below average during 1976-1984 then primarily above average thereafter. SW1 scale growth was more random compared with previous life stages, but it tended to be below average during brood years 1976-1980 and 1993-1999. SWPL scale growth was above average during 1977-1982 then highly variable. Adult length of Unalakleet coho salmon did not exhibit a long-term trend. FW2 and FW1 were inversely correlated ($r = -0.41$), as was SW1 and FW2 (-0.45), suggesting the possibility of compensatory growth in Unalakleet coho salmon.

Scale growth of Kuskokwim coho salmon was positively correlated with that of Unalakleet coho salmon during FW1 ($r = 0.36$) and SWPL ($r = 0.40$) but not during FW2 and SW1, 1977-2006. Adult length-at-age (age-2.1) extracted from the ASL database was correlated between the two stocks ($r = 0.54$). Commercial catch of Kuskokwim coho salmon was positively correlated with catch of Unalakleet coho salmon, 1965-2007 ($r = 0.52$).

Scale Growth and Environmental Variables

Scale growth of Kuskokwim coho salmon during the first year at sea (SW1) was significantly correlated with SST in the North Pacific Ocean (Latitude: 48° to 59°N) during winter ($r = 0.46$) and spring ($r = 0.50$) prior to seaward migration, 1964-2005. SW1 was also correlated with the annual PDO ($r = 0.51$) and the Aleutian Low ($r = -0.44$). Growth during freshwater was not correlated with Bethel air temperature during May through September.

Scale growth of Unalakleet coho salmon, which was limited to years after the 1977 ocean regime shift, was not correlated with Nome air temperature during spring through summer, SST during winter through early summer, date of ice out in Norton Sound, or with the Aleutian Low and PDO indices. Commercial harvest of Unalakleet coho salmon was positively correlated with June SST during the year of harvest ($r = 0.48$), but harvest was not correlated with other environmental variables.

Interactions with Pink Salmon

Commercial catch of Kuskokwim and Unalakleet coho salmon were 49% and 33% greater during even- versus odd-numbered years, 1965-2007. Differenced catch values, which removed long-term trends and highlighted the alternating-year patterns (Fig. 22), were significantly greater during even-numbered years for both the Kuskokwim ($df = 1, 41$; $F = 12.694$; $P < 0.001$) and Unalakleet ($df = 1, 41$; $F = 9.360$; $P = 0.004$) stocks. Likewise, differenced Kuskokwim coho CPUE ($df = 1, 40$; $F = 8.760$; $P = 0.005$) and Unalakleet coho CPUE in the test fishery ($df = 1, 20$; $F = 8.509$; $P = 0.008$) were greater in even-numbered years. The alternating year patterns suggested coho salmon may interact with pink salmon, which have a two-year life cycle that leads to cyclic abundances.

Growth of juvenile coho produced by the more numerous even-year parents was significantly lower during both the first and second years in freshwater (Kuskokwim) or just in the first year (Unalakleet, Fig. 23, Table 1). During the FW1 stage, coho salmon were too small to consume pink salmon fry, but coho produced by odd-year broods may have had access to food provided by spawned-out pink salmon carcasses near the end of FW1, as suggested by cumulative scale growth of Kuskokwim coho salmon (Fig. 24). Kuskokwim coho produced by odd-year broods continued to have relatively greater growth during early FW2 (Figs. 23 and 24), possibly because they had access to pink salmon fry during spring. Alternatively, greater growth of odd-brood year coho salmon may reflect lower densities of coho salmon because fewer adult coho salmon return in odd-numbered years. Alternating-year growth of Unalakleet coho salmon was not apparent during FW2.

Progeny of even-year brood coho salmon in the Kuskokwim River experienced significantly greater growth during the first year at sea (SW1), a pattern that was not apparent among Unalakleet coho salmon (Fig. 23, Table 1). These coho entered the Bering Sea in odd-numbered years and may have consumed numerous pink salmon fry produced by the dominant even-year broods in western Alaska. However, examination of cumulative scale growth trends indicated that differential growth occurred during late SW1 growth (i.e., circuli 21-43) indicating Kuskokwim pink salmon fry were not likely a key factor in SW1 growth (Fig. 24). Both coho stocks exhibited a marked shift in growth during the latter portion of SW1. The ocean location in which this shift in growth occurs was unknown, but the distribution of tagged maturing coho salmon from western Alaska was south to 47°N and east to 145°W (tagged May to July; Myers et al. 1996). Therefore, AYK coho salmon likely crossed multiple ocean habitats during their first growing season at sea. Adult Kuskokwim coho returning in even-numbered years experienced significantly greater growth during SW1, and these fish were more abundant than those returning in odd-numbered years as noted above.

Most coho salmon return to the AYK region in August and scale growth and circuli counts during the homeward migration (SWPL) were approximately 60% less than during SW1. Kuskokwim and Unalakleet coho salmon produced by odd-year parents experienced greater growth during the homeward migration (Figs. 23 and 24; Table 1). Greater growth occurred during odd-numbered years at sea. Adult length of Kuskokwim and Unalakleet coho salmon (scale data and total ASL database) did not significantly differ between even- and odd-years of return, probably reflecting tradeoffs in growth during SW1 and SWPL (Fig. 23; Table 1).

Male versus Female Coho Salmon Length

Length of age-2.1 male coho salmon was not significantly different from female coho salmon (paired t-test using ASL database, $df = 66$, $P = 0.247$). It is noteworthy that size of male versus female Kuskokwim coho salmon significantly declined beginning with the 1997 El Niño through 2006 (Fig. 25; $df = 1, 38$; $F = 18.019$; $P < 0.001$), corresponding with the sharp decline in coho abundance beginning in 1997 (Fig. 22).

Kuskokwim Coho Salmon Productivity

CPUE of Kuskokwim coho salmon was positively correlated with scale growth during the first year in freshwater (FW1; $r = 0.47$) and during the first year at sea (SW1; $r = 0.55$) from 1965 to 2006 ($P < 0.001$). CPUE was not correlated with FW2 or SWPL ($P > 0.05$).

Residuals from the linear regression of CPUE on SW1 were typically low from 1965-1977, moderate from 1978-1988, high from 1989-1996, and low to average from 1997-2006. These periods of growth correspond with ocean regime shifts in 1977 and 1989 and the 1997/98 El Niño (Kruse 1998, Hare and Mantua 2000). Thus, the effects of ocean regime shifts on coho CPUE were tested using “dummy” variables, where the value was “1” within the shift period, or “0” otherwise.

Kuskokwim coho CPUE was explained by the following multivariate relationship (Fig. 26):

$$5) \text{ CPUE} = -15.43 + 12.192 (\text{SW1}) + 5.076 (\text{period 1977-1988}) + 8.345 (\text{period 1989-1996}),$$

which explained 67% (adjusted for independent variables) of coho CPUE variability during the past 41 years ($P(\text{SW1}) < 0.001$, $P(\text{Shift 1977-1988}) < 0.001$, $P(\text{Shift 1989-1996}) < 0.001$, autocorrelation $P > 0.05$). The model indicates that coho CPUE increased with greater growth during the first year at sea, and that CPUE also increased during 1977-1988 and further increased in 1989-1996, then declined to pre-1977 values beginning with the 1997 El Niño (Kruse 1998). Other scale growth variables (e.g., FW1), seasonal SST, Bering Sea ice cover index, and climate indices (Aleutian Low, PDO) did not add significant information to explain coho CPUE.

Coho salmon growth during the first year at sea (SW1) was positively correlated with the spawning biomass of pollock in the Bering Sea (NPFMC 2007) and with pink salmon abundance in Eastern Kamchatka (Ruggerone et al. 2008), 1964-2005. The multivariate model was (Fig. 27):

$$6) \text{ SW1 (mm)} = 1.527 + 0.104 (\text{pollock}) + 0.00172 (\text{pink salmon}).$$

Pollock spawning biomass (millions mt) and Eastern Kamchatka pink salmon abundance (millions of adults) explained 60% of the variability in coho scale growth during the first year at sea ($P(\text{Pollock}) < 0.001$; $P(\text{pink salmon}) = 0.012$). Autocorrelation among residuals at lags of one to six years was non-significant ($P > 0.05$). Collinearity among the independent variables was negligible (VIF 1.04). Standardized partial regression coefficients indicated pollock (0.68) explained much more of the variability in SW1 than pink salmon (0.28).

Models 5 and 6 suggested that coho CPUE was linked to pollock spawning biomass and pink salmon through their effects on growth. The effect of these variables on Kuskokwim coho CPUE is shown in the following multivariate equation (Fig. 28):

$$7) \text{ CPUE} = 0.643 + 2.4 (\text{Pollock}) + 3.6 (\text{period 1977-1988}) + 6.7 (\text{period 1989-1996}) \\ + 0.29 (\text{pink salmon}).$$

Model 7 explained 80% of coho CPUE variability during the past 41 years ($P(\text{Pollock}) < 0.001$, $P(\text{Shift 1977-1988}) < 0.001$, $P(\text{Shift 1989-1996}) < 0.001$, $P(\text{pink salmon}) = 0.043$). Autocorrelation among residuals at lags of one to six years was non-significant ($P > 0.05$) and collinearity among the independent variables was negligible (VIF 1.1-1.3). Standardized partial regression coefficients indicated that pollock (0.52) and the 1989 regime shift (0.50) explained most of the variability in CPUE followed by the 1977 regime shift (0.31) and pink salmon (0.16). Seasonal SST did not add significant information to the model ($P > 0.05$).

These models suggest coho salmon, which are highly piscivorous (Farley et al. 2008), grew faster during their first year at sea when pollock spawning biomass was high and many larval pollock were likely available. Ocean regime shifts in 1977 and in 1989 led to progressively greater coho CPUE followed by markedly lower CPUE during and after the 1997 El Niño (Fig. 22). The positive correlation of coho CPUE with Eastern Kamchatka pink salmon abundance was the opposite of that observed in Bristol Bay sockeye salmon (Ruggerone et al. 2003, 2005) but

consistent with alternating-year growth of AYK Chinook salmon (Ruggerone et al. 2007a). Presumably, the positive correlation of coho CPUE and Asian pink salmon abundance reflects the higher trophic level of coho (and Chinook) salmon versus pink and sockeye salmon and a cascading trophic effect caused by numerous Asian pink salmon.

Unalakleet Coho Salmon Productivity

Commercial catch of Unalakleet coho salmon (1980-2006) was not correlated with scale growth during each life stage or with adult length-at-age ($P > 0.05$). Catch of Unalakleet coho salmon (1965-2006) was positively correlated with catch of Kuskokwim coho salmon ($r = 0.52$), December to March SST ($r = 0.41$) and June SST ($r = 0.48$) in the North Pacific Ocean, annual PDO index ($r = 0.34$), and North Pacific Index (April-July; $r = 0.32$). These variables explained less than 27% of the variability in Unalakleet coho catch during the past 41 years.

CPUE of Unalakleet coho salmon in the test fishery (1985-2004) was positively correlated with abundance of Eastern Kamchatka pink salmon abundance during the previous year ($r = 0.63$) and negatively correlated with scale growth during the homeward migration (SWPL; $r = -0.53$) but only when the exceptionally high CPUE during 2005-2007 was excluded. The relationship with pink salmon was consistent with that between SW1 scale growth and pink salmon. Other scale growth variables, environmental variables and local pink salmon indices were not correlated with CPUE of Unalakleet coho salmon.

CONCLUSIONS

Kwiniuk Chum Salmon

- 1) Early marine growth of age-0.3 and age-0.4 Kwiniuk chum salmon was less during odd-numbered years, i.e., years when pink salmon fry were relatively abundant in Norton Sound. Early marine growth of Kwiniuk chum salmon was inversely correlated with abundance of adult Kwiniuk pink salmon during the previous year, indicating competition for prey between chum and pink salmon during early marine life.
- 2) Odd- and even-year growth of age-0.3 and age-0.4 chum salmon differed during the second (SW2) year at sea, suggesting migration pattern and/or diet may vary between the two age groups.
- 3) Scale growth of age-0.3 chum salmon was significantly greater than that of age-0.4 chum salmon during each year at sea, including the homeward migration. The percentage of age-0.3 chum returning from a parent spawning year (brood year) was positively correlated with scale growth of age-0.3 salmon during the third year at sea (SW3). Male salmon grew faster than female chum salmon.
- 4) Length-at-age and SW2 growth of Kwiniuk chum salmon was inversely related to abundance of Asian hatchery chum salmon and total Asian chum salmon.

- 5) Productivity of Kwiniuk chum salmon (R/S) decreased with greater parent spawners, decreased with greater adult abundance of Asian chum salmon, decreased with greater adult abundance of Eastern Kamchatka pink salmon, and increased with an index of early marine productivity. These variables explained 68% of the variability in productivity during the past 37 years.

Norton Sound Chum Salmon

- 1) Productivity (R/S) and adult recruits of Norton Sound chum salmon were highly correlated with that of Kwiniuk chum salmon, suggesting common factors affect all Norton Sound chum salmon stocks.
- 2) Like Kwiniuk chum salmon, productivity of Norton Sound chum salmon (R/S) decreased with greater parent spawners, decreased with greater adult abundance of Asian chum salmon, decreased with greater adult abundance of Eastern Kamchatka pink salmon, and increased with an index of early marine productivity. These variables explained 71% of the variability in productivity during the past 32 years.
- 3) The findings involving Kwiniuk and Norton Sound chum salmon indicated that competition with Asian chum salmon (dominated by hatchery salmon) and pink salmon from Norton Sound and Kamchatka may have adversely affected productivity of Norton Sound chum salmon.

Kuskokwim and Unalakleet Coho Salmon

- 1) Commercial catch of Kuskokwim and Unalakleet coho salmon were 49% and 33% greater during even- versus odd-numbered years, 1965-2007, providing evidence for interaction with alternating-year abundances of pink salmon.
- 2) Scale growth of juvenile Kuskokwim and Unalakleet coho salmon produced by the less numerous odd-year parents was significantly greater during the first (FW1) of two years in freshwater. These juvenile coho salmon may have benefited from reduced density of juvenile coho salmon and prey associated with pink salmon carcasses during late summer and fall.
- 3) Scale growth of juvenile Kuskokwim coho salmon during the second year in freshwater was significantly greater during odd-numbered years when numerous pink salmon fry would have been produced by adult pink salmon returning in even-numbered years.
- 4) Scale growth of juvenile Kuskokwim coho salmon during the first year at sea was significantly greater during odd-numbered years; however, greater scale growth occurred primarily during late summer when encounter rates with young pink salmon fry would have been minimal. Greater scale growth may be related to a cascading trophic effect caused by Russian pink salmon, but new research is needed to test this hypothesis.

- 5) Catch per unit effort (CPUE) of Kuskokwim coho salmon in the commercial fishery was positively correlated with scale growth during the first year at sea (SW1), 1965 to 2006. A multivariate analysis indicated SW1 growth, ocean climate shifts in 1977 and 1989, and the 1997 El Niño significantly affected CPUE of Kuskokwim coho salmon, explaining 67% of coho CPUE variability during the past 41 years.
- 6) SW1 growth of coho salmon was positively influenced by abundance of spawning pollock, which provide prey (larvae) for coho salmon. Approximately 80% of the variability in CPUE of Kuskokwim coho salmon was explained when SW1 growth was replaced with the pollock variable in the multivariate model.
- 7) These findings indicated that pink salmon and pollock may have a beneficial effect on growth and abundance of coho salmon.

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REFERENCES

- Alverson, D.L. 1992. A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. *Reviews in Aquatic Sciences* 6:203-256.
- Anderson, P.J. and J.F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189:117-123.
- Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative (AYK SSI). 2006. Arctic-Yukon-Kuskokwim Salmon Research and Restoration Plan. Bering Sea Fishermen's Association, 705 Christensen Drive, Anchorage, AK.
- Banducci, A., T. Kohler, J. Soong, and J. Menard. 2007. 2005 annual management report Norton Sound, Port Clarence, and Kotzebue. Alaska Department of Fish and Game, Fishery Management Report No. 07-32, Anchorage, AK.
- Brannian, L.K., M.J. Evenson, and J.R. Hilsinger. 2006. Escapement goal recommendations for select Arctic-Yukon-Kuskokwim region salmon stocks, 2007. Alaska Department of Fish and Game, Fishery Manuscript No. 06-07, Anchorage, AK (with 2-15-2007 revision)
- Davis, N.D., M. Fukuwaka, J.L. Armstrong, and K.W. Myers. 2005. Salmon food habits studies in the Bering Sea, 1960 to present. North Pacific Anadromous Fish Commission Technical Report 6:24-28.

Davis, N.D., J.L. Armstrong, and K.W. Myers. 2004. Bering Sea salmon diet overlap in fall 2002 and potential for interactions among salmon. North Pacific Anadromous Fish Commission Document 779.

Farley, E.V., J. Murphy, Jr., J. Moss, A. Feldman, and L. Eisner. 2008. Juvenile western Alaska salmon research along the Eastern Bering Sea shelf, August 2 – October (2002 – 2006). Proceedings of the 2007 AYK SSI Symposium, Anchorage, AK. In review.

Fisher, J.P. and W.G. Pearcy. 2005. Seasonal changes in growth of coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington and concurrent changes in the spacing of scale circuli. Fishery Bulletin 103:34-51.

Fukuwaka, M., and M. Kaeriyama. 1997. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. Canadian Journal Fisheries and Aquatic Sciences 54:631-636.

Gaudet, D.M. and G. Schaefer. 1982. Migrations of salmon in Norton Sound, Alaska determined by tagging in 1978-1979. Alaska Department of Fish and Game Informational Leaflet no. 198. Anchorage, AK.

Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103-146.

Hilborn, R., R. Lessard, D. Goodman, B. Bue, M. Adkison, J. Stanford, D. Whited, and E. Knudsen. 2007. Alternative methods for setting escapement goals in AYK. Prepared for the Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project.

Holt, C.A., M.B. Rutherford, and R.M. Peterman. 2008. International cooperation among nation-states of the North Pacific Ocean on the problem of competition among salmon for a common pool of prey resources. Marine Policy 32:607-617.

Hunt, G.L., P. Stabeno, G. Walters, E. Sinclair, R.D. Brodeur, J.M. Napp, and N.A. Bond. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Research Part II 49:5821-5853.

Joy, P. and D.J. Reed. 2007. Estimation of coho salmon abundance and spawning distribution in the Unalakleet River 2004 - 2006. Alaska Department of Fish and Game, Fishery Data Series No. 07-48, Anchorage, AK.

Kent, S. 2007. Salmonid escapements at Kwiniuk, Niukluk and Nome Rivers, 2006. Alaska Department of Fish and Game, Fishery Data Series No. 07-09, Anchorage, AK.

Koo, T.S., 1962. Studies of Alaska Red Salmon. University of Washington Press, Seattle.

Kruse, G.H. 1998. Salmon run failures in 1997-1998: a link to anomalous ocean conditions? Alaska Fishery Research Bulletin 5:55-63.

Larsen, W.A. and S.J. McCleary. 1972. The use of partial residual plots in regression analysis. *Technometrics* 14:781-790.

Mantua, N.J., S.R. Hare, Y., Zhang, J.M., Wallace, and R.C., Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin American Meteorological Society* 78:1069-1079.

Menard, J. and D.J. Bergstrom. 2006. Norton Sound Golovin and Moses Point Subdistricts chum salmon stock status and action plan, 2007; a report to the Alaska Board of Fisheries. Alaska Department of Fish and Game, Special Publication No. 06-32, Anchorage, AK.

Myers, K.W., K.Y. Aydin, R.V. Walker, S. Fowler and M.L. Dahlberg. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956-1995. North Pacific Anadromous Fish Commission Document 192.

Myers, K.W., R.V. Walker, N.D. Davis, and J.L. Armstrong. 2004. Diet Overlap and competition between Yukon River chum salmon and hatchery salmon in the Gulf of Alaska in summer. Final Report to the Yukon River Drainage Fisheries Association. SAFS-UW-0407. School of Aquatic and Fisheries Sciences, University of Washington, Seattle.

North Pacific Fishery Management Council (NPFMC). 2007. Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. Prepared for the North Pacific Fishery Management Council, Anchorage, AK.
<http://www.afsc.noaa.gov/refm/stocks/assessments.htm>

Overland, J.E. and P.J. Stabeno. 2004. Is the climate of the Bering Sea warming and impacting the ecosystem? *Eos, Transactions of the American Geophysical Union* 85:309-310.

Pyper, B.J., F.J. Mueter, and R.M. Peterman. 2005. Across-species comparisons of spatial scales of environmental effects on survival rates of northeast Pacific salmon. *Transactions of the American Fisheries Society* 134:86-104.

Rogers, D.E. 1984. Trends in abundance of Northeastern Pacific stocks of salmon. Pp. 100-127 in Percy, W.G. (ed.), *The influence of ocean conditions on the production of salmonids in the North Pacific*. Oregon State University Press, Corvallis.

Ruggerone, G.T. and F. Goetz. 2004. Survival of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*O. gorbuscha*). *Canadian Journal Fisheries and Aquatic Sciences* 61:1756-1770.

Ruggerone, G.T., and J.L. Nielsen. 2004. Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Reviews in Fish Biology and Fisheries* 14:371-390.

- Ruggerone, G.T. and M.L. Link. 2006. Collapse of Kvichak sockeye salmon production during brood years 1991-1999: population characteristics, possible factors, and management implications. Prepared for North Pacific Research Board and the Bristol Bay Science and Research Institute. Anchorage, AK. (http://doc.nprb.org/web/03_prjs/r0321_final1.pdf)
- Ruggerone, G.T., M. Zimmermann, K.W. Myers, J.L. Nielsen, and D.E. Rogers. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fisheries Oceanography* 12:3:209-219.
- Ruggerone, G.T., E. Farley, J. Nielsen, and P. Hagen. 2005. Seasonal marine growth of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) in relation to competition with Asian pink salmon (*O. gorbuscha*) and the 1977 ocean regime shift. *Fishery Bulletin* 103:2:355-370.
- Ruggerone, G.T., J.L. Nielsen, and B. Agler. 2007a. Retrospective analysis of AYK Chinook salmon growth. Prepared for the Arctic Yukon Kuskokwim Sustainable Salmon Initiative, Anchorage, AK. (http://www.aykssi.org/docs/Project_Docs/Final_Reports/107.pdf)
- Ruggerone, G.T., J.L. Nielsen, and J. Bumgarner. 2007b. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955-2002. *Deep Sea Research II* 54:2776-2793.
- Ruggerone, G.T., R.M. Peterman, B. Dorner, and K.W. Myers. 2008. Abundance and relative contribution of hatchery and wild pink, chum, and sockeye salmon in the North Pacific Ocean. In review.
- Salo, E.O. 1991. Life history of chum salmon (*Oncorhynchus keta*). Pp. 231-309 in C. Groot and L. Margolis (eds.), *Pacific Salmon Life Histories*. University of British Columbia, Vancouver.
- Smoker, W.W. 1984. Genetic effect on the dynamics of a model of pink salmon (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon. *Canadian Journal Fisheries and Aquatic Sciences* 41:1446-1453.
- Ward, T.C., M. Coffing, J.L. Estensen, R.L. Fisher, and D.B. Molyneaux. 2003. Annual management report for the subsistence and commercial fisheries of the Kuskokwim Area 2002. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A03-27, Anchorage, AK.
- Whitmore, C., M. Martz, J.C. Linderman Jr., R.L. Fisher, and D.G. Bue. 2008. Annual management report for the subsistence and commercial fisheries of the Kuskokwim area, 2004. Alaska Department of Fish and Game, Fisheries Management Report No. 08-25, Anchorage, AK.
- Woodruff, S.D., H.F. Diaz, J.D. Elms, and S.J. Worley. 1998. COADS Release 2 Data and Metadata Enhancements for Improvements of Marine Surface Flux Fields. *Physics and Chemistry of Earth* 23:517-527.

Table 1. Analysis of Variance (ANOVA) to test for scale growth and adult body length differences between even- and odd-numbered years of Kwiniuk chum salmon (A) and Kuskokwim and Unalakleet coho salmon (B). Mean growth values are shown in Figs. 11 and 21. Tests were conducted on differenced values.

A:	Life stage	Age-0.3 chum salmon				Age-0.4 chum salmon			
		n	F-value	P-value	Larger growth year	n	F-value	P-value	Larger growth year
	SW1 ₁₋₁₀	19	16.031	< 0.001	Even	20	4.988	0.038	Even
	SW1	25	4.158	0.053	Even	25	0.676	0.418	
	SW2	25	2.353	0.139		25	4.698	0.041	Even
	SW3	25	0.879	0.358		25	19.946	< 0.001	Odd
	SW4	NA				25	1.44	0.242	
	SWPL	25	1.728	0.202		25	1.446	0.242	
	Length (scales)	25	2.541	0.125		25	0.029	0.865	
	Length (ASL)	29	1.375	0.251		29	0.096	0.759	

B:	Life stage	Kuskokwim coho salmon				Unalakleet coho salmon			
		n	F-value	P-value	Larger growth year	n	F-value	P-value	Larger growth year
	FW1*	36	4.575	0.037	Even	26	4.575	0.037	Even
	FW2	36	5.594	0.024	Odd	26	0.099	0.826	
	SW1	36	12.133	0.001	Odd	26	1.284	0.268	
	SWPL*	36	33.662	< 0.001	Odd	26	33.662	< 0.001	Odd
	Length (scales)*	36	1.217	0.274		26	1.217	0.274	
	Length (ASL)*	36	2.815	0.099		36	2.815	0.099	

* Two factor ANOVA (stock, stage: df = 1, 58). Interaction effect was non-significant (P > 0.05).

Table 2. Brood table for Kwiniuk chum salmon in the Moses Point subdistrict of Norton Sound, Alaska. Source: T. Hamazaki (ADFG).

Year	Spawning		Total Run	Age Specific Recruits:				Total Recruits	R/S
	Escap.	Harvest		Age 0.2	Age 0.3	Age 0.4	Age 0.5		
1965	29,575	5,109	34,684	1,869	27,639	1,927	0	31,434	1.1
1966	31,381	22,545	53,926	860	81,256	15,247	183	97,546	3.1
1967	23,327	5,154	28,481	586	47,901	34,286	324	83,098	3.6
1968	19,134	11,502	30,636	381	9,442	14,754	399	24,977	1.3
1969	19,315	10,341	29,655	1,925	30,589	17,348	0	49,863	2.6
1970	67,438	16,331	83,769	8,377	40,014	4,494	207	53,091	0.8
1971	38,304	25,226	63,530	8,707	29,706	9,075	309	47,798	1.2
1972	29,996	15,841	45,837	103	5,475	6,601	208	12,386	0.4
1973	28,519	25,526	54,045	0	38,883	18,603	0	57,486	2.0
1974	35,325	31,144	66,468	5,776	31,594	10,706	116	48,192	1.4
1975	14,175	20,128	34,303	1,559	30,326	2,759	98	34,743	2.5
1976	6,462	8,295	14,757	625	25,007	16,579	1,904	44,115	6.8
1977	22,367	29,201	51,568	1,162	32,174	23,923	966	58,225	2.6
1978	20,592	31,372	51,964	344	55,379	38,737	703	95,163	4.6
1979	11,957	29,700	41,657	1,573	67,173	20,424	131	89,301	7.5
1980	18,908	10,136	29,044	429	35,489	4,061	159	40,137	2.1
1981	33,626	15,570	49,196	1,529	8,842	17,012	645	28,029	0.8
1982	42,920	39,858	82,778	65	19,517	13,426	517	33,525	0.8
1983	56,229	51,076	107,305	3,061	11,619	7,493	768	22,940	0.4
1984	53,365	4,758	58,123	129	17,570	10,881	505	29,085	0.5
1985	8,697	4,402	13,099	258	3,115	5,218	0	8,591	1.0
1986	24,046	15,703	39,749	0	10,940	12,111	0	23,051	1.0
1987	15,475	10,345	25,819	168	8,416	8,434	488	17,507	1.1
1988	12,643	13,196	25,838	0	3,969	9,601	674	14,244	1.1
1989	13,623	1,141	14,764	0	6,183	11,124	1,773	19,080	1.4
1990	13,298	3,534	16,831	0	21,911	17,726	1,443	41,080	3.1
1991	18,913	1,614	20,527	0	24,817	14,137	228	39,182	2.1
1992	11,657	747	12,404	0	13,272	10,489	130	23,891	2.0
1993	15,278	994	16,272	0	12,085	5,511	71	17,668	1.2
1994	31,678	2,031	33,710	0	20,226	4,619	40	24,885	0.8
1995	41,445	2,871	44,316	130	4,191	1,707	172	6,199	0.1
1996	27,880	972	28,852	36	11,690	15,240	383	27,349	1.0
1997	19,575	3,226	22,801	0	1,304	2,525	76	3,905	0.2
1998	23,867	2,131	25,997	446	35,278	8,100	210	44,034	1.8
1999	8,515	401	8,916	77	4,321	3,055	61	7,514	0.9
2000	12,487	950	13,437	101	6,783	2,074	177	9,135	0.7
2001	16,299	864	17,163	451	9,395	9,648	0	19,494	1.2
2002	37,511	751	38,262						
2003	11,561	1,036	12,597						
2004	10,134	365	10,499						
2005	11,884	317	12,201						
2006	39,114	629	39,743						
Avg.	24,488	11,358	35,846	1,101	22,797	11,612	380	35,890	1.8

Table 3. Brood table for chum salmon in Norton Sound, Alaska. Values exclude salmon returning to Norton Bay and Shaktoolik subdistricts. See data cautions in methods section.

Year	Spawning Escap.	Harvest	Total Run	Age Specific Recruits:				Total Recruits	R/S
				Age 0.2	Age 0.3	Age 0.4	Age 0.5		
1965									
1966									
1967									
1968									
1969									
1970	604,605	108,527	713,132	36,491	210,452	52,801	8,570	308,314	0.5
1971	383,322	131,649	514,971	33,656	354,020	156,352	5,467	549,495	1.4
1972	177,747	89,644	267,391	26,213	69,031	100,492	4,104	199,840	1.1
1973	211,588	105,587	317,175	629	285,315	168,368	2,562	456,874	2.2
1974	225,874	134,749	360,623	28,422	290,711	78,831	844	398,808	1.8
1975	280,042	152,993	433,035	8,845	178,895	43,404	560	231,704	0.8
1976	154,372	80,210	234,582	3,569	350,796	180,424	8,618	543,406	3.5
1977	247,032	172,663	419,695	12,178	277,838	106,392	4,035	400,443	1.6
1978	330,083	141,945	472,028	1,961	212,589	199,785	8,835	423,171	1.3
1979	151,791	112,065	263,856	6,145	315,274	203,418	4,466	529,304	3.5
1980	245,075	162,147	407,222	3,229	381,792	140,140	3,851	529,012	2.2
1981	294,107	166,676	460,783	14,610	227,900	154,973	8,416	405,898	1.4
1982	168,848	164,897	333,745	1,346	164,340	158,382	5,618	329,686	2.0
1983	268,367	253,956	522,323	17,845	139,301	89,262	5,375	251,784	0.9
1984	482,186	126,416	608,602	2,024	175,684	120,839	5,880	304,427	0.6
1985	244,116	129,736	373,852	2,203	81,394	87,711	744	172,052	0.7
1986	189,210	151,798	341,009	0	127,710	151,696	5,564	284,970	1.5
1987	200,025	108,098	308,123	2,822	179,836	170,526	17,690	370,874	1.9
1988	172,969	99,797	272,767	0	40,201	156,554	6,860	203,615	1.2
1989	174,098	33,510	207,608	655	102,761	115,245	25,107	243,768	1.4
1990	161,580	62,542	224,123	509	189,782	173,354	34,030	397,675	2.5
1991	257,706	74,570	332,277	273	168,679	166,068	7,341	342,362	1.3
1992	146,628	70,317	216,946	740	111,531	152,818	1,134	266,222	1.8
1993	229,912	47,602	277,514	0	126,590	52,781	1,146	180,518	0.8
1994	280,064	32,097	312,161	941	167,141	51,284	427	219,793	0.8
1995	308,357	59,524	367,881	1,436	69,201	40,575	5,032	116,243	0.4
1996	280,783	30,846	311,629	931	90,428	147,621	3,253	242,233	0.9
1997	243,000	44,689	287,689	228	44,515	30,262	290	75,294	0.3
1998	201,285	21,207	222,492	3,101	168,423	36,958	618	209,100	1.0
1999	102,085	20,477	122,562	4,248	97,566	67,092	2,437	171,343	1.7
2000	118,102	13,556	131,658	386	50,004	23,401	3,480	77,272	0.7
2001	176,772	23,497	200,269	8,675	159,701	88,389	1,711	258,476	1.5
2002	192,800	13,385	206,185						
2003	126,611	8,589	135,200						
2004	118,005	8,383	126,388						
2005	186,816	7,951	194,767						
2006	286,898	12,311	299,209						
Avg.	233,050	85,908	318,959	7,010	175,294	114,569	6,065	302,937	1.4

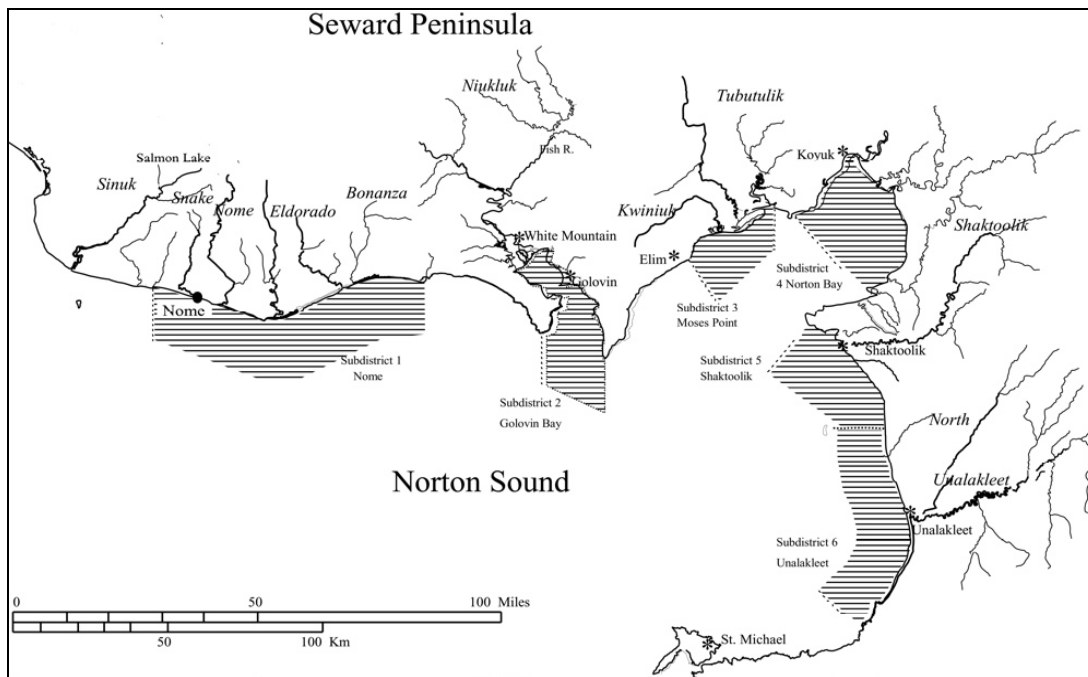


Fig. 1. Map of salmon fishing districts in Norton Sound and the location of Kwiniuk (Moses Point) and Unalakleet rivers. Source: Menard and Bergstrom (2006).



Fig. 2. Map of salmon fishing districts in the Kuskokwim area. Districts W-1 and W-2 are within the Kuskokwim River. Source: Whitmore et al. (2008).

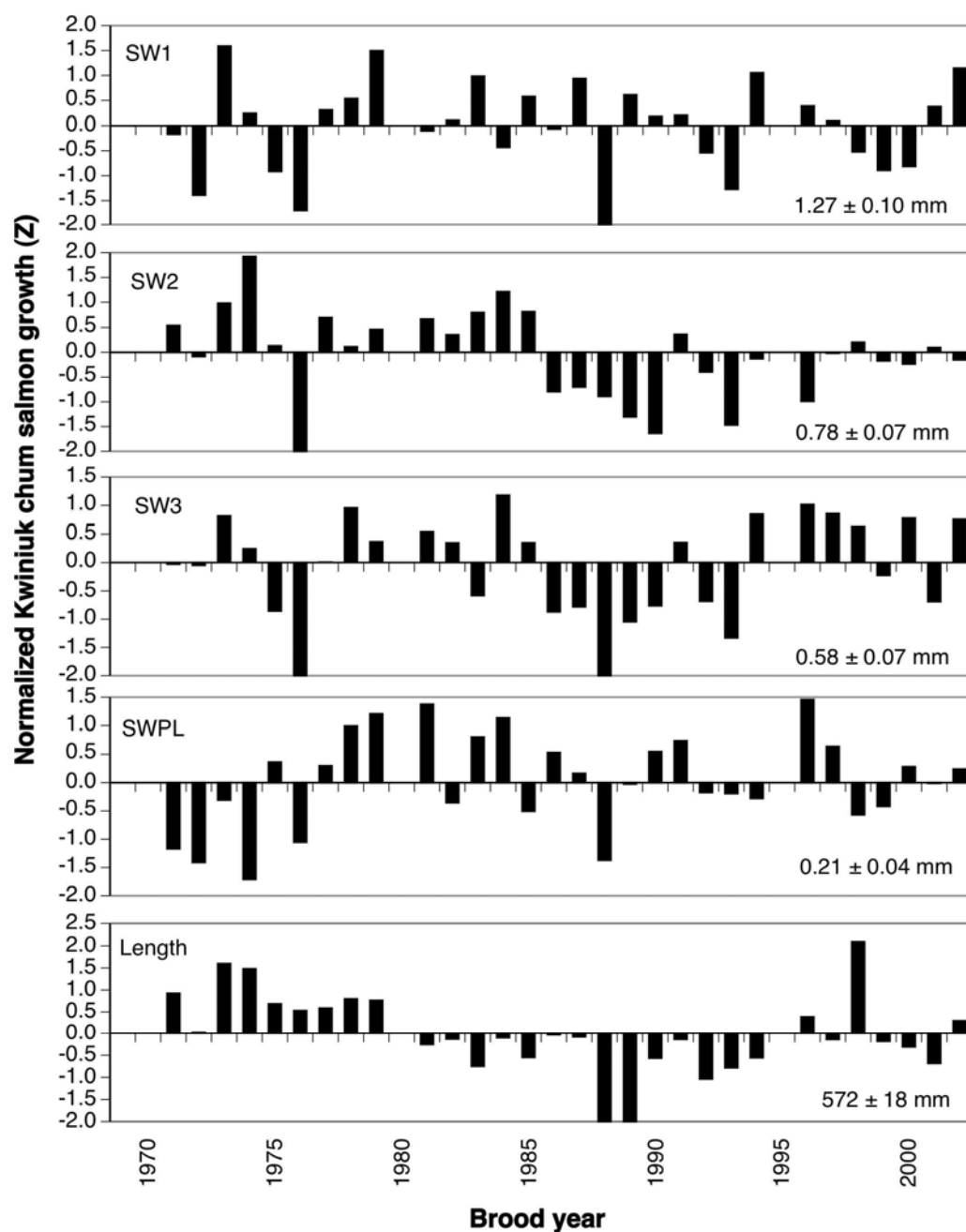


Fig. 3. Mean annual growth of age-0.3 Kwiniuk chum salmon during each life stage, brood years 1971-2002. Life-stage growth organized by brood year is based on individuals produced by the same parents. Values are standard deviations above and below the long-term mean. Unweighted mean \pm 1 SD during each stage is shown.

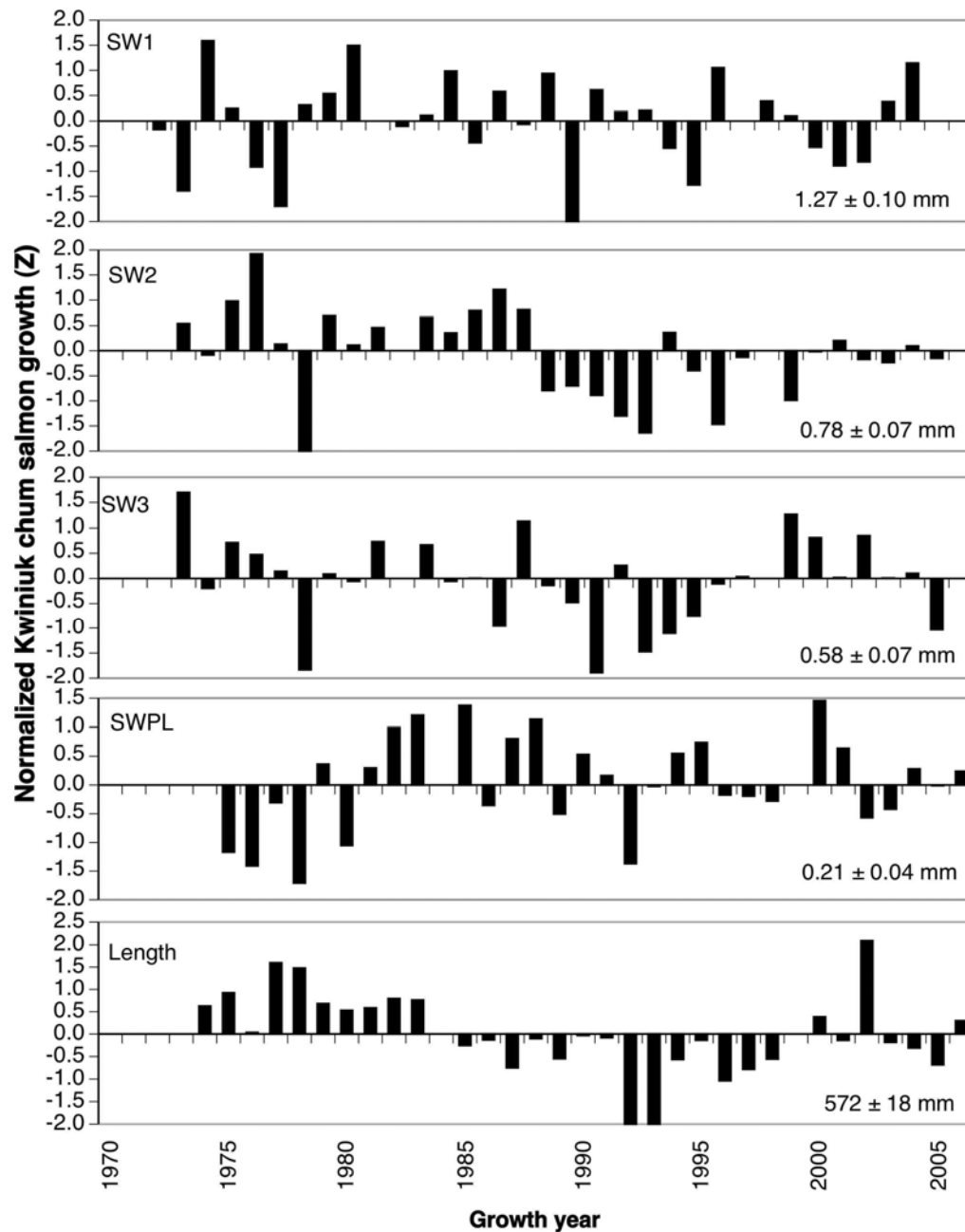


Fig. 4. Mean annual growth of age-0.3 Kwiniuk chum salmon during each life stage, growth years 1973-2006. Life stage growth organized by growth year is based on fish of different ages co-occurring in the ocean during the same year. Values are standard deviations above and below the long-term mean. Unweighted mean \pm 1 SD during each stage is shown.

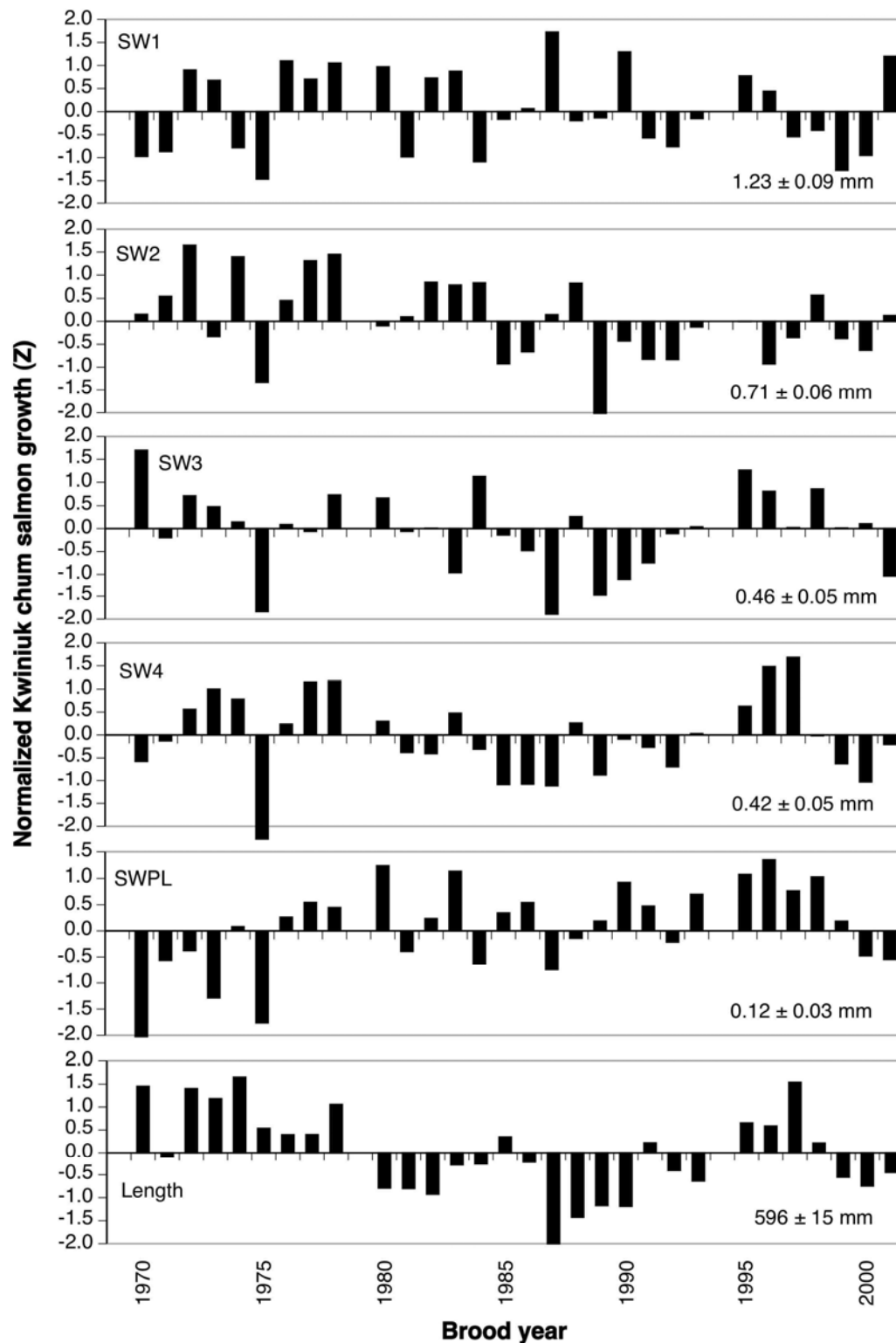


Fig. 5. Mean annual growth of age-0.4 Kwiniuk chum salmon during each life stage, brood years 1970-2001. Values are standard deviations above and below the long-term mean. Unweighted mean \pm 1 SD during each stage is shown.

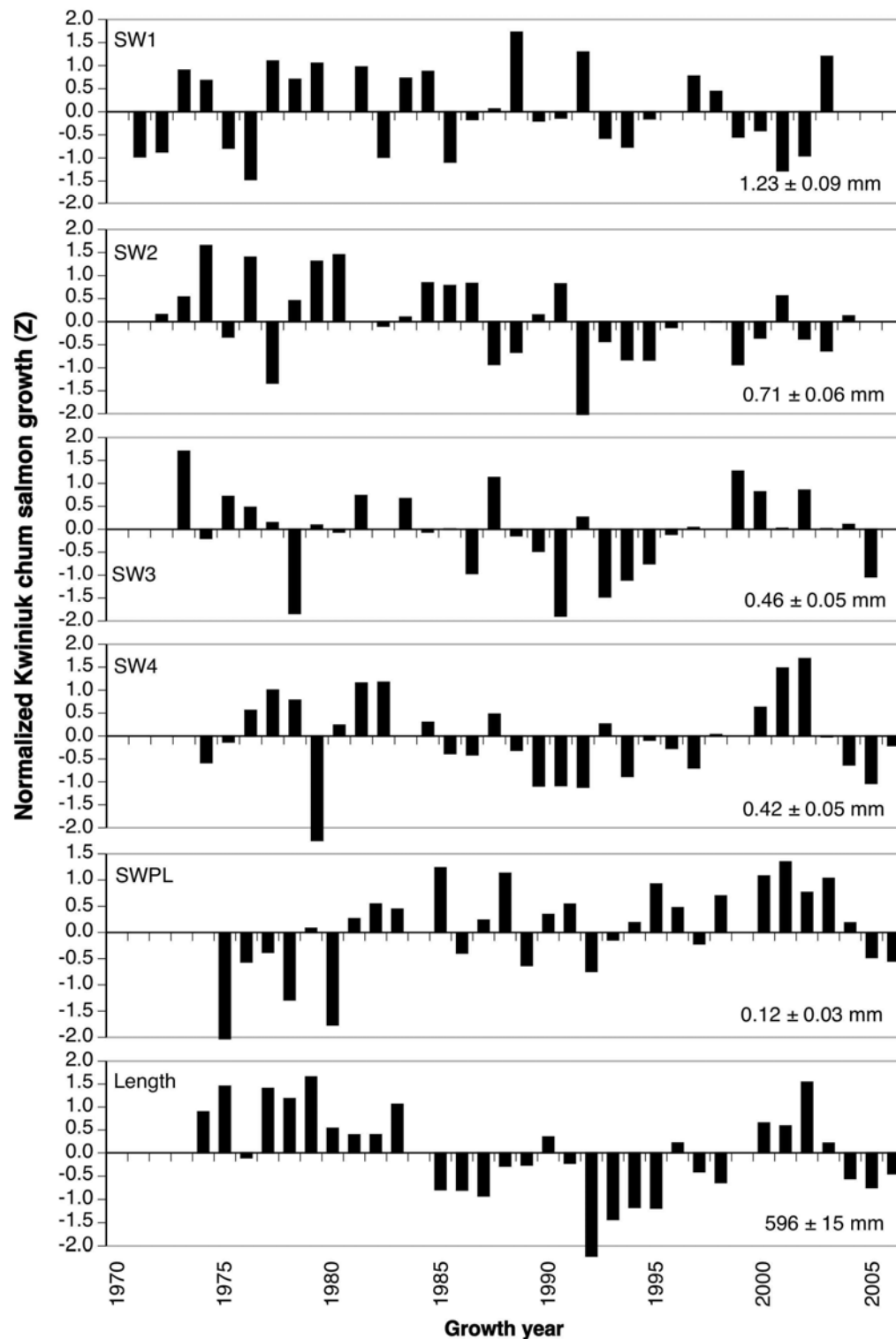


Fig. 6. Mean annual growth of age-0.4 Kwiniuk chum salmon during each life stage, growth years 1971-2006. Values are standard deviations above and below the long-term mean. Unweighted mean \pm 1 SD during each stage is shown.

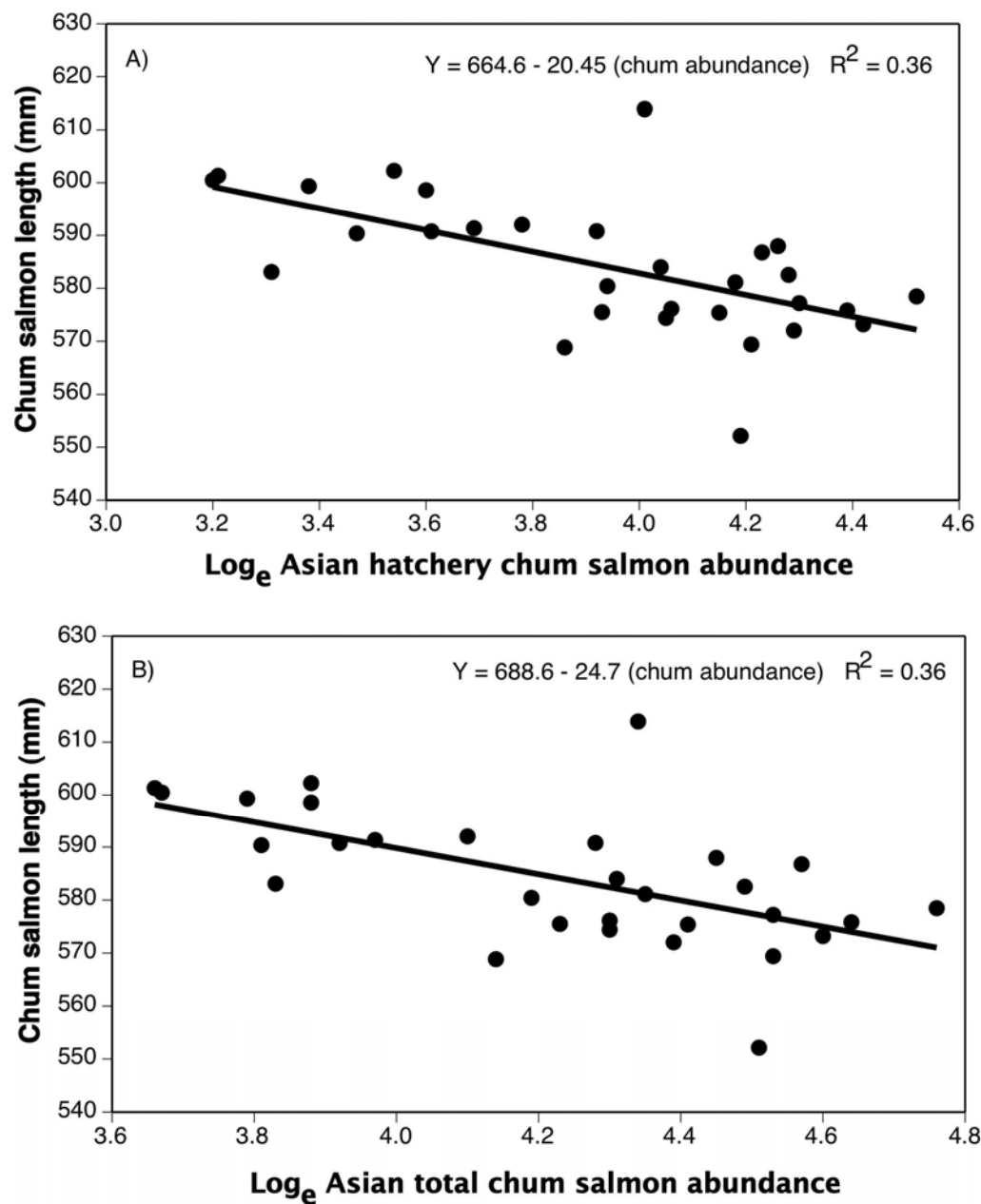


Fig. 7. Mean length-at-age of Kwiniuk chum salmon in relation to A) abundance of Asian hatchery chum salmon and B) total Asian chum salmon during the same year of return, 1974-2005. Asian salmon abundances are Log_e millions of fish.

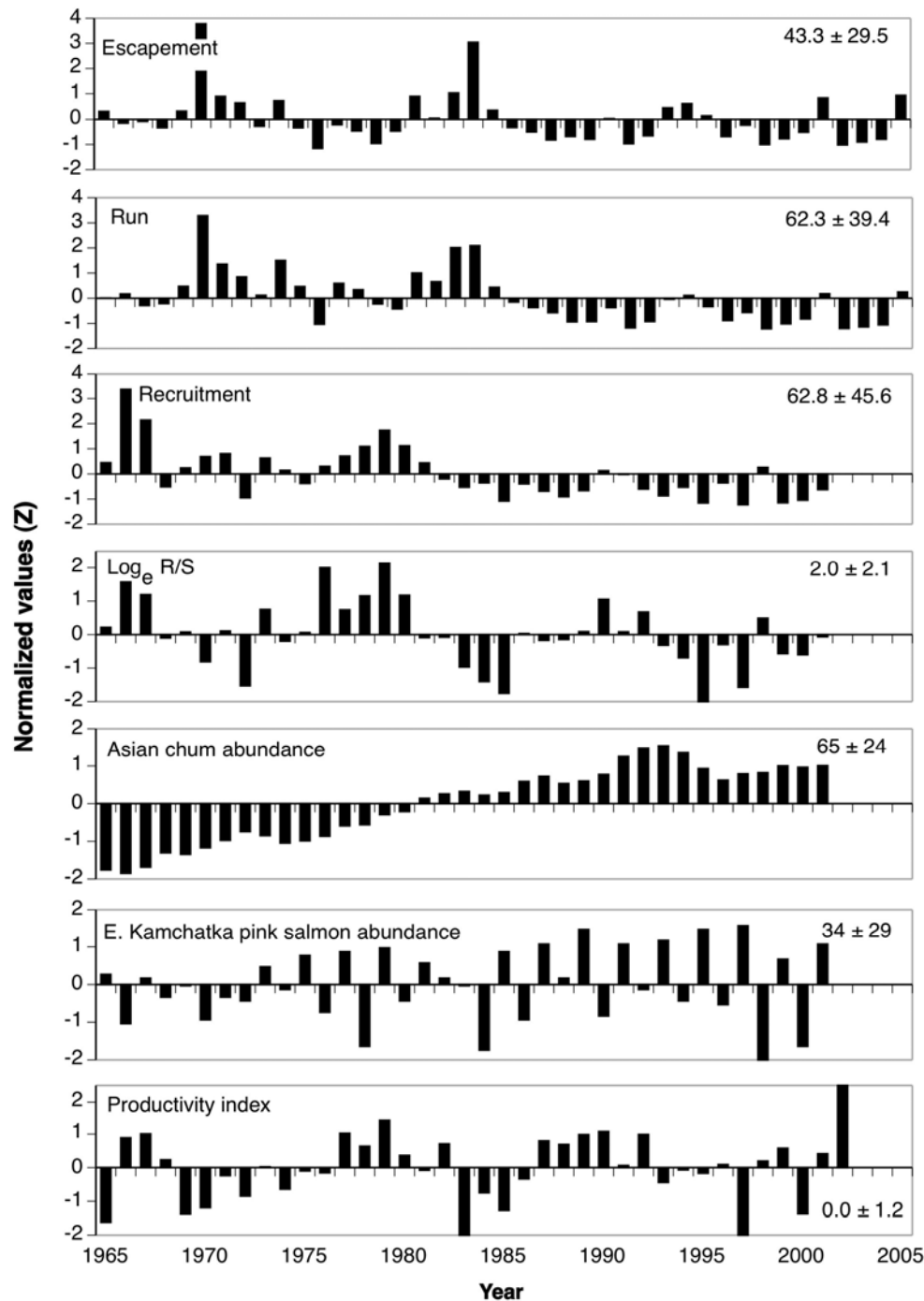


Fig. 8. Normalized statistics of Kwiniuk chum salmon production (1,000s of fish), Asian chum salmon abundance, Eastern Kamchatka pink salmon abundance, and an early marine life productivity index. Asian chum salmon is the moving mean adult abundance two to four years later, Kamchatka pink salmon abundance is the adult return two years later. Productivity index is the residual of Kwiniuk pink salmon return (escapement) regressed on parent escapement while also incorporating a negative effect of Kamchatka pink salmon. Mean \pm 1 SD of untransformed statistics are shown.

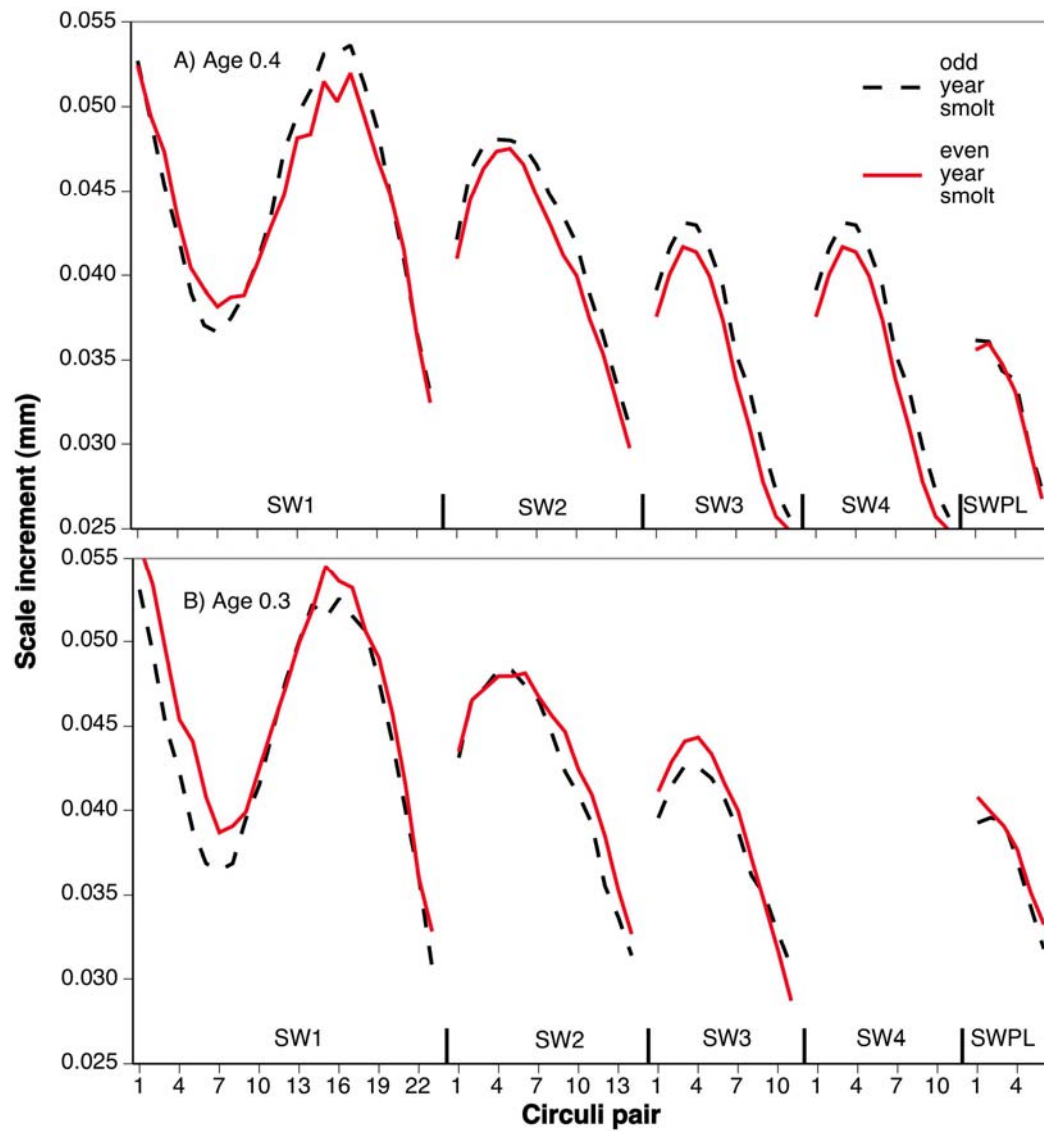


Fig. 9. Average seasonal scale growth of age-0.4 (A) and age-0.3 (B) Kwiniuk chum salmon that entered Norton Sound during even- versus odd-numbered years. Values are based on mean incremental scale growth during brood years 1970-2002.

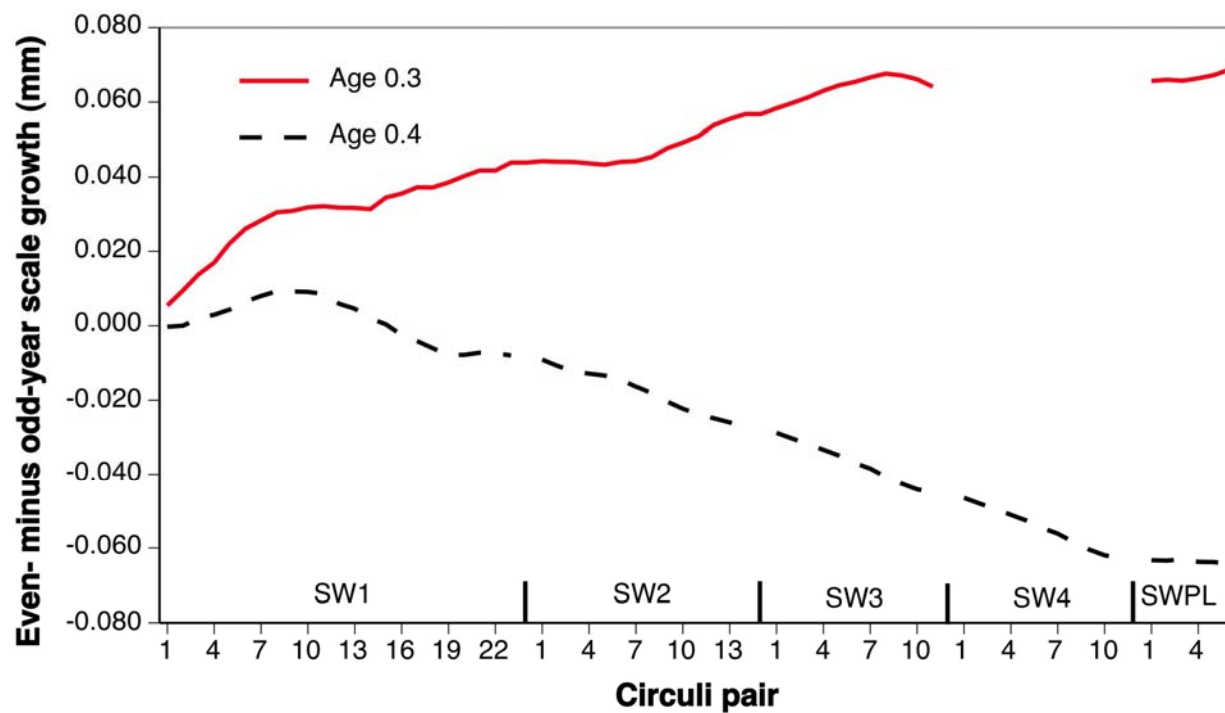


Fig. 10. Cumulative incremental scale growth difference between even- versus odd-year chum salmon smolts from the Kwiniuk River. Values are based on mean incremental scale growth during brood years 1970-2002.

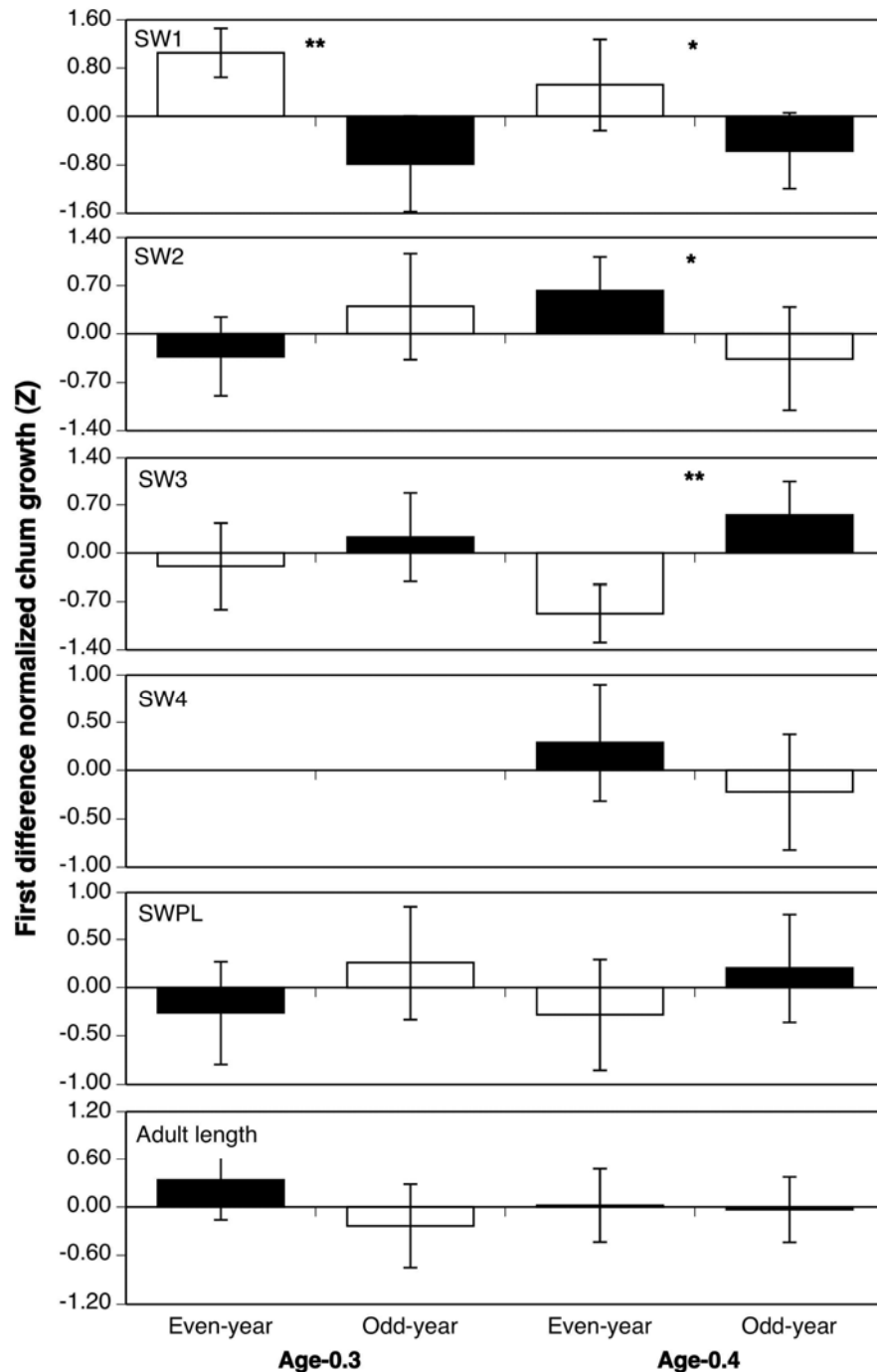


Fig. 11. Comparison of age-0.3 and age-0.4 Kwiniuk chum salmon growth during even- versus odd-numbered years at sea of each life stage, adult return years 1974-2006. SW1 values represent scale growth during the first 10 circuli (excluding focus) when chum and pink salmon are likely migrating through coastal waters; SW1 values exclude years prior to 1979 when Norton Sound pink salmon abundance was low. Salmon produced by even-year parent spawners are identified by black bars. Annual values were differenced to remove long-term trends (see methods).

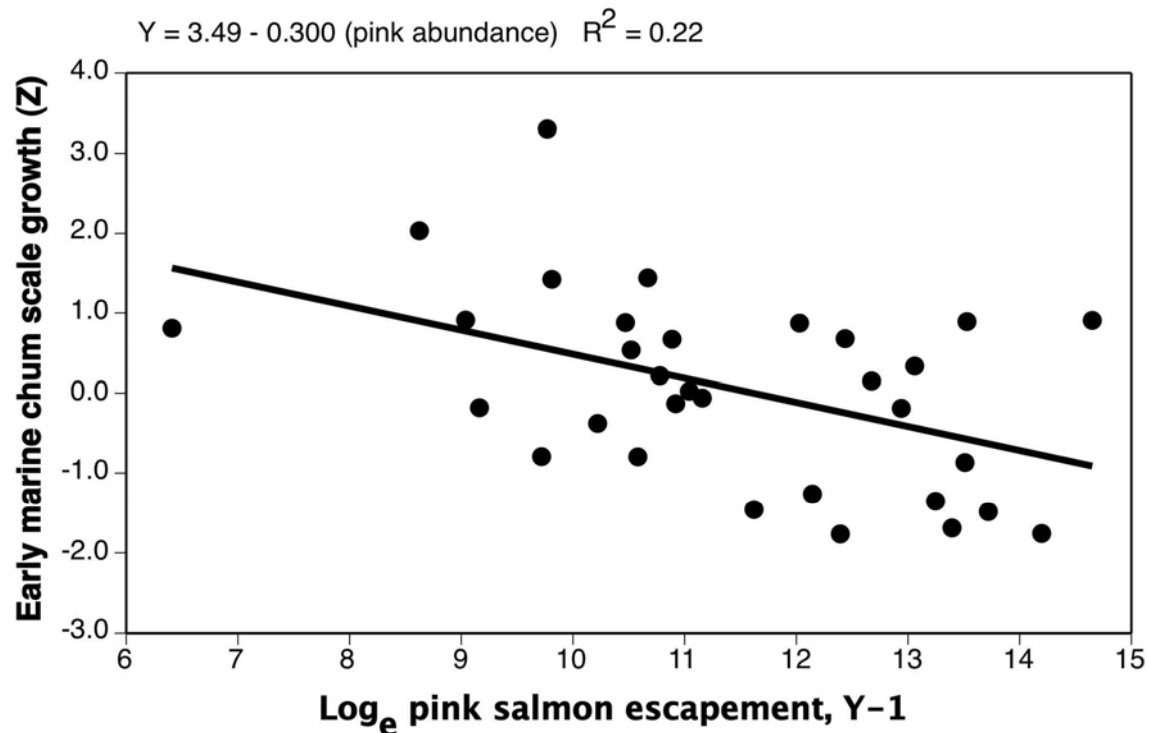


Fig. 12. Relationship between early marine scale growth of Kwiniuk chum salmon and an index of pink salmon fry entering Norton Sound, brood years 1971-2002. Early marine chum growth is the differenced value of the normalized (Z) first 10 circuli of age-0.3 and age-0.4 chum salmon during their first year. Pink salmon fry index is based on the escapement of adult pink salmon into the Kwiniuk River during the previous year.

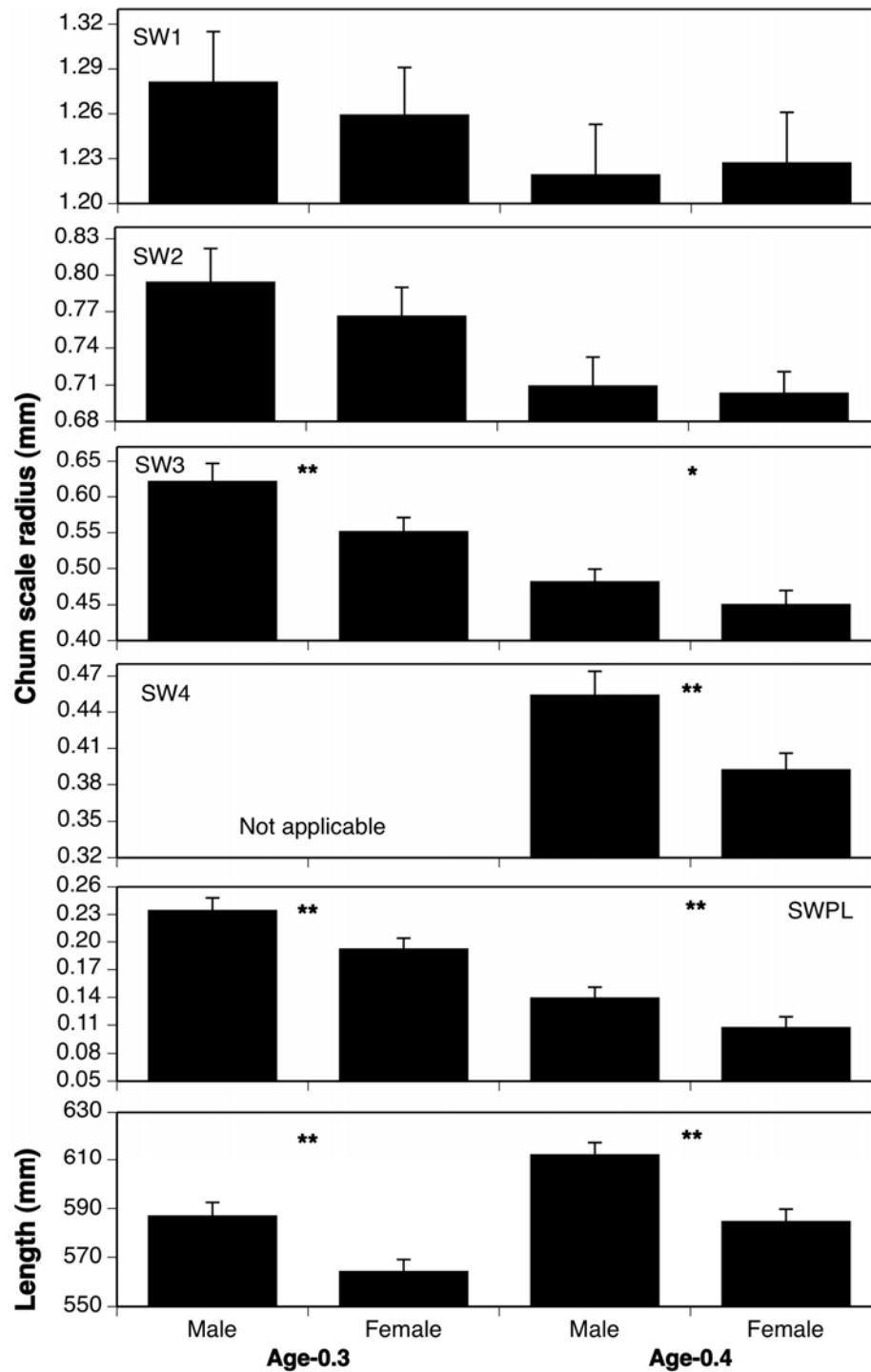


Fig. 13. Scale radius measurement of age-0.3 and age-0.4 male and female Kwiniuk chum salmon during each life stage, return years 1969-2006. Values are mean \pm 95% CI. Age-0.3 salmon were significantly bigger than age-0.4 salmon at all life stages ($P < 0.05$). Male salmon were bigger than female salmon beginning in third year at sea (SW3) and thereafter (“*” $P < 0.05$; “**” $P < 0.01$).

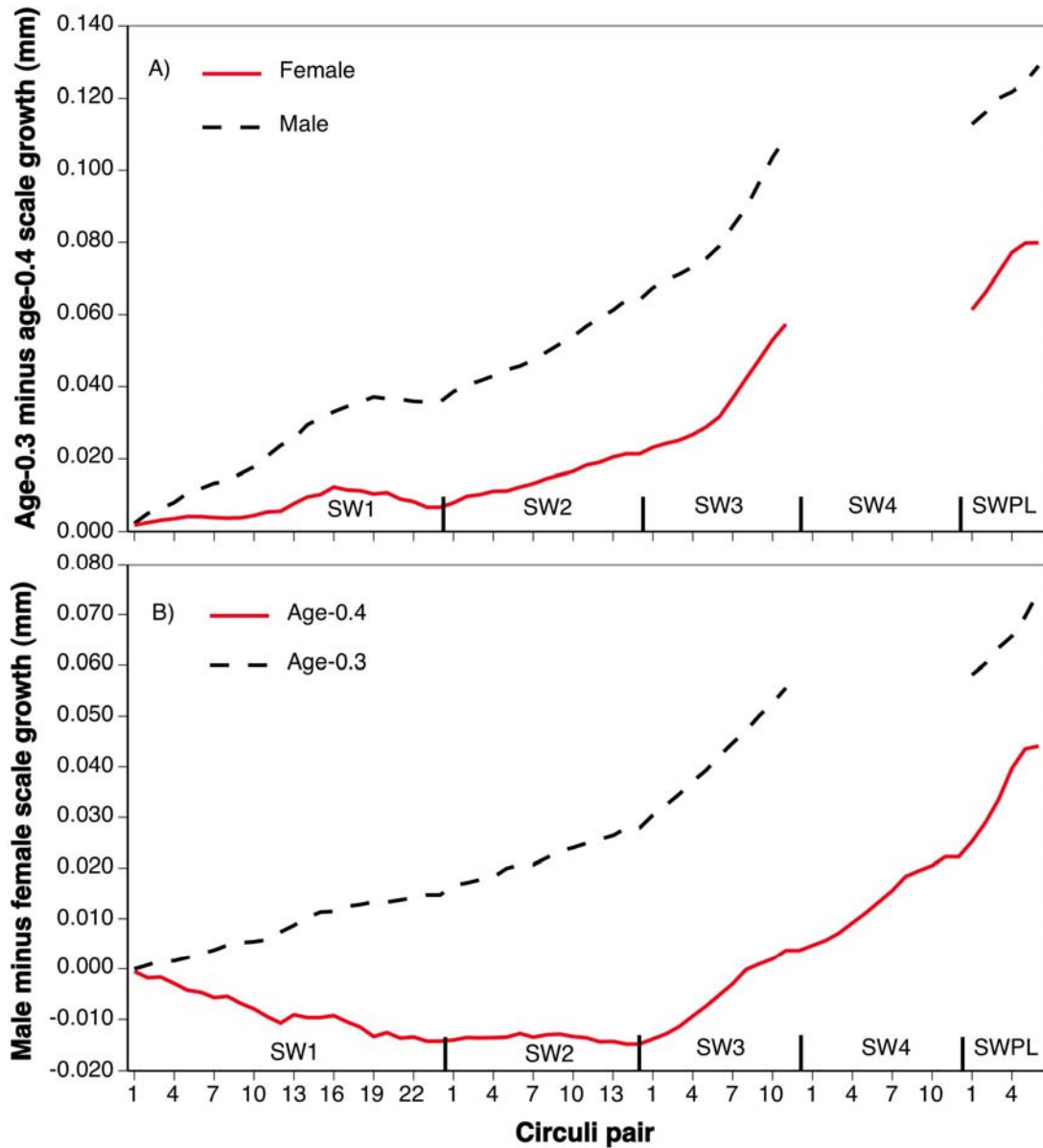


Fig. 14. Cumulative scale growth differential of age-0.3 versus age-0.4 Kwiniuk chum salmon within gender (A) and between gender (B). Circuli pairs included only when 90% or more of chum salmon produced the circuli.

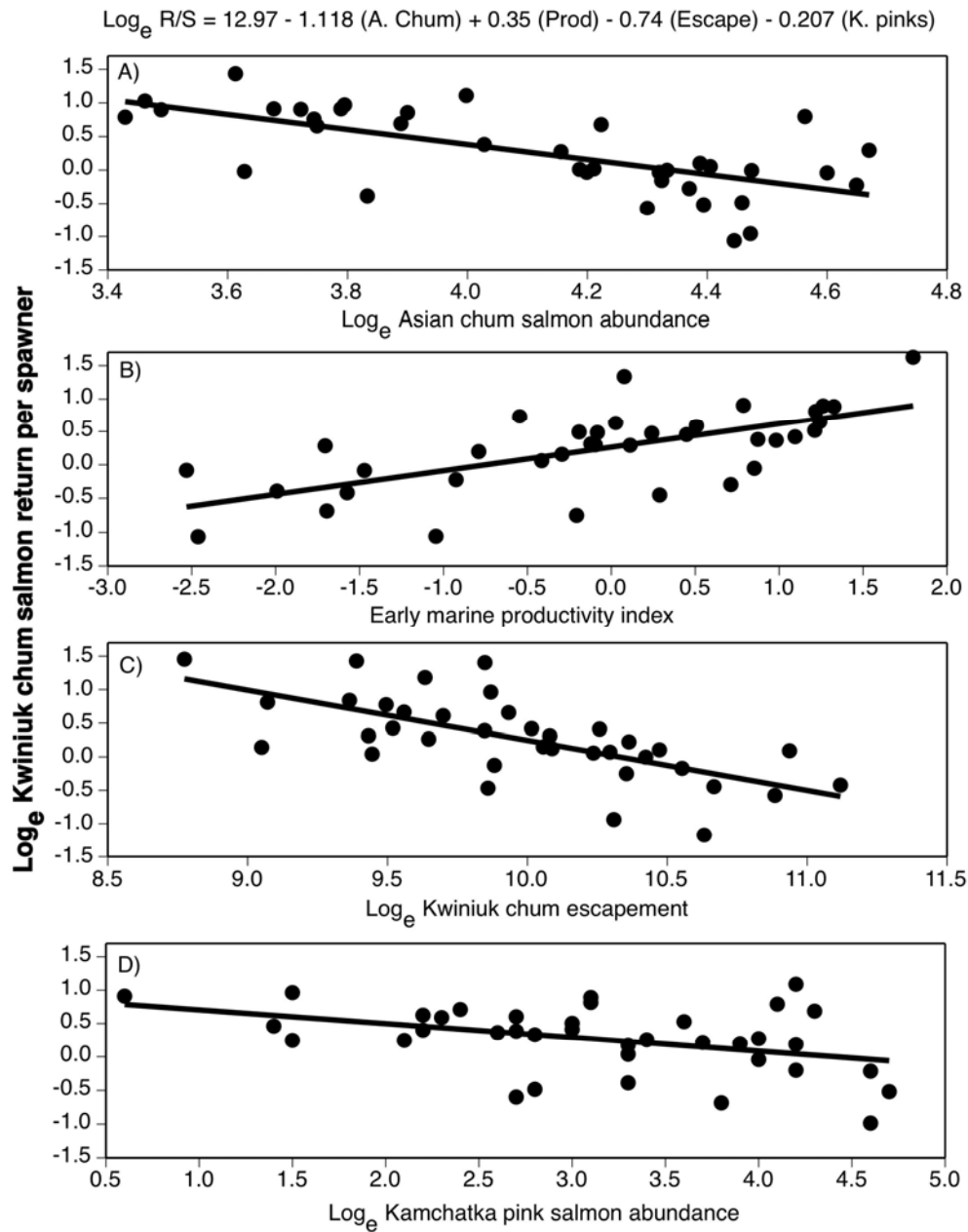


Fig. 15. Multivariate relationship showing the effect on Kwiniuk chum salmon return per spawner of A) average Asian adult chum salmon abundance two to four years after the Kwiniuk chum salmon brood year, B) an index of early marine productivity based on Kwiniuk pink salmon return per spawner, C) parent spawner escapement in Kwiniuk River, and D) abundance of Eastern Kamchatka adult pink salmon abundance two years after the Kwiniuk chum salmon brood year.

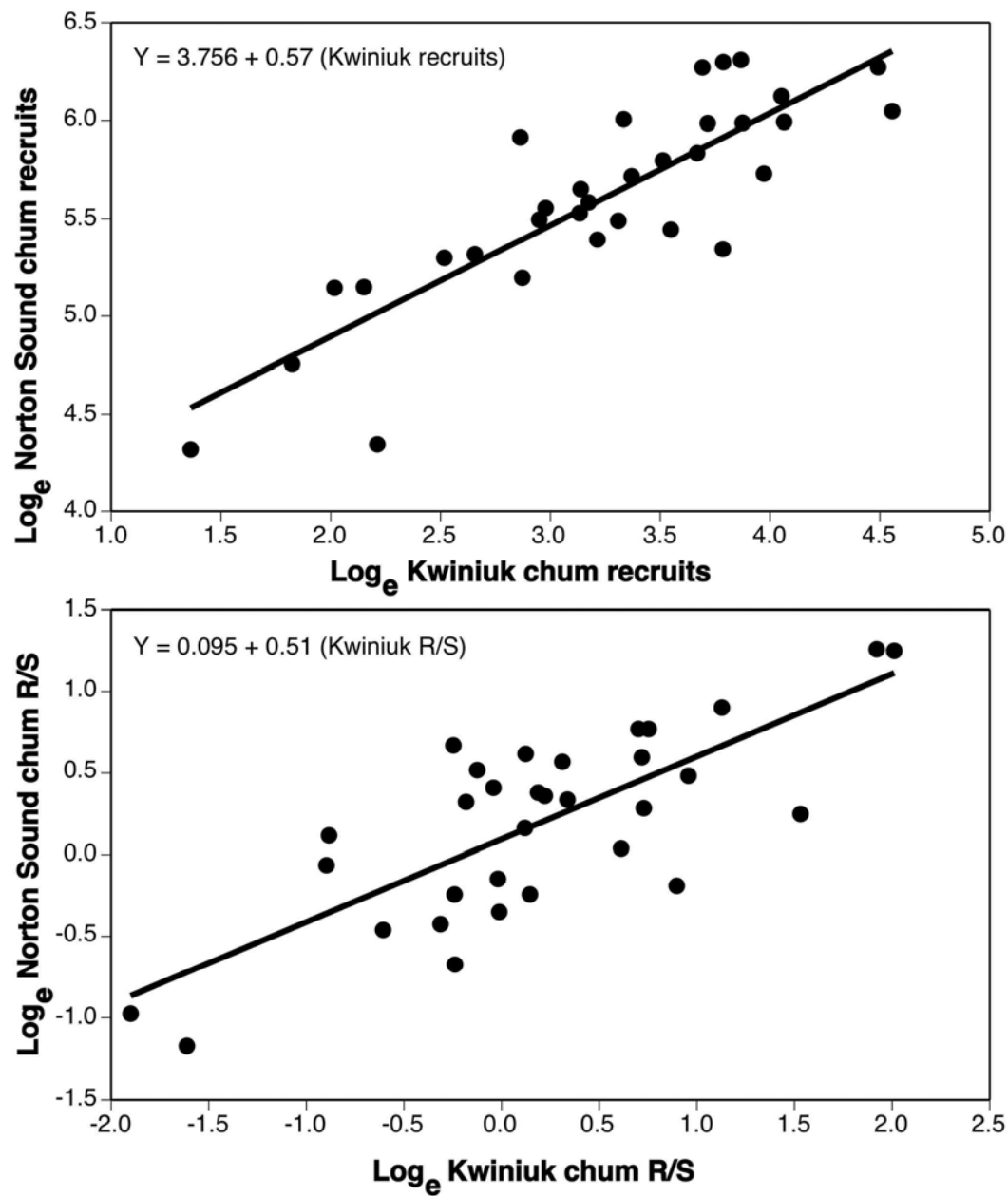


Fig. 16 Correlation between chum salmon production in Norton Sound and the Kwiniuk watershed. Salmon recruits from parent spawners are in 1,000s of fish.

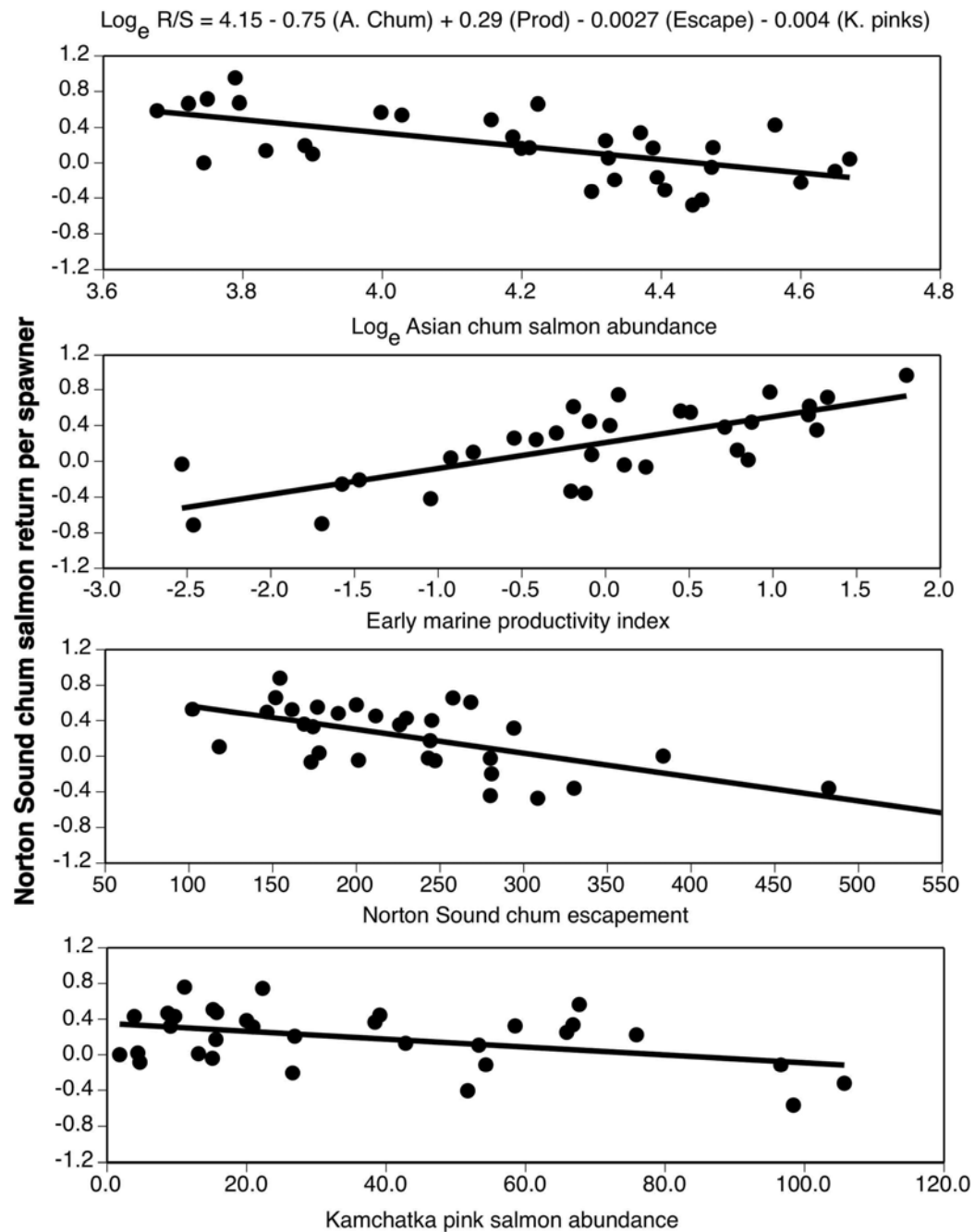


Fig. 17. Multivariate relationship showing the effect on Norton Sound chum salmon R/S of A) average Asian adult chum salmon abundance two to four years after the Norton Sound chum salmon brood year, B) an index of early marine productivity based on Kwiniuk pink salmon return per spawner, C) parent spawner escapement in Norton Sound, and D) abundance of Eastern Kamchatka adult pink salmon abundance two years after the Norton Sound chum salmon brood year.

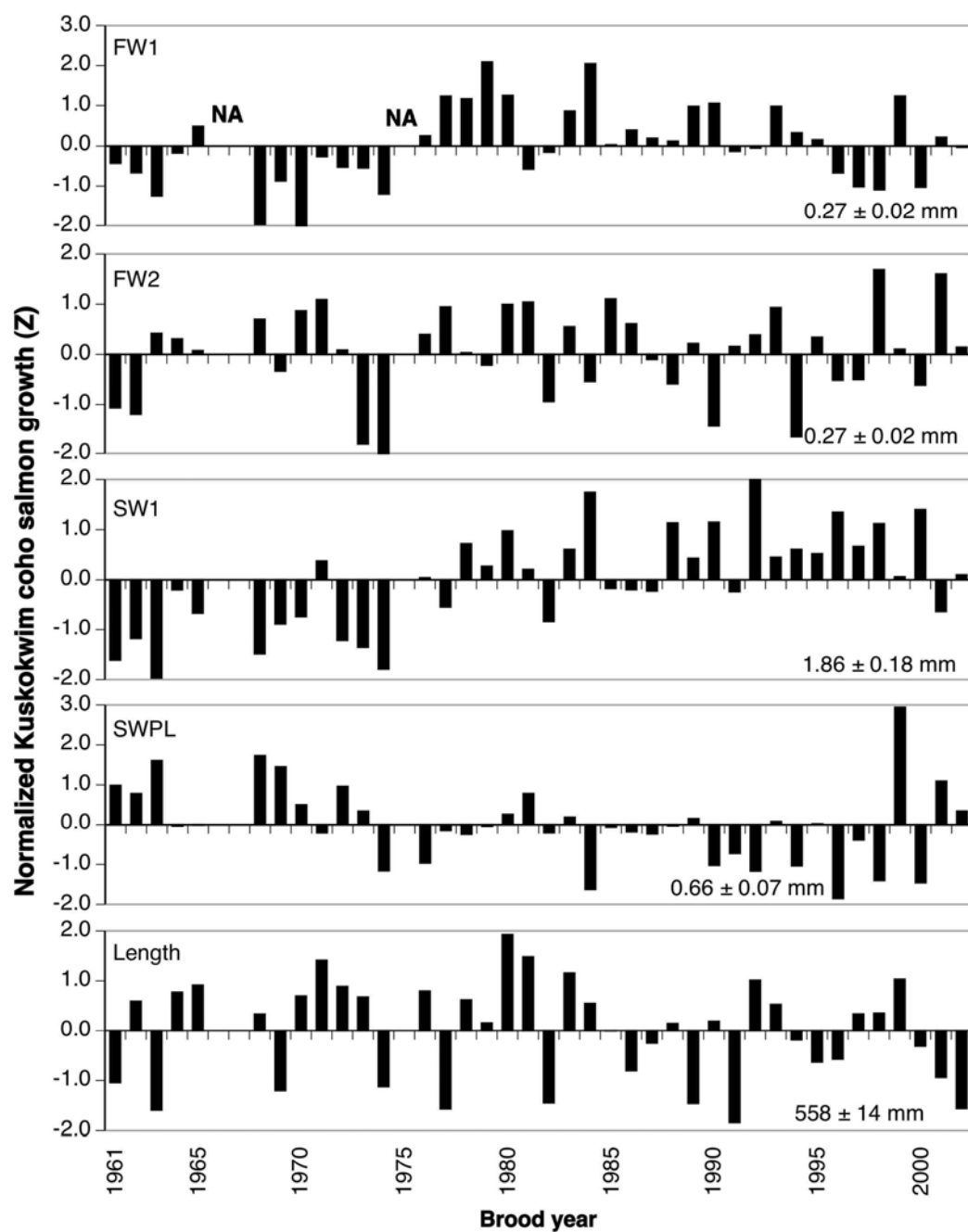


Fig. 18. Mean annual growth of age-2.1 Kuskokwim coho salmon during each life stage, brood years 1961-2002. Life-stage growth organized by brood year is based on individuals produced by the same parents. Values are standard deviations above and below the long-term mean.

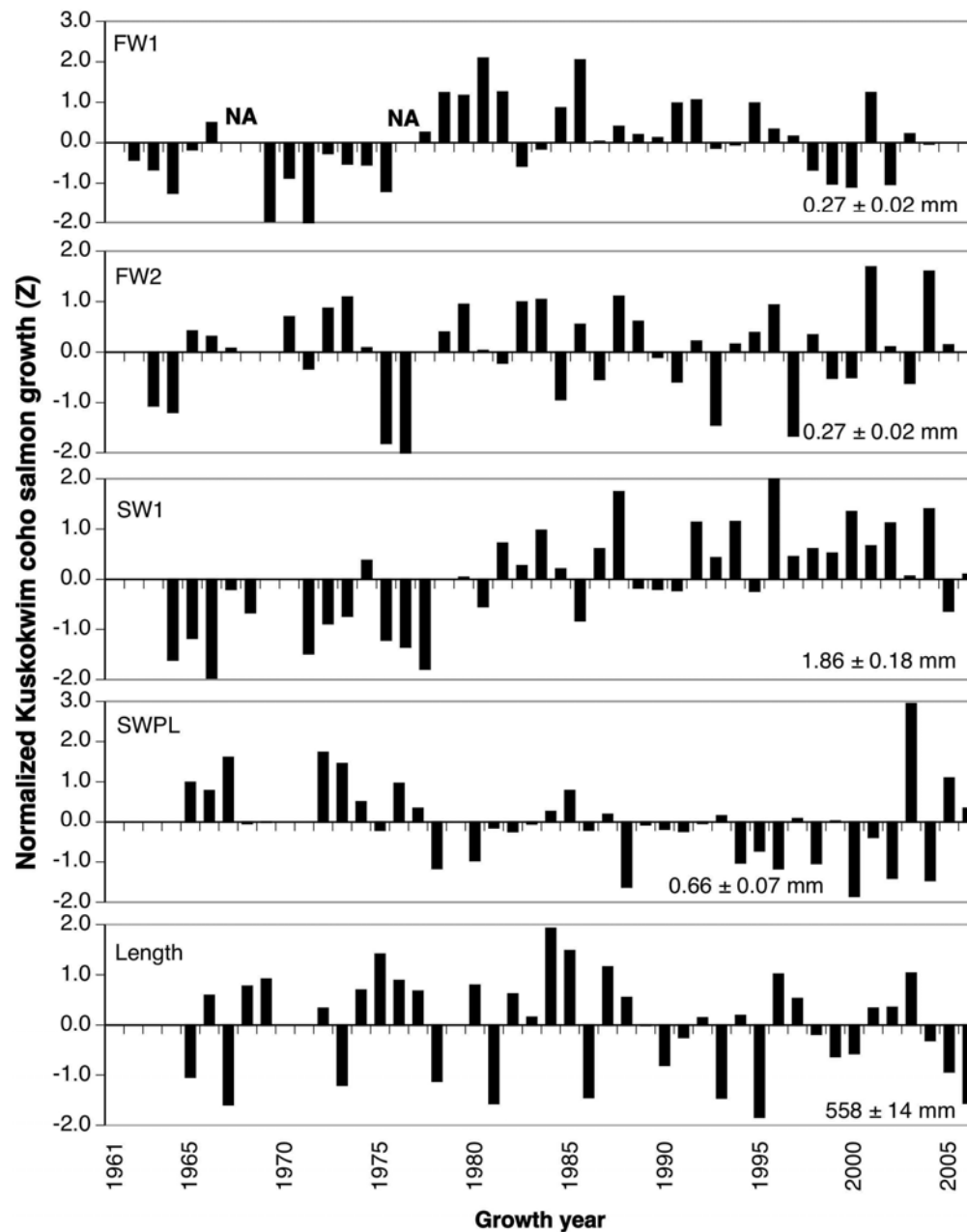


Fig. 19. Mean annual growth of age-2.1 Kuskokwim coho salmon during each life stage, growth years 1961-2006. Life stage growth organized by growth year is based on fish of different ages co-occurring during the same year. Values are standard deviations above and below the long-term mean.

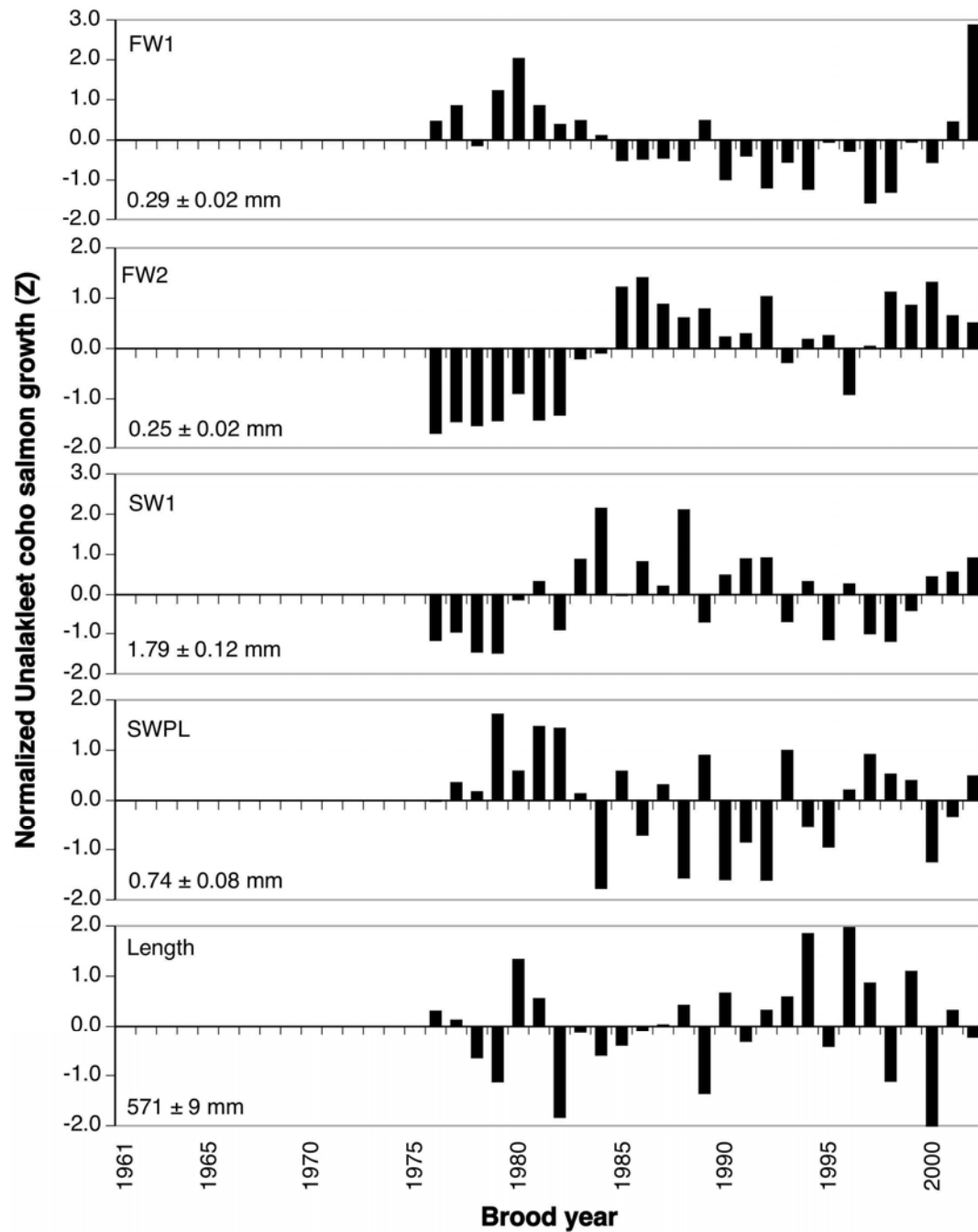


Fig. 20. Mean annual growth of age-2.1 Unalakleet coho salmon during each life stage, brood years 1976-2002. Values are standard deviations above and below the long-term mean.

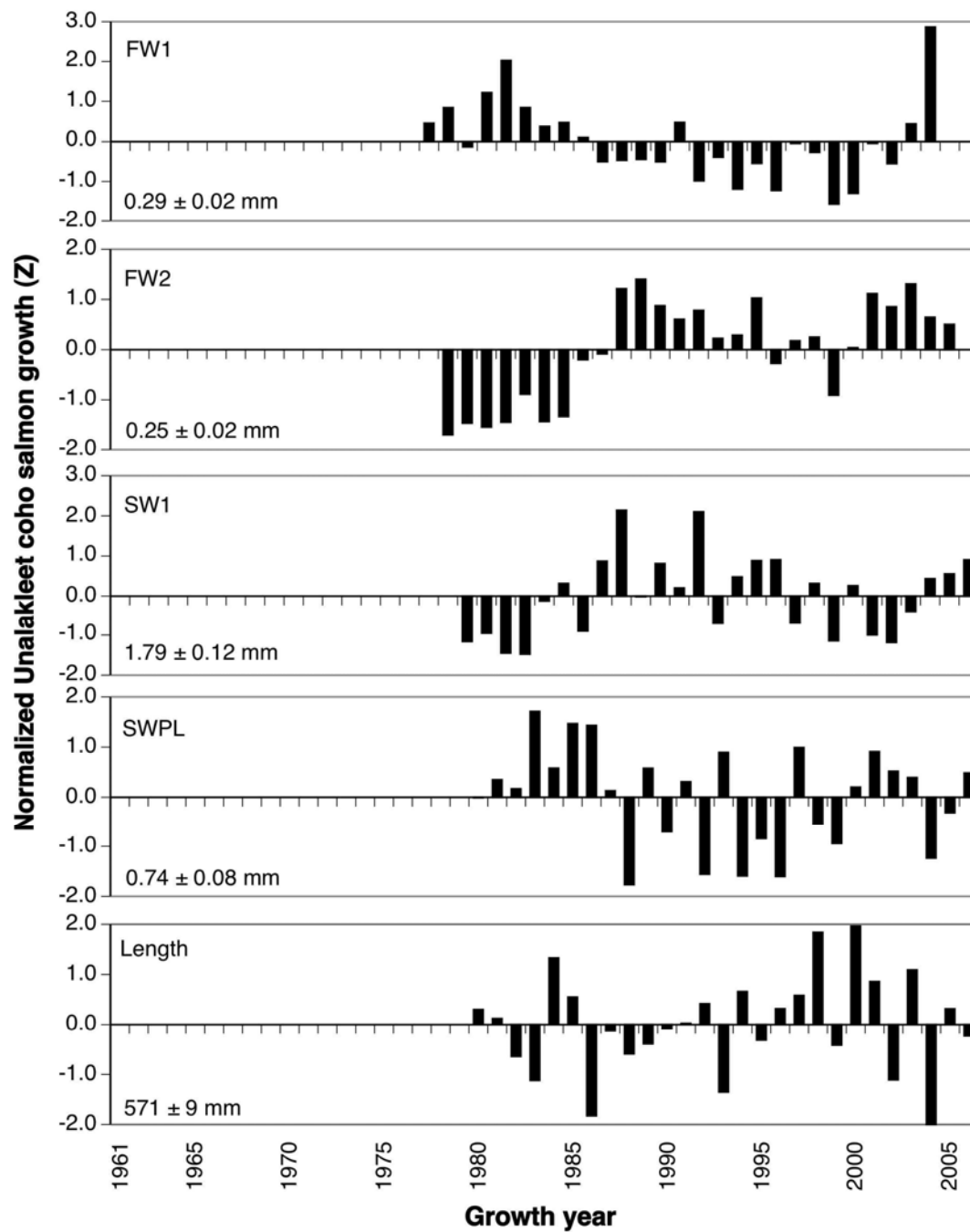


Fig. 21. Mean annual growth of age-2.1 Unalakleet coho salmon during each life stage, growth years 1977-2006. Values are standard deviations above and below the long-term mean.

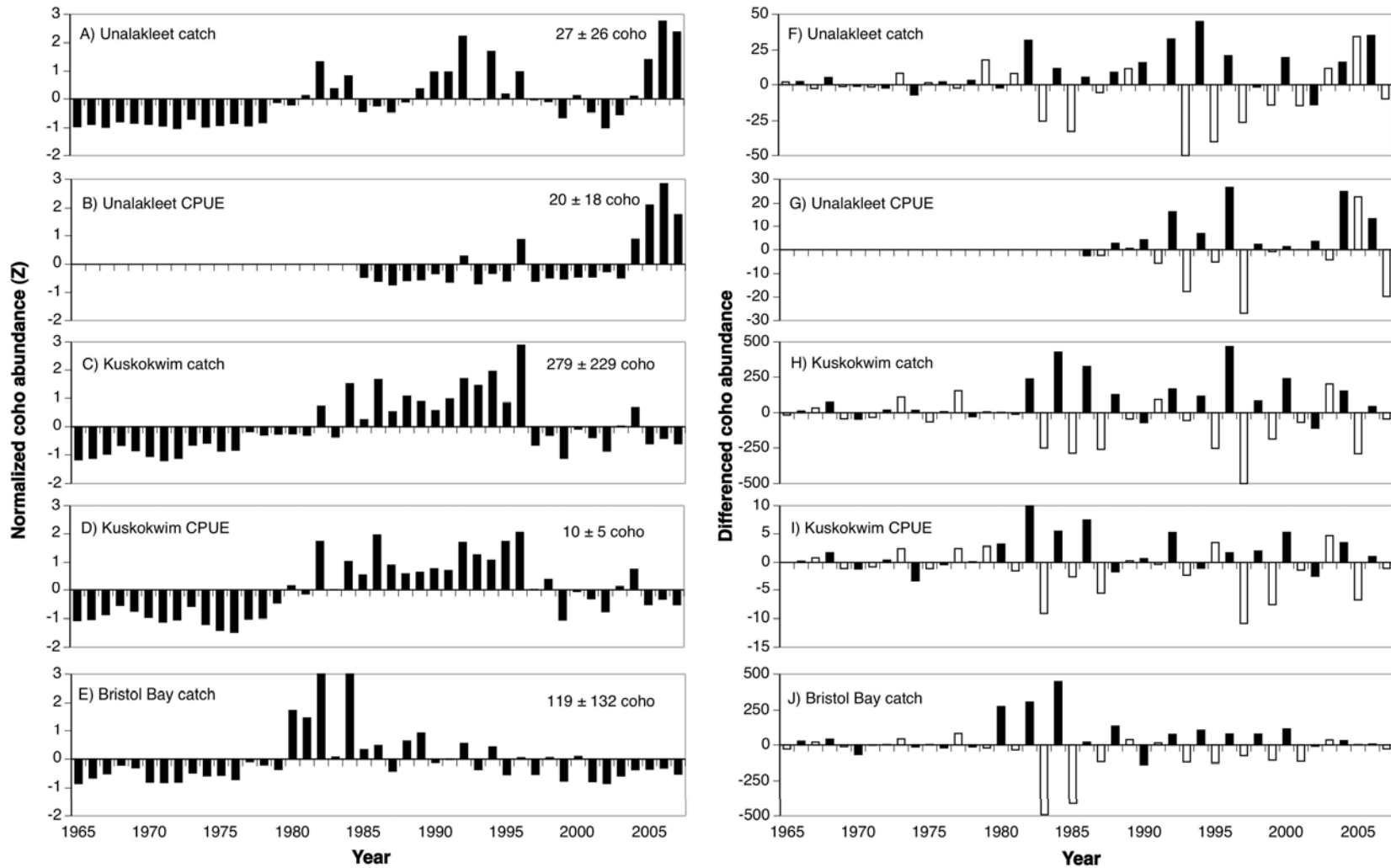


Fig. 22. Commercial harvest and CPUE trends of coho salmon in Unalakleet subdistrict, Kuskokwim River, and Bristol Bay, 1965-2007. Values are normalized (A, B, C, D, E) to highlight long-term trends and differenced (F, G, H, I, J) to highlight alternating-year patterns. Mean catch values and are 1,000s of fish.

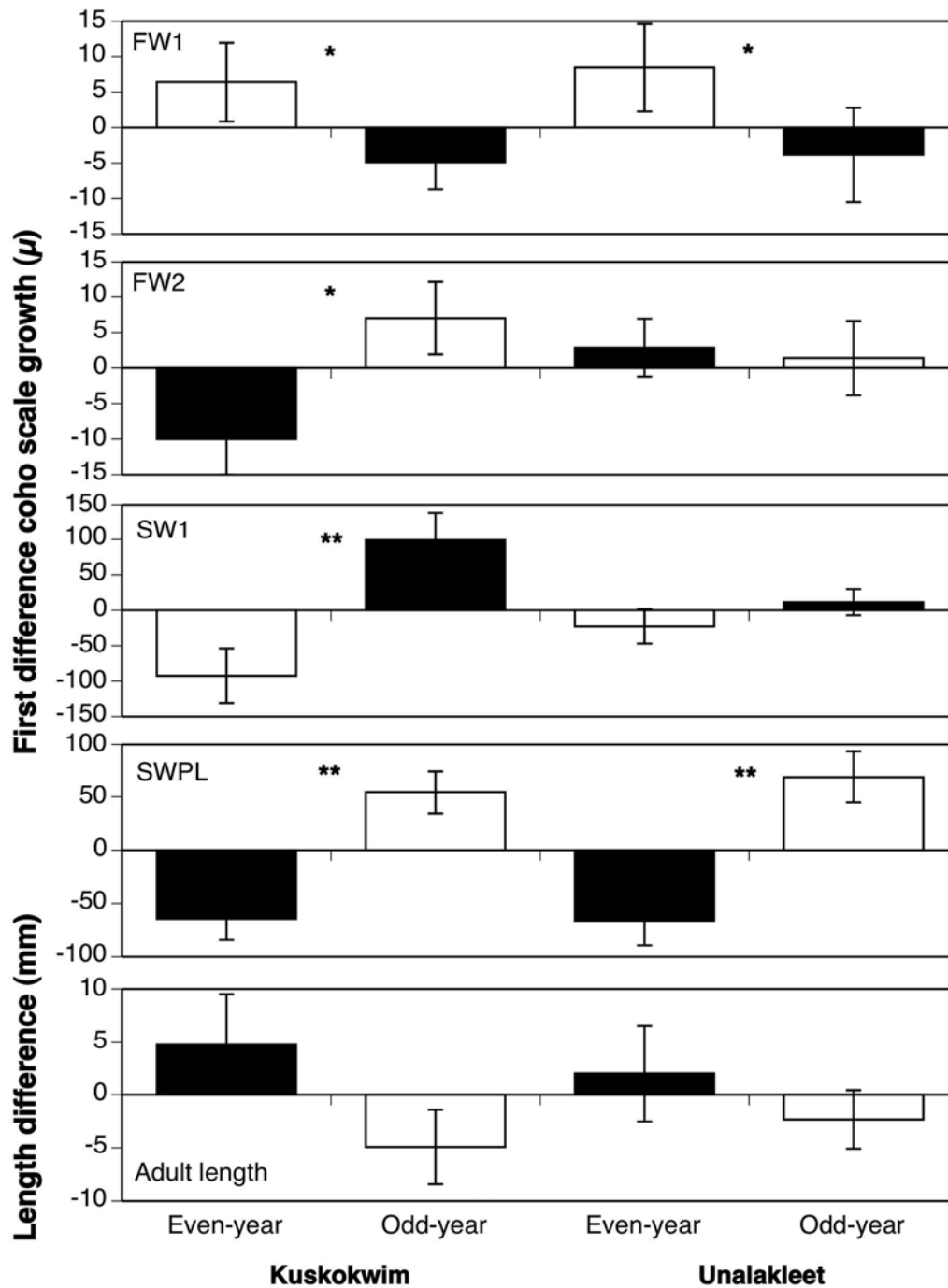


Fig. 23. Comparison of age-2.1 coho salmon growth from the Kuskokwim and Unalakleet rivers during even- versus odd-numbered growth years of each life stage, including adult length. Salmon produced by even-year parent spawners (more numerous) are identified by black bars. Annual values (mean \pm 1 SE) were differenced to remove long-term trends (see methods).

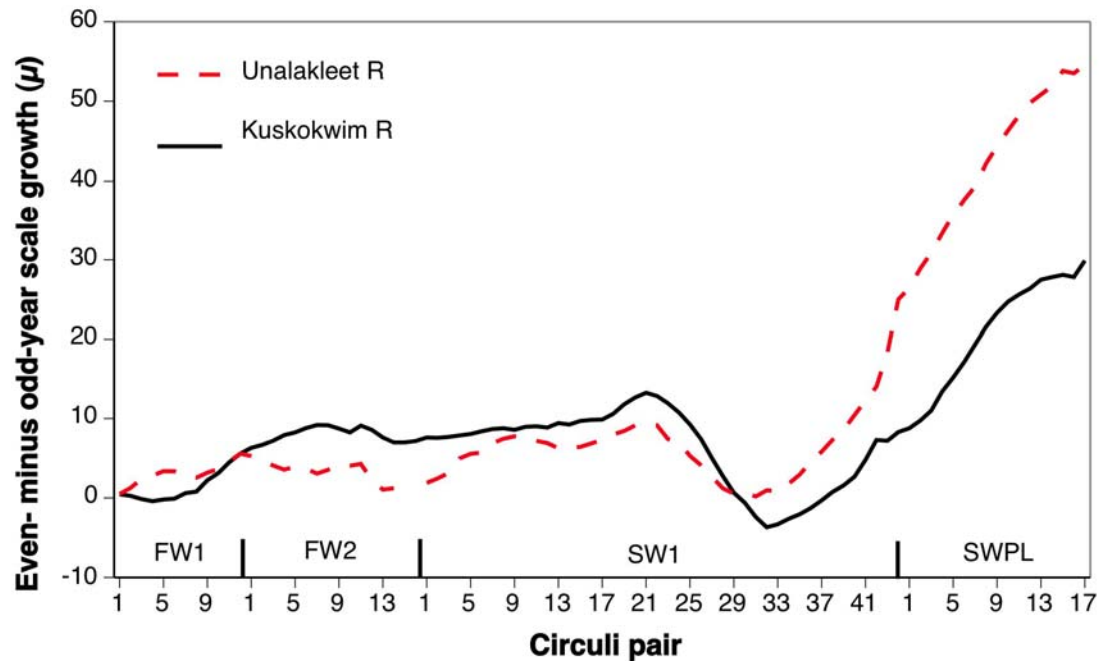


Fig. 24. Cumulative incremental scale growth difference between coho salmon emerging into streams in even- versus odd-years. Values are based on mean incremental scale growth during brood years during 1961-2002 (Kuskokwim) and 1976-2002 (Unalakleet).

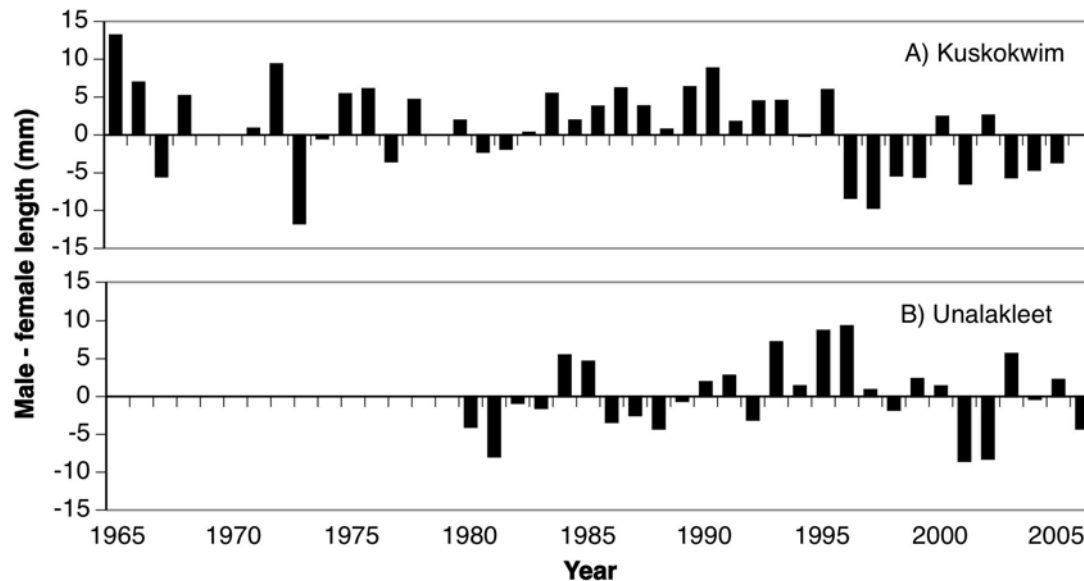


Fig. 25. Comparison of age-2.1 male versus female coho length in the Kuskokwim and Unalakleet rivers. Values are based on the ADFG age-sex-length database. Differential growth of Kuskokwim coho salmon significantly declined with the 1997 El Niño.

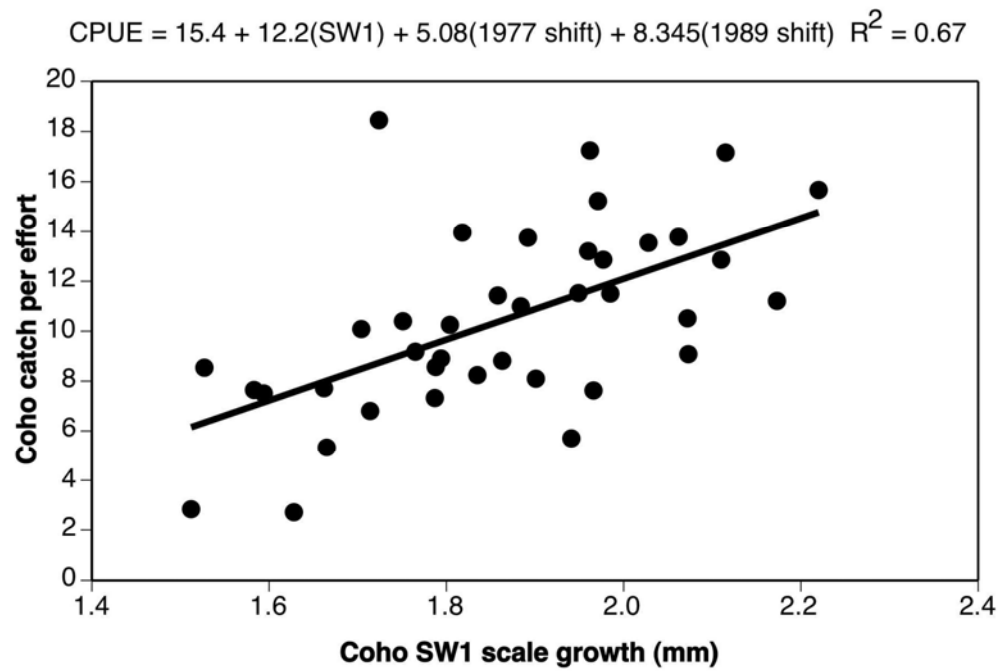


Fig. 26. Catch per unit effort (CPUE) of adult coho salmon in the Kuskokwim River in relation to coho growth during the first year at sea (SW1), 1965-2006. CPUE values are partial residuals (Larsen and McCleary 1972), which reflect this relationship after accounting for the effects of ocean regime shifts in 1977-1988 and 1989-1996.

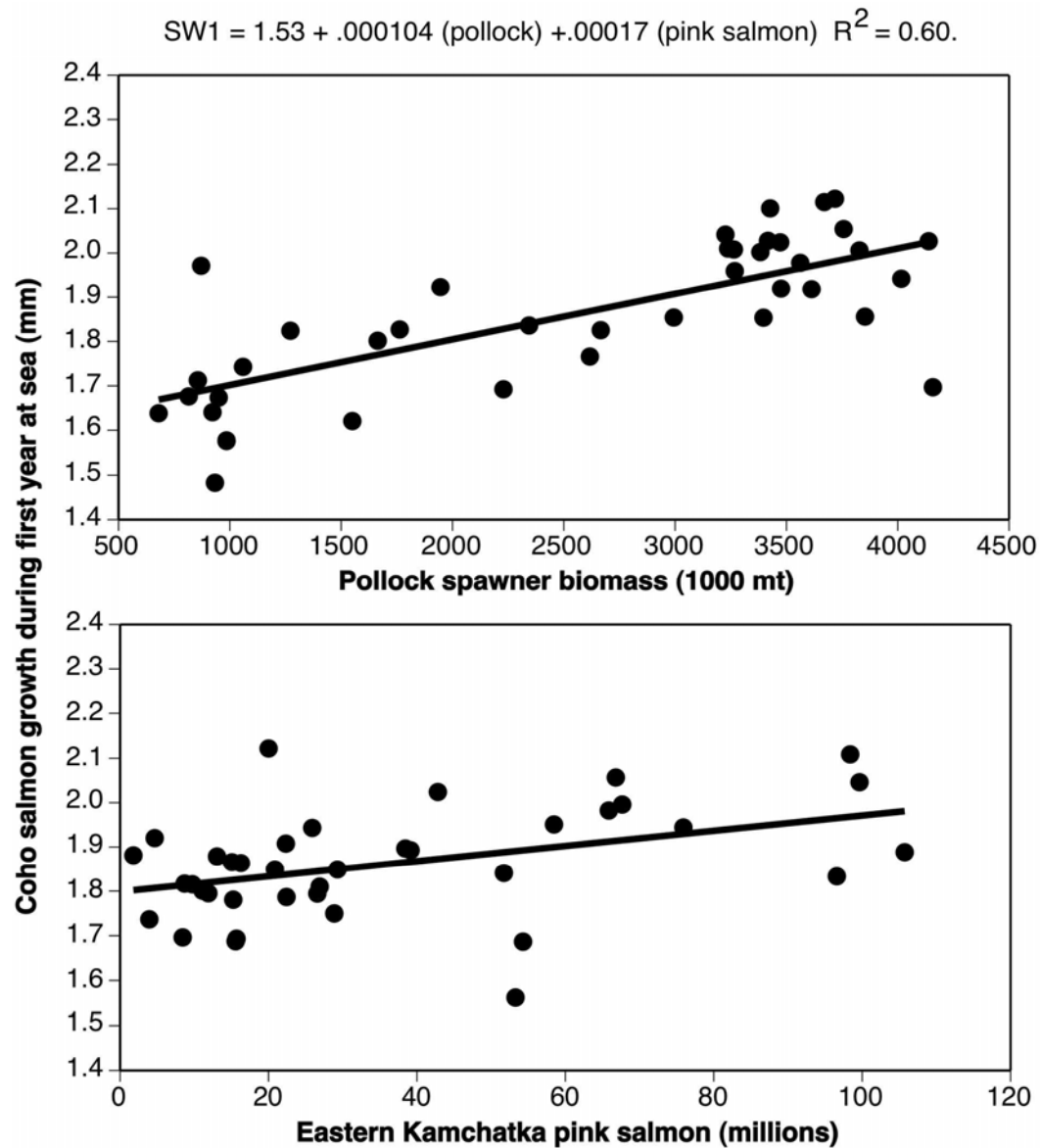


Fig. 27. Multivariate relationship showing the effect on Kuskokwim coho growth during the first year at sea (SW1) of pollock spawning biomass and abundance of adult Eastern Kamchatka pink salmon during coho growth years 1964-2005.

$$\text{CPUE} = 0.643 + .0024 (\text{pollock}) + .029 (\text{pink salmon}) + 3.6 (1977 \text{ shift}) + 6.7 (1989 \text{ shift}) \quad R^2 = 0.80$$

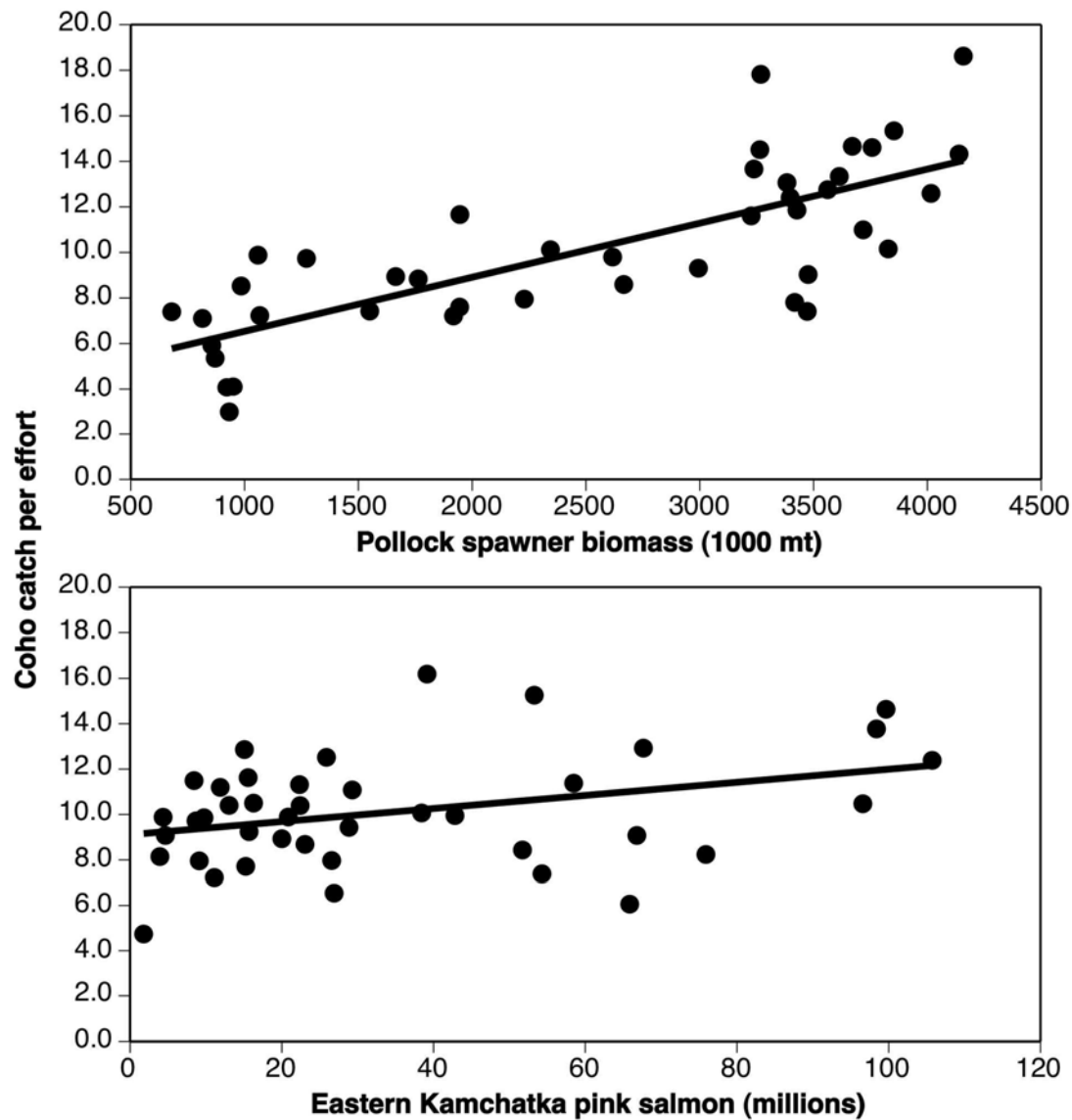


Fig. 28. Catch per unit effort (CPUE) of adult coho salmon in the Kuskokwim River in relation to pollock spawning biomass and abundance of adult Eastern Kamchatka pink salmon during the year prior to harvest, 1965-2006. Values are partial residuals, which reflect this relationship after accounting for the effects of ocean regime shifts in 1977-1988 and 1989-1996.