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Productivity of Kuskokwim Juvenile Coho

by:

G.T. Ruggerone[2], B.A. Agler[3], and D.B. Molyneaux[4]

[2] Natural Resources Consultants, Inc.
4039 21st Avenue West, Ste 404, Seattle, WA 98199
GRuggerone@nrccorp.com

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

[4] ADF&G Division of Commercial Fisheries
333 Raspberry Rd, Anchorage, AK 99518
doug.molyneaux@alaska.gov

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SUMMARY

Coho salmon occur throughout much of the Kuskokwim River Area, spawning in tributaries that range from 10 to over 1,500 km from the ocean. We back-calculated growth of juvenile coho salmon from adult salmon scales collected from weirs located in eight spatially-distributed tributaries from 2003 to 2007 (Middle Fork Goodnews, Kanektok, Kwethluk, Tuluksak, George, Tatlawiksuk, Kogrukluk, and Takotna rivers) and from adult salmon scales sampled on the Kuskokwim River near Bethel during 1966-2006. These scale measurements were used to test whether coho growth varied among tributaries, and if so, whether growth was influenced by habitat characteristics associated with each tributary (e.g., area of floodplain habitat, watershed gradient, water temperature, and/or pink salmon). We also examined long-term trends in juvenile length-at-age in relation to climate shifts and air temperature. The back-calculated lengths of coho salmon were compared with lengths of smolts from other regions. The back-calculated coho lengths described here were salmon lengths after the fish experienced size-dependent mortality, i.e., loss of smaller than average fish from the population.

Coho Length v. Scale Radius

We developed relationships between live length of juvenile coho salmon from five Kuskokwim River watersheds and their scale radius. Comparison of these relationships among watersheds indicated little or no difference from watershed to watershed, as might occur if fish body shape at a given size changed among the watersheds. Thus, all scale/fish length data were combined to develop a geometric regression of coho length on scale radius. This relationship was used to back-calculate juvenile length-at-age from adult scale measurements.

Coho Length-at-age, 1965-2006

The time series of juvenile coho lengths (estimated from adult scales collected near Bethel, Alaska) revealed distinct shifts in size during the first year in freshwater and total smolt length. At the end of the first growing season, coho length was below average from 1962 to 1975 (smolt years), above average during 1977 to 1996, then typically below average from 1997 to 2005. Length of age-2 smolts followed a similar pattern over time, largely reflecting growth experienced during the first growing season. The increase in back-calculated smolt length corresponded with the 1976/77 ocean regime shift and with mean winter air temperature at the Bethel Airport (December to April). The variable but somewhat lower juvenile coho length beginning in 1997 corresponded with the 1997/1998 El Niño.

Coho Growth Dependency

Growth of individual coho salmon during the second year in freshwater was weakly correlated with late season scale growth during the first year in freshwater. Likewise, scale growth of individual coho salmon during the first year in the ocean tended to be positively correlated with total growth in freshwater. Scale growth during the final

(second) year at sea (SWPL) was correlated with previous scale growth. These findings are consistent with observations of growth dependency on prior growth among Kuskokwim and Yukon River Chinook salmon. Greater size of coho and Chinook salmon may provide the fish with greater opportunities for consuming larger and more evasive preferred prey, such as forage fishes and squid.

Coho Length in Watersheds

Mean length of coho salmon smolts in the Kuskokwim River Area tended to be greater among stocks originating from watersheds farther from the ocean, largely in response to greater growth during the second year in freshwater. However, further analyses suggested that length at the end of the first year in freshwater was positively correlated with greater floodplain area and greater mean summer water temperature of the watershed and negatively correlated with average elevation of the watershed. The importance of floodplain habitat, which was the primary variable in the model, makes sense because coho salmon often rear and feed upon prey in side channels, which are more common in floodplain habitat. Growth of juvenile coho salmon during the second year in freshwater (i.e., yearlings) was positively correlated with mean summer water temperature of the watershed and negatively correlated with watershed gradient. Mean length of age-2 coho smolts was best explained by growth during the first year in freshwater and by mean summer water temperature. Biological variables, such as coho density and coho productivity which were exploratory indices, did not explain variability in mean length among the watersheds.

Adult length of coho salmon returning to the Kuskokwim area watersheds was inversely related to the distance of those watersheds from the ocean. Larger size of lower river adult coho salmon, such as Kuskokwim Bay stocks, probably reflects the tendency for lower river adult coho salmon to enter freshwater somewhat later in the summer, thereby allowing additional foraging and growth in the ocean.

Coho Length vs. Pink Salmon

Downstream tributaries (Middle Fork Goodnews, Kanektok, Kwethluk rivers), which support relatively abundant populations of adult pink salmon, produced subyearling and yearling coho salmon that were longer during odd-numbered years, i.e., years when numerous pink salmon fry would be present in spring. Subyearling coho salmon were too small to consume pink salmon fry that were abundant during spring of odd-numbered years, but they could potentially benefit from consumption of pink salmon eggs and adult carcasses during August and September. Additionally, pink salmon carcasses during the previous year might have led to greater production of insects that may be consumed by subyearling coho during odd-numbered rearing years.

In the lower Kuskokwim River Area tributaries that support adult pink salmon, greater growth of yearling coho salmon during odd-numbered years may reflect the availability and consumption of pink salmon fry produced by adult pink salmon spawners in the previous even-numbered year. However, examination of coho salmon stomach contents revealed that yearling coho salmon also consumed pink salmon eggs during late summer of even-numbered years. These feeding opportunities may have off-set alternating-year growth patterns, as was expected if coho only fed on pink salmon fry.

Length of age-2 coho smolts and early marine scale growth of coho salmon smolts did not vary between odd- and even-numbered years, suggesting that coho salmon smolts may not have consumed numerous pink salmon fry during odd-year smolt migrations.

Length of Kuskokwim vs. Other Coho Stocks

Age-1 Kuskokwim Area coho salmon were smaller than age-1 coho smolts from other watersheds even though the Kuskokwim Area coho salmon had undergone potential size-selective mortality. This size difference likely reflects larger size of age-1 smolts compared with age-1 salmon that smolt during the following year. Age-2 coho smolts from the Kuskokwim area (avg. 129 mm) were large compared with age-2 smolts from other northern regions (avg. 113 mm). This size difference reflects size-dependent mortality that Kuskokwim salmon had experienced, but it also suggests that many coho salmon in Kuskokwim area grow rapidly, especially during the second year in freshwater.

Conclusions

Growth of juvenile coho salmon varied among Kuskokwim area watersheds, and the amount of floodplain habitat was the key habitat feature that affected coho salmon growth. Longer coho salmon were observed in watersheds that had greater amounts of floodplain habitat. Average water temperature and the presence of pink salmon fry (prey) also influenced growth of juvenile coho salmon. Back-calculated length of Kuskokwim coho salmon smolts appeared to be relatively long compared with coho smolts from other regions. Large size of Kuskokwim coho smolts probably contributes to the great abundance of coho salmon in the watershed. We conclude that floodplain habitat should be protected in order to maintain the high productivity of coho salmon in the Kuskokwim area.

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INTRODUCTION

Coho salmon (*Oncorhynchus kisutch*) is the primary species harvested in the Kuskokwim River commercial salmon fishery, averaging approximately 495,000 coho salmon per year from 1980 to 1996 (Whitmore et al. 2008). However, during 1997 to 2009 coho harvests declined 65% to an average of 175,000 coho per year (www.cf.adfg.state.ak.us/region3/ayk_harvest.php). Approximately 35% of the statewide Alaska subsistence catch of coho salmon occurs in the Kuskokwim area. Thus, commercial harvests of coho salmon are vital to the local economy, and they enable many subsistence fishermen to purchase the gas and equipment needed to catch salmon and other species for subsistence use.

Growth is a key factor affecting the survival and life history characteristics of Pacific salmon (e.g., Healey 1986, Friedland et al. 2006, Farley et al. 2007, Ruggerone et al. 2007a,b). Growth appears to be especially important to coho salmon because they are relatively short-lived, aggressive foragers, and fast growing compared with other salmonids (Ruggerone 1989, Ruggerone and Rogers 1992). Using measurements of returning adult scales, Ruggerone and Agler (2008) reported that harvest and catch per effort of Kuskokwim coho salmon during 1965-2006 was positively correlated with scale growth during the first year at sea. Furthermore, coho salmon abundance and growth at sea was correlated with an abundance index of larval pollock. They reported that freshwater growth of Kuskokwim coho salmon scales varied between odd- and even-numbered years, suggesting a potential link to juvenile pink salmon production, which is relatively high in some tributaries during odd-numbered years (adult pink salmon return in higher abundance during even-years). Williams et al. (2009) noted that coho smolt size in the Nome River tended to be positively correlated with juvenile pink salmon abundance, which provide prey for coho salmon. In addition to the positive effect of growth on survival, greater size of maturing coho salmon may lead to greater fecundity and egg size (Quinn et al. 2004), and thus to greater production of progeny.

The Kuskokwim River is the second largest watershed in Alaska and relatively little information is available on growth of juvenile coho salmon that originate from tributaries of the Kuskokwim River and Kuskokwim Bay, i.e., the Kuskokwim River Area. Growth of juvenile coho salmon, which typically inhabit freshwater for two growing seasons, likely reflects the productivity of the watershed in which they live. This growth information is important because threats to salmon habitat, such as mining, may continue or possibly increase in the future.

In this study, we back-calculated coho length-at-age from adult scales and compared the growth of juvenile coho salmon originating from eight major drainages of the Kuskokwim River Area to examine the productivity of these watersheds. Back-calculated salmon lengths from adult scales would over-estimate juvenile length to the extent that size selective mortality at sea removed smaller individuals from the population. The fish examined in this study spent two winters in freshwater before emigrating to sea. We also tested the hypotheses that growth of juvenile coho salmon in Kuskokwim River Area tributaries was:

- Correlated with indices of adult coho salmon productivity and density in those tributaries,
- Associated with the presence of pink salmon fry as prey in those tributaries,
- Associated with habitat characteristics, such as water temperature, distance from the ocean, amount of floodplain habitat, sinuosity of floodplain habitat, and density of stream nodes, and
- Equal to growth and length-at-age of coho in other watersheds.

Specific Objectives

1) Develop a quantitative relationship between juvenile coho length and scale radii measurements.

2) Reconstruct Kuskokwim coho lengths (mm) at the end of the first and second years of freshwater residence, 1967-2006, using previously measured adult coho scales collected near Bethel (AYK SSI Project 45486) and the regression equation to estimate juvenile length (mm) from its scale radius (Objective 1).

3) Determine whether freshwater growth of coho salmon varied among eight Kuskokwim River Area tributaries (five adult return years: e.g., 2003-2007).

4) Determine whether mean growth of juvenile coho salmon originating from the eight tributaries was correlated with habitat characteristics, such as a) distance from the Bering Sea, b) average summer water temperature, c) sinuosity of floodplain habitat, d) amount of floodplain habitat, and e) density of stream nodes (connections).

5) Determine whether mean growth of juvenile coho salmon in the eight tributaries was correlated with biotic factors, such as a) indices of adult coho production, b) an index of juvenile coho density, and c) pink salmon abundance (i.e., tributaries and cycle year).

6) Compare length-at-age of Kuskokwim coho salmon with that of coho salmon smolts from other regions.

METHODS

Adult Scale Collections and Measurements

Adult coho salmon scales from the Kuskokwim River were obtained from the Alaska Department of Fish and Game (ADFG) regional archive in Anchorage, Alaska. Scales were collected annually for quantifying age composition beginning in 1965. For back-calculating juvenile coho salmon length during 1965-2006, we used adult scales primarily sampled with drift gillnets (5.6-6.0 inch stretched mesh) near Bethel (river kilometer (RK) 106) during approximately late July through late August. For back-calculating length of juvenile coho salmon originating from each of the eight watersheds in the Kuskokwim area, we used scales collected from adult salmon sampled at weirs on the following rivers during 2003-2007:

<u>Rivers Sampled for Adult Scales:</u>

Middle Fork (MF) Goodnews River
Kanektok River
Kwethluk River
Tuluksak River
George River
Tatlawiksuk River
Kogrukluk River
Takotna River

The goal was to measure 25 male and 25 female coho salmon scales each year from age-2.1 salmon, which represent approximately 89% of all adult coho salmon. These salmon spent two winters in freshwater and one winter in the ocean before retuning to the Kuskokwim area. 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. Scales collected at the weirs exhibited resorption along the sides of the scales and slight resorption was present along the measurement axis of these fish, but freshwater zones were not affected. Scales were not available for some stocks in 2003 (Tatlawiksuk River), 2005 (Kwethluk River), and 2006 (Kanektok River).

Scale measurements followed procedures described by Hagen et al. (2001). After selecting a scale for measurement, the scale was scanned from a microfiche reader and stored as a high resolution digital file. High resolution 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 digital image was measured with Optimas 6.5 image processing software. The scale image was displayed on a LCD monitor, and the scale measurement axis was defined as the longest axis extending from the scale focus to outer scale edge. Distance (mm) between circuli was measured within each growth zone, i.e., growth through the first winter in freshwater from the scale focus to the outer circulus of the first freshwater annulus (FW1), growth during the second year in freshwater (FW2), the first ocean growth zone (SW1), and from the ocean annulus to the edge of the scale (SWPL). Spring plus growth (FWPL) was rarely observed. Data associated with the scale, such as date of collection, location, gender, fish length and capture method, were included in the dataset.

Juvenile Scale Collections and Measurements

Juvenile coho salmon were collected during 2008 by field crews located at four weir sites (e.g., George, Kogrukluk, Takotna, MF Goodnews rivers) and a smolt trap on the lower Kwethluk River. At the weir locations, coho salmon were collected with baited minnow traps, preserved in 10% buffered formaldehyde, and shipped to the NRC lab where species identification was confirmed, fork lengths measured, and scales removed from the preferred area for measurement. The goal was to collect scales and fork lengths from coho salmon evenly distributed across the range of available sizes, e.g., 45 mm to 150 mm (preserved length). Scales were mounted on numbered scale cards, linked to fish length data, and the scale cards were pressed into heated acetate cards. Both live and preserved fork lengths were available for some fish, and these data were used to develop a regression equation to predict live length from preserved length. All reported lengths are live lengths unless noted otherwise. Juvenile scales were measured along the longest axis.

Relationship Between Juvenile Length and Scale Radius

We developed a coho length versus scale radius relationship for coho in each watershed (Kwethluk, George, Kogrukluk, Takotna, MF Goodnews rivers), so that juvenile length could be back-calculated from adult scale measurements. A variety of approaches have been used to back-calculate fish lengths from scale radii measurements (Francis 1990). We explored the Fraser-Lee procedure recommended by Ricker (1992). However, the Fraser-Lee procedure was not appropriate to back-calculate juvenile salmon length from adult salmon scales because 1) some adult scales were resorbed along the outer edge, and 2) allometry of scales and salmon length changed from juvenile to adult life stages (Fisher and Pearcy 2005). Therefore, as recommended by Fisher and Pearcy (2005), we utilized geometric regression of juvenile salmon length (mm) on total scale radius (mm) to back-calculate juvenile length from adult scales collected in the watershed. Pierce et al. (1996) concluded that various back-calculation methods produced equivalent results, especially when variability in the fish length versus scale radius relationship was low. The slope of the geometric regression was calculated from the ratio of length standard deviation to scale radii standard deviation. The Y-intercept of the regression could then be calculated using algebra because the regression crosses mean Y and mean X values.

The relationships were plotted and visually compared to search for evidence that the fish length-scale radius relationship might vary between watersheds. ANCOVA was considered but not used to test for statistical differences in the regression relationships because the range in fish sizes available from each watershed was different and a statistical comparison could lead to spurious relationships.

We also tested the hypothesis that the longest axis of juvenile and adult coho scales may not be the same, leading to an underestimate of back-calculated juvenile length from the adult scales. For 30 adult coho scales, the longest axis was independently identified for the juvenile scale radius and total scale radius. Distance along each of these axes was measured and compared using a paired t-test. It is noteworthy that the longest axis of the juvenile scale radius can only be equal to or longer than that measured along the longest axis of the adult scale. Thus, it was anticipated that some measurements along the adult scale longest axis might lead to an underestimate of back-calculated juvenile length. The key objective here was to determine the degree to which this may have biased the back-calculated length of juvenile coho salmon.

In three of eight watersheds, adult coho scales were not available in one year. Therefore mean length of these missing values was estimated using an iterative approach in Excel. Mean length of the missing stock was estimated based on the length ratio of the missing stock to other stocks while adjusting for the ratio of mean length in the missing year relative to mean length of all years.

Growth of Juvenile Coho Salmon, 1967-2006

Length of juvenile coho salmon was back-calculated from adult scales collected from fish caught near Bethel during 1967-2006 and the fish length/scale radius relationship described previously. Length was estimated at the end of the first growing season (FW1) and as smolts (FW1 & FW2). Spring plus growth on the coho scales (FWPL) was rarely present but included in the smolt length calculation, if present.

Growth of Juvenile Coho Salmon by Watershed

Length of juvenile coho salmon was back-calculated from adult scales collected from weirs during 2003-2007 and the fish length/scale radius relationship described above. Length was estimated at the end of the first growing season (FW1) and as smolts (FW1 & FW2). Spring plus growth on the coho scales (FWPL) was rarely present but included in the smolt length calculation, if present. Analysis of Variance (ANOVA) was used to test the null hypothesis that coho length-at-age was similar among all eight tributaries.

Watershed Habitat Characteristics

Habitat Features

Geomorphologic characteristics of each watershed in the Kuskokwim area were obtained from the Riverscape Analysis Project (RAP), Flathead Lake Biological Station, University of Montana (http://rap.ntsg.umt.edu). RAP is a publicly available database of riverine and watershed physical structure encompassing the majority of watersheds draining into the Pacific and Arctic Oceans from California to the Kamchatka Peninsula in the Russian Far East (Luck et al. 2010). Data generated by RAP were provided by D. Whited, Flathead Lake Biological Station. Variables included watershed area, mean elevation of the watershed, elevation gain in the watershed, area of floodplain habitat, ratio of floodplain area to watershed area, floodplain sinuosity (sum of all main channel lengths found in floodplains divided by the sum of all floodplain lengths), average nodes per km (channel separation or convergence), and watershed gradient (elevation gain per km^2 of watershed; Table 2). Floodplain habitat is associated with side channel and off-channel habitats where many juvenile Kuskokwim coho occur (Ruggerone et al. 2009). Distance of each watershed from the Bering Sea was based on the location of the weir where adult salmon scales were collected.

Water Temperature

Water temperature loggers were deployed in the aforementioned tributaries during 2008 and 2009 as a means to document water temperature that might influence growth of coho salmon during summer. Temperature loggers were deployed in the mainstem river typically near the weir site and they recorded temperature each hour. Average summer temperature calculations were restricted to July and August because temperature was consistently available for each tributary during these months only. Water temperature was not available in George and Takotna rivers in 2009. Therefore, when calculating mean temperature for 2008 and 2009, we estimated the 2009 temperatures for these two rivers by applying the temperature ratio in 2009:2008 to the 2008 observed temperature values.

Adult Coho Density, Production and Productivity

Daily weir counts of coho salmon in each watershed were examined in order to estimate total spawning escapement each year. Weirs were removed before the end of the coho salmon migration in some watersheds, therefore linear interpolation was used to expand escapement counts through an anticipated ending date based on coho counts in other watersheds. Average expansions of the observed escapements counts were as follows:

MF Goodnews River:	9.8%
Kanektok River:	12.8%
Kwethluk River:	11.6%
Tuluksak River:	10.8%
George River:	0.9%
Tatlawiksuk River:	0.7%
Kogrukluk River:	2.1%
Takotna River:	0.8%

Averaged escapement of adults coho salmon during 2003-2007 was calculated from the expanded escapement counts and used as an index of coho production that could be compared with the average growth that these fish experienced in freshwater. An index of coho production in each watershed was calculated from the ratio of average spawning escapement (2003-2007) and either total watershed area or floodplain area upstream of the counting weir. These values provided an index of adult coho production per unit of habitat, which was compared with their juvenile growth in the freshwater habitat.

The average escapement of coho salmon during 1999-2003 (parents) was calculated as an index of juvenile abundance that may have negatively influenced growth of juveniles (e.g., competition) that returned as adults during 2003-2007. An index of juvenile density in each watershed was calculated from the ratio of average spawning escapement (1999-2003) and either total watershed area or floodplain area upstream of the counting weir. These data were used in an exploratory analysis to evaluate if there was evidence for competition among juvenile coho salmon.

Additionally, we compared coho growth patterns with estimates of coho productivity, which was based on calculations of spawner returns per spawner (S/S) during brood years 1999-2005. The S/S analysis was considered exploratory because only five years of data were available for these calculations and because the return of spawners may not fully account for trends in the total return of adult coho salmon because some fish were harvested. However, it is noteworthy that harvest rates were relatively low during this period (e.g., ~10-40% in Kuskokwim River; Estensen et al. 2009). Regression analysis was used to test the hypothesis that S/S and adult coho production were dependent on mean size of juvenile coho salmon, or that mean size of juvenile coho salmon was negatively correlated with coho density.

Pink Salmon

The hypothesis involving pink salmon was tested using the dominant even-year cycle of adult pink salmon in the Kuskokwim area. Very few adult pink salmon occur in odd-numbered years (Whitmore et al. 2008). Additionally, the eight watersheds were qualitatively ranked as having relatively high versus low abundances of pink salmon during even-numbered years. Although some pink salmon are counted at weirs, most are small and readily pass through the weir without being counted. Therefore, we used a qualitative ranking of pink salmon abundance (Doug Molyneaux (ADFG), pers. observation):

Kwethluk River:	Medium
George River:	Low
Takotna River:	Low (rare)
Tatlawiksuk River:	Low (nearly rare)
Kogrukluk River:	Low
Tuluksak River:	Low
Kanektok River:	High (maximum for Kuskokwim Area)
MF Goodnews River:	High (maximum for Kuskokwim Area)

RESULTS

Live vs. Preserved Juvenile Coho Length

Fork length of live juvenile coho salmon (n = 57, $P < 0.001$) was highly correlated (R^2 = 0.997) with their preserved length (Fig. 2). Live length could be estimated using the following equation

1) Live coho length (mm) = -1.352 + 1.052 (preserved length).

Coho Length vs. Scale Radius

Juvenile coho length and scale radius were highly correlated, and there was no evidence that this relationship varied among the five watersheds (Fig. 3). Therefore, all data were combined in order to develop the relationship to predict coho length from scale radius measurements.

Approximately 86% of the variability in juvenile coho length was explained by scale radius measurements (Fig. 4, $P < 0.05$). The geometric regression relationship between live length of juvenile coho salmon and scale radius was:

2) Live coho length (mm) = 17.847 + 199.94 (scale radius).

Comparison of longest axis measurements of juvenile growth (FW1 & FW2) on adult coho salmon scales using the axis for juvenile versus total scale radius revealed that the longest axis was the same for 19 of 30 scales. However, on average, the longest axis along the juvenile scale was significantly longer than the juvenile portion of the adult (paired t-test, n = 30, P = 0.013). This difference equated to juvenile coho length of approximately 1.1 mm, or 1% of fork length, on average. This finding was not unexpected because the longest axis of the juvenile portion of the scale could only be equal to or greater than the longest axis of the juvenile portion measured along the total scale longest axis. In order to account for the 1% bias, we multiplied Equation 2 by 1.01 to yield the following length-scale relationship that was used to back-calculate juvenile coho length from adult salmon scales:

3) Live juvenile coho length (mm) = 18.025 + 201.94 (scale radius).

Adult Coho Length vs. Scale Radius

Length of adult coho salmon sampled at Bethel was correlated with their total scale radius. Adult length was significantly correlated with total scale radius in 79% of 39 years (Table 1). The slope was positive in 97% of years, including non-significant slopes. Average correlation coefficient (r) was 0.43. Correlation was not expected to be high because salmon in their final stages of maturation resorb scales and also allocate energy to body growth and fecundity rather than to maintaining scales (Bilton 1985).

Juvenile Coho Length-at-Age, 1965-2006

Back-calculation of juvenile coho length-at-age from adult scales (i.e., smolts that survived ocean residence) collected near Bethel indicated that coho salmon averaged 72.6 ± 3.9 mm (SD) after the first year and 126.7 ± 5.5 mm when they migrated as smolts after spending two winters in freshwater (Fig. 5). Growth during the second year was approximately 54.1 ± 3.6 mm.

The time series of juvenile coho lengths revealed distinct shifts in growth during the first year in freshwater and total smolt length (Fig. 5). At the end of the first growing season, coho length was typically below average from 1962 to 1975 (69.4 ± 3.1), above average during 1977 to 1996 (75.0 ± 2.8), then below average from 1997 to 2003 (71.3 ± 3.4). Size of the age-2 smolts followed a similar pattern over time, largely reflecting growth experienced during the first growing season. However, growth during the second growing season was variable, and it did not show a distinct pattern.

The increase in back-calculated smolt length corresponded with the 1976/77 ocean regime shift (Fig. 5). Winter air temperature at Bethel (December to April) also increased in 1977 and 1978 and remained relatively high through 2006 (Fig. 5). Exploratory analyses indicated that mean air temperature of the three winters prior to smolt migration (i.e., winters that influenced rearing conditions) explained 26% of the variation in smolt length. Mean length of parent-year coho salmon did not explain length of their progeny ($P > 0.05$). Thus, although a shift in air temperature corresponded with the shift in smolt length-at-age, air temperature explained only a small percentage in year to year variability in smolt length, indicating other factors in the watershed contributed to smolt length or that smolt length back-calculated from scales was influenced by variable size-dependent mortality at sea.

Juvenile Coho Growth Dependency on Prior Growth

Growth of <u>individual</u> coho salmon during the second season in freshwater was sometimes negatively correlated with growth during the first season, although only 28% of the 39 years of sampling near Bethel yielded statistically significant relationships (Table 1) and two of the eleven significant relationships were positive. The average correlation coefficient was low ($r = -0.10$) and 69% of the annual relationships were negative.

In contrast, scale growth of individual salmon during the second season in freshwater tended to be positively correlated with scale growth during the last four circuli of the first growing season (Table 1). Approximately 97% of the annual correlations were positive and 41% were statistically significant ($P < 0.05$), suggesting that second year growth was weakly related to late summer growth during the previous year. The average correlation coefficient was low ($r = 0.23$).

Approximately 82% of the correlations between FW2 and FW1 excluding the last four circuli were negative, including non-significant correlations. Interestingly, four of the seven positive correlations occurred during 1977-1981, i.e., immediately after the regime shift.

Scale growth of individual salmon during the first season in the ocean (SW1) was positively correlated with total growth in freshwater during 92% of the 39 years, and 41% of these relationships were statistically significant (Table 1).

Scale growth of individual coho salmon during the second and final season in the ocean (SWPL) was positively correlated with total previous scale growth (FW1, FW2, SW1), but SWPL growth was primarily correlated with maximum scale growth (5 circuli) during the first year in the ocean (SW1) (Table 1). Approximately 97% of the relationships with SW1 had positive slopes and 79% were statistically significant.

Adult length (mm) of individual coho salmon was positively, albeit weakly, correlated with smolt length, which was back-calculated from their scales. Approximately 77% of the annual correlations were positive (avg. $r = 0.14$) and 23% of the annual relationships were statistically significant (Table 1).

Juvenile Coho Length in Watersheds

Mean back-calculated length of juvenile coho salmon at the end of the first growing season (rearing years 2001-2005) ranged from 65.8 ± 3.4 mm in the Kanektok River to 73.9 ± 3.3 mm in the Takotna River (Fig. 6). The maximum difference in mean growth among the watersheds was approximately 8.1 mm or 12% of body length.

Kanektok (120.5 ± 3.1 mm) and Takotna (142.7 ± 9.7 mm) rivers also produced the smallest and largest smolts (smolt years 2002-2006), respectively (Fig. 6). Difference in maximum versus minimum mean smolt length in the eight tributaries was approximately 22 mm or 18% of total body length. Growth during the second year in freshwater was greatest in the Takotna and Tatlawiksuk rivers and lowest in the two coastal watersheds, Kanektok and MF Goodnews rivers (Fig. 7).

Two factor ANOVAs (stock, cohort) indicated that the interaction between stock and year was statistically significant ($df = 4, 1230$; $F = 4.84$, $P < 0.05$), suggesting that stock-specific growth during each year in freshwater was not consistent among all cohorts. This test was limited to the five stocks that had length measurements during all five years. Single factor ANOVAs for each cohort indicated that growth in each watershed was typically significantly different from growth in other watersheds ($P < 0.05$, Fig. 8). Stocks having relatively high average growth (e.g., Takotna) tended to have relatively high growth in each year, and visa versa.

Comparison of annual mean lengths of juvenile coho salmon (Fig. 8) suggested that coho salmon originating farther upriver from the ocean tended to produce larger smolts, largely in response to growth during the second rather than first year in freshwater. Statistical analyses of mean annual growth confirmed this observation (Fig. 9). Length of coho smolts and growth during the second year in freshwater increased with distance (km) from the ocean ($n = 37$, $P < 0.05$). Distance from the ocean explained approximately 20% and 18% in annual mean 2nd-year growth and total length of coho salmon, respectively. Coho length at the end of the first growing season was not significantly correlated with distance from the ocean ($r = 0.21$, $P > 0.05$).

In contrast to the positive relationship between smolt length and distance from the ocean, length of adult coho salmon (age-2.1) was inversely related to distance from the ocean ($P < 0.05$). Distance from the ocean explained 30% of the variability in annual mean length of the coho salmon stocks (Fig. 9c).

Juvenile Coho Length vs. Watershed Characteristics

Back-calculated length of juvenile coho salmon after one year in freshwater (mean of smolt years 2002-2006) was positively correlated with the amount of floodplain habitat in the watershed ($r = 0.82$), summer water temperature ($r = 0.73$), and floodplain sinuosity ($r = 0.70$). The adult coho production index (fish per km^2), adult productivity index (S/S), and the juvenile density index (competition) were not associated with back-calculated juvenile length at the end of the first year in freshwater ($P > 0.05$).

The following multivariate model described approximately 94% in the mean length of coho salmon (mean of smolt years 2002-2006) after one year in the watershed (Fig. 10):

4) Age-1 length (mm) = 58.2 + 0.022(Floodplain area) + 1.21(Temperature) – 0.02(Elevation),

where overall $P < 0.001$, P(floodplain area) = 0.004, P(temperature) = 0.026, and P(watershed elevation) = 0.017. This model suggests that coho length during the first year in freshwater was primarily influenced by the amount of floodplain habitat in the watershed followed by average summer water temperature in the mainstem river, and negatively influenced by average elevation of the watershed.

Growth of juvenile coho salmon during the second year in freshwater (mean of smolt years 2002-2006) was positively correlated with water temperature ($r = 0.95$) and distance from the ocean ($r = 0.69$, $P = 0.057$). Coho growth was negatively correlated with index of juvenile coho abundance ($P < 0.05$), but this relationship was likely spurious because it was no longer significant when water temperature was included in the model. Mean summer water temperature in the watershed explained the greatest amount of variability in mean coho salmon growth during the second year in freshwater (90%; Fig. 11). After inclusion of water temperature in the growth model, watershed gradient was a statistically significant variable as shown in the following multivariate model:

5)   Age-2 coho growth (mm) = 5.75 + 5.0(Temperature) – 4.13(Gradient),

where overall $P < 0.001$, P(Temperature) < 0.001, P(Gradient) = 0.046. This model explained 95% of the variability in mean coho growth during the second year in freshwater. Growth was primarily influenced by water temperature, but growth may have been reduced in watersheds having steeper gradient. No other variables were significant after inclusion of water temperature in the model.

Length of age-2 coho salmon smolts was positively correlated with mean summer water temperature ($r = 0.94$), age-2 growth ($r = 0.96$), and age-1 length ($r = 0.87$). Age-2 coho smolt length could be explained by the following multivariate model (Fig. 12):

6)   Age-2 coho length (mm) = -4.08 + 5.47(Temperature) + 1.036(Age-1 coho length),

where overall $P < 0.001$, P(Temperature) = 0.005, and P(age-1 length) = 0.03. Approximately 94% if the variability in mean age-2 coho smolt length in the watersheds was explained by water temperature and length after the first year of growth. The model indicates that water temperature had a greater influence in explaining mean smolt length than first year growth. Exploratory analyses involving the indices of juvenile coho productivity and density (competition) did not provide significant information for explaining variation in length of age-2 coho salmon in the watershed.

Juvenile Coho Length vs. Pink Salmon

Length-at-age of juvenile coho salmon was first examined in tributaries having relatively few adult pink salmon (e.g., Tuluksak, George, Kogrukluk, Tatlawiksuk, and Takotna rivers) in both even- and odd-numbered years. Back-calculated length of age-1 juveniles, age-2 smolts, and growth during the second year in freshwater did not significantly differ between odd- and even-numbered years of rearing (two-factor ANOVAs (odd/even year, river), df = 1, 1198; $P > 0.05$). As reported above, length was significantly different among the rivers (df = 4, 1198; $P < 0.05$). The interaction between odd-even year and river was non-significant for age-1 length ($P > 0.05$), but statistically significant for age-2 smolt length and growth during year two (df = 4, 1198; $P < 0.05$). The significant interaction effect suggests the effect of river on coho length was not consistent among odd- and even-numbered years. For example, length of juvenile coho salmon produced from Tuluksak, George, and Kogrukluk rivers tended to be greater when returning to rivers in even-numbered years as adults, whereas length of juvenile coho salmon produced from the uppermost tributaries (Tatlawiksuk[1] and Takotna) tended to be greater when returning to rivers in odd-numbered years.

In contrast, the odd/even year effect on juvenile coho salmon growth was significant for tributaries that typically receive moderate to large numbers of adult pink salmon in even-numbered years, e.g., MF Goodnews, Kanektok, and Kwethluk rivers. In these rivers, length of age-1 coho salmon was significantly greater in odd rearing years, corresponding with parents that returned in the previous even-numbered year (two-factor ANOVA (odd/even year, river), df = 1, 648; $P < 0.001$). On average, age-1 length was 5.4 mm or 8% longer in odd- versus even-numbered rearing years. Length varied significantly among the three rivers (df = 2, 648; $P < 0.001$, but interaction between the two factors was not significant ($P > 0.05$), indicating the odd-even effect was consistent among rivers.

Growth of coho salmon during the second year in freshwater (rivers with numerous pink salmon only) was significantly greater during odd-numbered rearing years (two-factor ANOVAs (odd/even year, river), df = 1, 648; $P = 0.015$). Numerous pink salmon fry would have been available for these coho salmon in odd-numbered years. On average, coho salmon growth during the second year was 1 mm or 2% longer in odd versus even-numbered rearing years. Growth varied significantly between the three rivers (df = 2, 648; $P < 0.001$, but interaction between the two factors was non-significant ($P > 0.05$) indicating the odd-even effect was consistent among the rivers.

Length of age-2 coho smolts was not significantly different during odd- versus even-numbered years (df = 1, 648; $P > 0.05$), reflecting the opposing growth patterns during the first and second years in freshwater. Growth varied significantly among the three rivers (df = 2, 648; $P < 0.001$, but interaction between the two factors (odd/even year, river) was not significant ($P > 0.05$), indicating the odd-even effect was consistent among the rivers.

Early marine growth of age-2 smolts (1st six circuli and 12 circuli) was not significantly greater during odd-numbered years, as would be expected if they consumed numerous pink salmon fry. This finding was consistent for the lower three tributaries that supported relatively great numbers of pink salmon (df = 1, 648; $P > 0.05$) and for all eight tributaries examined (df = 1, 1846; $P > 0.05$).

Length of Kuskokwim vs. Other Juvenile Coho Stocks

Average length of age-1 Kuskokwim area coho salmon, based on back-calculation from adult scales, ranged from 67 mm in Kuskokwim Bay tributaries, to 70 mm for six Kuskokwim River tributaries, and to 73 mm for the aggregate juvenile population

[1] The confluence of the Tatlawiksuk and Kuskokwim rivers is upstream of the confluence of the Holitna and Kuskokwim rivers. Kogrukluk River is a tributary of the Holitna River. If this growth pattern was real, and verified with additional years of data, then it would worthwhile to know whether or not the growth pattern was related to genetic composition, environment, or both.

sampled at Bethel during the past 39 years (Table 4). Average length of the age-2 Kuskokwim coho salmon groupings was 122 mm, 133 mm, and 131 mm, respectively. On average, age-2 Kuskokwim area smolts gained approximately 84% more length by staying in freshwater for an additional year. Approximately 89% of adult Kuskokwim coho salmon returned after spending two winters in freshwater, indicating most smolts migrated at age-2 (based on analysis of coho sampled for age near Bethel, 1965-2006).

Age-1 and age-2 coho salmon smolts in other watersheds in Alaska, British Columbia, and Russia averaged 93 mm (range: 77-122 mm) and 112 mm (range: 94-135 mm), respectively (Table 4). On average, these coho salmon gained approximately 23% more length when migrating as age-2 versus age-1 smolts. Thus, back-calculated length of age-1 Kuskokwim coho salmon was less than length of age-1 smolts from other regions, but back-calculated length of age-2 Kuskokwim smolts was typically longer than age-2 smolts from other regions.

DISCUSSION

Juvenile Coho Length v. Scale Radius

A number of studies have shown that scale radii measurements are correlated with salmon length (e.g., Henderson and Cass 1991, Fukuwaka and Kaeriyama 1997, Fisher and Pearcy 2005, Ruggerone et al. 2009a,b). Our findings are consistent with these earlier studies. Length of juvenile coho salmon from the Kuskokwim area was highly correlated with scale radius. Furthermore, comparison of the length/scale radius relationships among five watersheds did not indicate this relationship differed from watershed to watershed, as might occur if fish body shape at a given size changed among the watersheds. The consistency in the length-scale relationships among the watersheds provides some evidence that the length-scale relationship may not change significantly from year-to-year. However, year-to-year variation in the length-scale relationship was not examined here, therefore this limitation should be considered when examining back-calculated coho lengths during years prior to the development of the length-scale relationship.

Juvenile Coho Length-at-age, 1965-2006

The time series of juvenile coho lengths revealed distinct shifts in size during the first year in freshwater and total smolt length. At the end of the first growing season, coho length was below average from 1962 to 1975 (smolt years), above average during 1977 to 1996, then typically below average from 1997 to 2005. Length of the age-2 smolts followed a similar pattern over time, largely reflecting growth experienced during the first growing season.

The increase in back-calculated smolt length corresponded with the 1976/77 ocean regime shift and with mean winter air temperature at Bethel Airport (December to April).

The variable but somewhat lower length beginning in 1997 corresponded with the 1997/1998 El Niño. Although winter air temperature seemed to explain the sudden increase in coho smolt length in the late 1970s, air temperature explained only 26% of the variation in coho smolt length throughout the time period. Air temperature did not explain the typically below average smolt size that began in 2000. As described previously, mean size of parent coho did not explain length of their progeny. We are continuing to explore other factors that may have influenced growth patterns of coho salmon, including seasonal flows in the Kuskokwim watershed.

Coho Growth Dependency

Growth of individual coho salmon during the second year in freshwater was not correlated with total growth during the first year. However, growth during the second year in freshwater was weakly correlated (positive) with late season scale growth during the first year in freshwater. Thus, late summer growth during the first year appeared to influence growth during the second year in freshwater.

Growth of individual coho salmon during the second year in freshwater tended to be negatively correlated with growth during the first year in freshwater after late summer growth (last four circuli) was excluded. This weak relationship might reflect evidence for catch-up growth and survival of coho salmon that grew relatively fast during the second year in freshwater. Interestingly, the relationship between early first year growth and that during the second year in freshwater was positive during years immediately after the 1977 regime shift, a period when first year growth was relatively great. This pattern might reflect a weaker relationship between catch-up growth and risk of mortality when initial growth is relatively great, as observed among AYK Chinook salmon (Ruggerone et al. 2009a). More research is needed to explore this possible relationship.

Scale growth of individual coho salmon during the first year in the ocean tended to be positively correlated with total growth in freshwater. Scale growth during the final (second) year at sea was correlated with previous scale growth. These findings were consistent with observations of growth dependency on prior growth among Kuskokwim and Yukon Chinook salmon (Ruggerone et al. 2009a). However, dependency of salmon growth on prior growth was stronger for Chinook salmon than coho salmon. Greater size of coho and Chinook salmon may provide greater opportunities for consuming larger and more evasive prey such as forage fishes and squid.

Juvenile Coho Length in Watersheds

Mean length of coho salmon smolts in the Kuskokwim area tended to be greater among stocks originating from watersheds farther from the ocean, largely in response to greater growth during the second year in freshwater. However, further analysis suggested that length at the end of the first year in freshwater was positively correlated with greater floodplain area and greater mean summer water temperature of the watershed, and negatively correlated with average elevation of the watershed. This model did not attempt to explain year-to-year variation in coho length. The amount of floodplain habitat was the primary variable in the model based on standardized regression coefficients. The importance of floodplain habitat makes sense because coho salmon often rear and feed upon insect prey and small fishes in side channels, which are more numerous in floodplain areas. Thus, this analysis suggests floodplain habitat should be protected because it is important in maintaining productivity (growth) of juvenile coho salmon.

The multivariate analysis involving coho growth in the first year assumed that the mean summer water temperature collected near the weir sites in 2008 and 2009 was representative of relative water temperature typically experienced by coho in each of the watersheds. The statistical model was biologically sensible, but coho salmon in a watershed potentially encounter a broad range of water temperatures that differ from those collected at the weir sites. But it was conceivable that water temperature in these side channel habitats was influenced by mainstem flow and temperature. Average elevation of the watershed was negatively correlated with age-1 coho length after one year. This variable may reflect potential effects of both water temperature and stream gradient, although watershed gradient did not provide information that explained length of subyearling coho salmon.

Growth of juvenile coho salmon during the second year in freshwater (i.e., yearlings) was positively correlated with mean summer water temperature of the watershed and negatively correlated with watershed gradient. This relationship makes biological sense, but it assumes water temperature at the weir was representative of rearing water temperature as noted above. Temperature was the most important variable. The negative effect of watershed gradient may reflect potentially greater habitat availability and quality in watersheds having a somewhat lower gradient.

Mean length of age-2 coho smolts was best explained by growth during the first year in freshwater and mean summer water temperature. As noted above, water temperature in addition to floodplain habitat appears to be a key variable influencing growth of Kuskokwim coho salmon. This makes biological sense because coho salmon in Alaska can process much more food when temperatures are relatively warm (Ruggerone 1989). Biological variables, such as coho density and coho productivity, which were exploratory indices, did not explain variability in mean length among the watersheds. The lack of a significant relationship could reflect the limited number of observations and/or accuracy of the indices.

Adult length of coho salmon returning to the Kuskokwim area watersheds was inversely related to the distance of those watersheds from the ocean. Larger size of lower river adult coho salmon, such as Kuskokwim Bay stocks, probably reflects the tendency for lower river coho salmon to enter freshwater somewhat later in the summer (e.g., Schaberg et al. 2010, Clark and Linderman 2007, 2008, Miller et al. 2008, Plumb and Harper 2008), thereby allowing additional foraging and growth in the ocean. Coho salmon returning to the Goodnews and Kanektok rivers in Kuskokwim Bay have the latest timing and the largest adult size-at-age. This size advantage may lead to greater reproductive potential of these fish to the extent that large female size leads to more numerous and larger eggs (Quinn et al. 2004).

Juvenile Coho Length vs. Pink Salmon

Subyearling coho salmon originating from downstream tributaries (MF Goodnews, Kanektok, and Kwethluk rivers), which support relatively abundant populations of adult pink salmon, were longer during odd-numbered years, i.e., years when numerous pink salmon fry would be present in spring. Subyearling coho salmon were too small to consume pink salmon fry that were abundant during spring of odd-numbered years, but they could potentially benefit from consumption of pink salmon eggs or carcasses during August and September. However, late season scale growth of subyearling coho salmon was not consistently greater during odd rearing years ($P > 0.05$). Growth of the scale focus, which might reflect egg size and size at emergence, was significantly greater among young-of-the-year coho during odd-numbered rearing years. Conceivably, pink salmon carcasses might lead to greater production of insects during the following year which may have led to greater growth of subyearling coho during odd-numbered rearing years. But we have no further evidence for this hypothesis. Because this test involved only five years of growth observations, we cannot rule out the potential confounding effect of water temperature or some other factor that was not measured during each of the five years.

The finding of greater odd-year growth of subyearling coho salmon in the tributaries that support relatively abundant populations of adult pink salmon was opposite of that observed when examining juvenile growth sampled from adult coho scales collected near Bethel during 1966-2006. Although statistically significant, the relationship involving scales from Bethel did not imply a major difference in growth during odd- versus even-numbered years. Tributaries upstream of Bethel support some pink salmon (e.g., Kwethluk and Kisaralik/Kasigluk Rivers) but numbers and densities of spawning pink salmon is generally low compared with tributaries downstream of Bethel and in Kuskokwim Bay. We did not detect an odd-even growth pattern among coho returning to the upstream tributaries during 2003-2007.

In the lower tributaries that support adult pink salmon, greater growth of yearling coho salmon during odd-numbered years may reflect the availability and consumption of pink salmon fry produced by adult pink salmon spawners in the previous even-numbered year. Examination of scale growth during spring and late summer periods did not reveal a significant difference between even- and odd-rearing years, probably because the annual difference in growth was small (1 mm). The observation of greater growth of yearling salmon during odd-numbered years was consistent with observations from sampling of adult coho scales near Bethel during 1966-2006. In August 2008 we observed a number of yearling coho stomachs from the MF Goodnews River containing salmon eggs, which we presumed were pink salmon eggs based on spawn timing and somewhat small size of some eggs. Thus, yearling coho salmon may consume pink salmon fry in the spring of odd-numbered years and pink salmon eggs in late summer of even-numbered years.

These feeding opportunities may off-set alternating-year growth patterns, as was expected if coho were only feeding on pink salmon fry.

Length of age-2 coho smolts and early marine scale growth of coho salmon smolts did not vary between odd- and even-numbered years, as would be expected if coho smolts consumed numerous pink salmon during migrations in odd-numbered years. This finding is consistent with the previous analysis involving scales collected near Bethel, 1966-2006 (Ruggerone and Agler 2008). In the earlier study, marine growth was greater during odd-numbered years at sea but only during the later portion of the scale growth zone corresponding to approximately late summer or fall in the ocean. In contrast, Williams et al. (2009) reported that coho smolts in Nome River were longer in 2005 and 2007 compared with 2004, 2006, and 2008, suggesting that coho smolts in Nome River may have consumed relatively abundant pink salmon fry during the odd-year smolt migration to sea.

Length of Kuskokwim vs. Other Juvenile Coho Stocks

A key difference between the length of Kuskokwim coho salmon and smolts from other regions (Alaska, British Columbia and Russia) is that the Kuskokwim coho lengths were back-calculated from scales of adult salmon that had undergone size-selective mortality. Size selective mortality, in which smaller smolts have lower survival rates, explains in part the large size of age-2 Kuskokwim smolts relative to coho in most other regions. However, favorable growing conditions also probably contributed to the large size of age-2 Kuskokwim coho salmon.

Age-1 Kuskokwim coho salmon were smaller than age-1 coho smolts from other watersheds (Table 4) even though Kuskokwim had undergone potential size-selective mortality. This size difference likely reflects larger size of age-1 smolts compared with age-1 salmon that did not migrate to sea until the following year. Faster growing juvenile salmon tend to emigrate to sea at a younger age (e.g., Burgner 1987). We back-calculated juvenile length of age-2.1 coho salmon from Unalakleet River and found that length at the end of the first growing season of these age-2 smolts was also relatively small compared with age-1 smolts (Ruggerone and Agler 2008). The relatively small size of Kuskokwim coho salmon after the first year in freshwater followed by relatively greater growth during the second year in freshwater is consistent with the high percentage of Kuskokwim smolts that migrate to sea after two years (89%) versus one year (11%) in freshwater, based on adult age composition. This characteristic is consistent with tradeoffs in growth and survival of Bristol Bay sockeye salmon smolts where juvenile salmon tend to rear in lakes for a second year when growth is relatively high and risk of mortality is low (Ruggerone and Link 2006).

A key unanswered question is why growth of age-2.1 coho salmon was relatively low during the first year, but high during the second year in freshwater. We speculate that this growth pattern might reflect the tendency for young of the year coho salmon to remain in side channels close to the spawning grounds where the water may be cooler and risk of predation might be less. During the second year, coho may move into downstream habitats where prey may be more abundant, water temperature warmer, and risk of predation less due to larger size of yearlings (e.g., see Ruggerone et al. 2009b). This behavior in juvenile coho salmon was observed in Chignik coho salmon where coho fry remained in tributaries then emigrated and reared in lakes (Ruggerone and Harvey 1995). Age-1 and age-2 coho salmon in Chignik Lake were highly piscivorous on small young of the year salmon but not on yearling salmon (Ruggerone and Rogers 1992).

Conclusions

Growth of juvenile coho salmon varied among Kuskokwim area watersheds, and the amount of floodplain habitat was the key habitat feature that affected coho salmon growth. Longer coho salmon were observed in watersheds that had greater amounts of floodplain habitat. Average water temperature and the presence of pink salmon fry (prey) also influenced growth of juvenile coho salmon. Back-calculated length of Kuskokwim coho salmon smolts appeared to be relatively high compared with coho smolts from other regions. Large size of Kuskokwim coho smolts probably contributes to the great abundance of coho salmon in the watershed. We conclude that floodplain habitat should be protected in order to maintain the high productivity of coho salmon in the Kuskokwim area.

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Table 1. Correlation between annual or cumulative scale growth of individual coho salmon and growth during the previous life stage from Kuskokwim River Area watersheds. Values are mean of annual correlations involving approximately 50 individual fish during each of 39 years of sampling near Bethel. SWPLMax5 is the largest five circuli during the homeward migration (SWPL).

Scale variables					
Dependent	Independent	n	r	% significant slopes	% positive slopes
FW2	FW1	39	-0.10 ±0.20	28%	31%
FW2	FW1, last 4 circuli	39	0.23 ±0.15	41%	97%
SW1	FW1 & FW2	39	0.27 ±0.19	41%	92%
SWPLMax5	FW1 & FW2 & SW1	39	0.28 ±0.23	62%	87%
SWPLMax5	SW1, maximum 8 circuli	39	0.43 ±0.19	79%	97%
Adult length	Smolt length	39	0.14 ±0.18	23%	77%
Adult length	Total scale	39	0.43 ±0.18	79%	97%

Table 2. Physical characteristics of Kuskokwim area watersheds, as estimated by the Riverscape Analysis Project (RAP), University of Montana (www.umt.edu/flbs/Research/default.htm). Source: D. Whited, Flathead Lake Biological Station, University of Montana.

Watershed	Distance from ocean (km)	Area (km^2)	Elevation range (m)	Avg. elevation (m)	Watershed gradient (m/km^2)	Floodplain area (km^2)	Floodplain area /watershed (%)	Floodplain sinuosity	Nodes per km	Water temperature (C)
MF Goodnews	16	719	869	186	1.209	64	0.09	1.08	1.82	10.9
Kanektok	68	2562	1255	339	0.490	120	0.05	1.11	2.17	10.5
Kwethluk	190	3847	1449	245	0.377	249	0.06	1.68	0.70	11.4
Tuluksak	222	2179	1077	209	0.494	188	0.09	1.99	0.03	10.9
George	453	3558	838	269	0.236	60	0.02	1.10	0.76	11.1
Tatlawiksuk	568	2060	946	245	0.459	87	0.04	1.46	0.64	12.5
Kogrukluk	710	2058	912	317	0.443	121	0.06	1.74	0.48	10.8
Takotna	835	5710	1253	281	0.219	288	0.05	1.86	0.38	13.0
Kuskokwim	0	118019	3549	353	0.030	8541	0.07	1.41	0.85	

[a] Water temperature is reported as average July-August values as determined from continuous monitoring data loggers located near the mainstem river weir.

Table 3. Biological characteristics of Kuskokwim River Area watersheds. Spawning escapement, spawning density, and back-calculated juvenile length data based on adults returning during 2003-2007.

Watershed	Avg spawning escapement	Coho adults per watershed area (km^2)	Coho adults per floodplain area (km^2)	Age-1 coho length (mm)	Age-2 coho length (mm)	Coho growth year 2 (mm)
MF Goodnews	36,065	61	686	68.9	124.4	55.5
Kanektok	64,524	40	860	65.8	120.5	54.7
Kwethluk	64,368	32	492	73.0	135.5	62.5
Tuluksak	18,173	11	131	70.7	128.6	58.0
George	19,096	6	333	66.9	128.5	61.6
Tatlawiksuk	10,558	5	123	70.3	136.8	66.5
Kogrukluk	36,277	18	301	68.0	125.3	57.3
Takotna	4,243	1	16	73.9	142.7	68.8

[a] Average spawning escapement was determined from annual weir escapements that include unofficial expansions for a standardized operational period.

Table 4. Comparison of mean coho salmon smolt length from the Kuskokwim River Area with those from other regions. Note that the Kuskokwim and Unalakleet length values were back-calculated from age 2.1 adult scales, i.e., fish that likely had experienced size-selective mortality. Back-calculated age 1 lengths are from fish that stayed in freshwater an additional year, not age 1 smolts.

Stock	Area	Habitat	No. years	Mean Length (mm) Age 1	Age 2	% increase	Source
Kuskokwim R (Bethel)	AYK	Stream	39	73	131	79%	This study, 1967-2006
Kuskokwim R (6 tributaries)		Stream	5	70	133	90%	This study, recent years
Kuskokwim Bay (2 tributaries)		Stream	5	67	122	82%	This study, recent years
Nome R	Norton Sound	Stream	5	93	108	16%	Williams et al. 2009
Unalakleet R		Stream	28	75	126	68%	Ruggerone & Agler 2008
Chignik	AK Peninsula	Lake	3	103	129	25%	Ruggerone 1989
Jordan Cr	Cook Inlet	Stream	4	85	111	30%	Briscoe et al. 2008
Duck Cr		Stream	2	106	131	23%	Briscoe et al. 2008
Resurrection Bay	Kenai Peninsula		-	122	135	11%	Sandercock 1991
Taku R	SEAK		5	92	114	23%	Yanusz et al. 1999
Yehring Cr		Stream	1	84	94	12%	Yanusz et al. 1999
Nakwasina R		Stream	5	79	99	24%	Tydingo 2006
Bridge Cr		Stream	3	80	97	20%	Tydingo 2006
Chilkat R			2	83	101	22%	Ericksen 2003
Chilkat Lake		Lake	1	101	128	27%	Ericksen 2003
Chilkat Trib		Stream	2	82	98	19%	Ericksen 2003
Slippery Cr		Lake	2	99	117	18%	Fleming 2005
Chuck Cr		Stream	4	99	115	17%	McCurdy 2009
Carnation Cr	British Columbia	Stream	-	77	101	32%	Sandercock 1991
Cowichan R			-	94	102	9%	Sandercock 1991
Paratunka R	Kamchatka		-	110	130	18%	Sandercock 1991

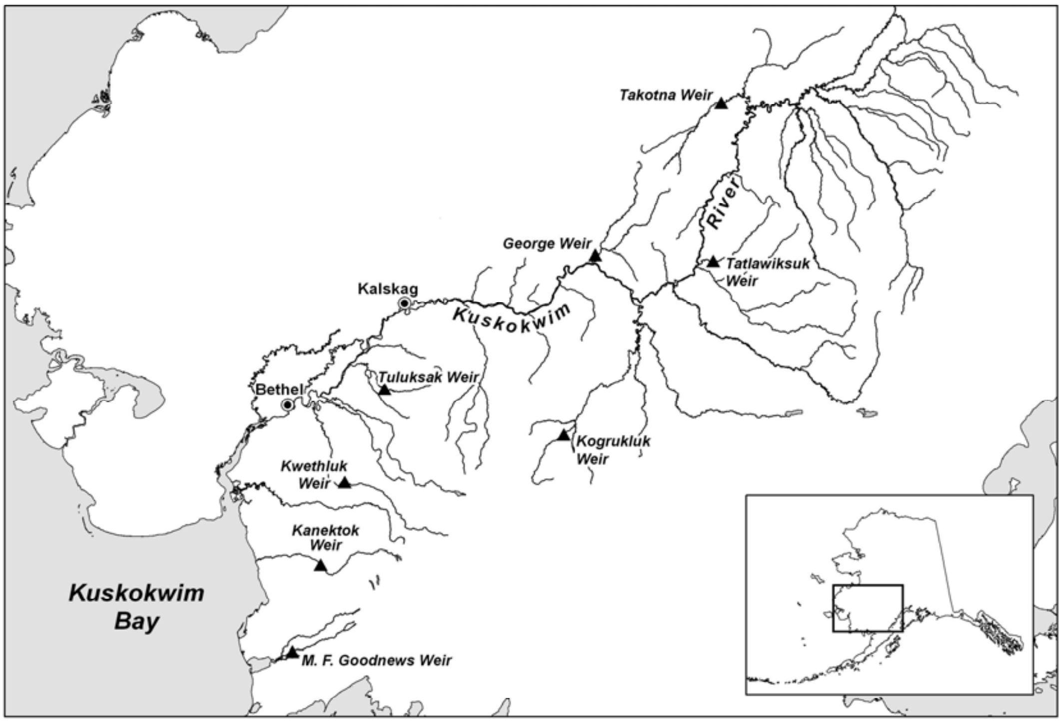

Fig. 1. Location of weirs on the Kuskokwim River and Kuskokwim Bay tributaries (Kuskokwim River Area) where coho salmon were sampled.

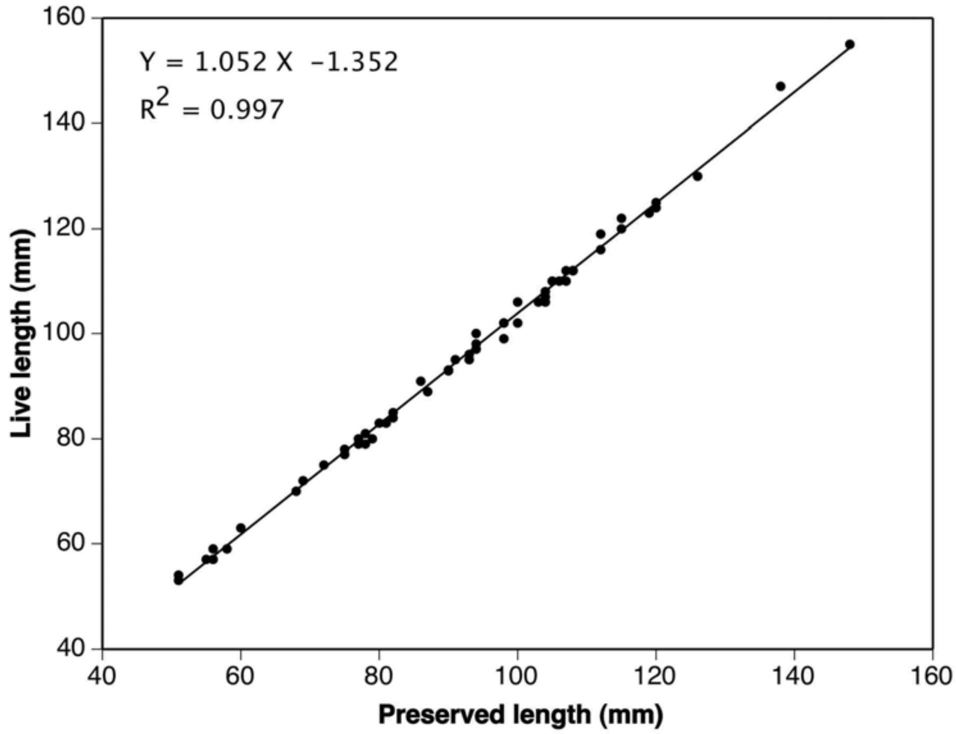

Fig. 2. Relationship between live and preserved fork length of juvenile Kuskokwim coho salmon.

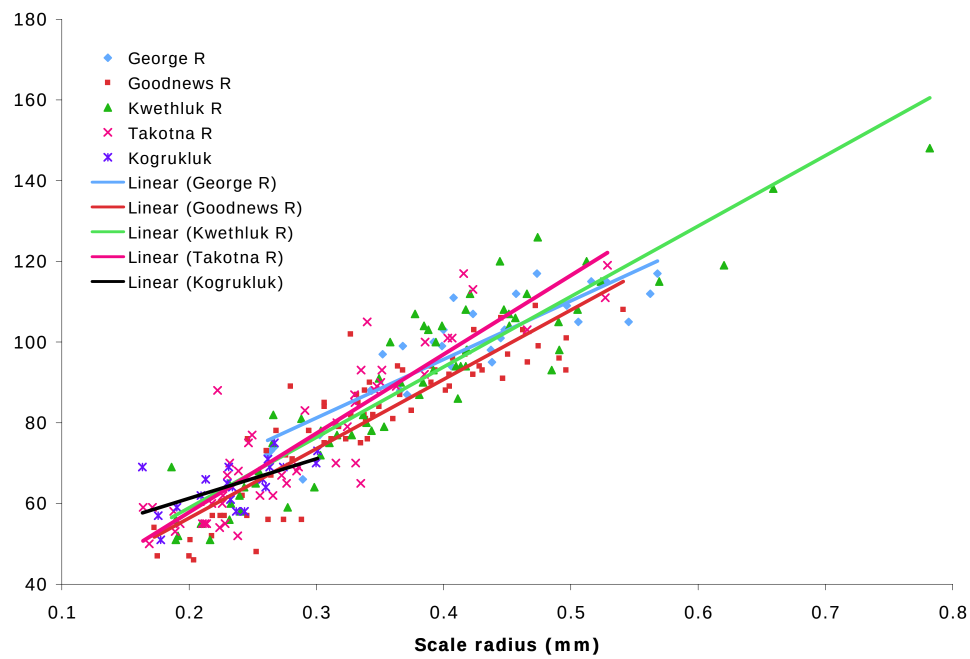

Fig. 3. Relationships between the preserved length of coho salmon collected from four Kuskokwim River Area watersheds and the total scale radius.

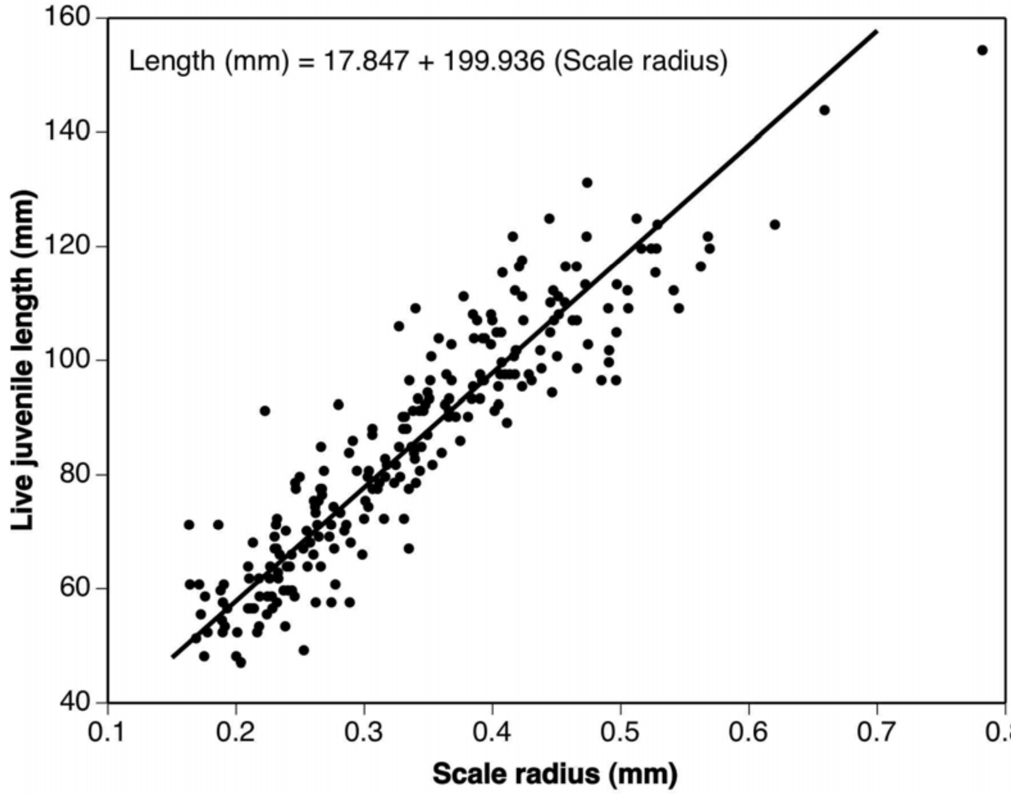

Fig. 4. Relationship between live length of juvenile coho salmon from the Kuskokwim River Area and their scale radius. Geometric regression equation is shown. See adjustment shown in equation 3.

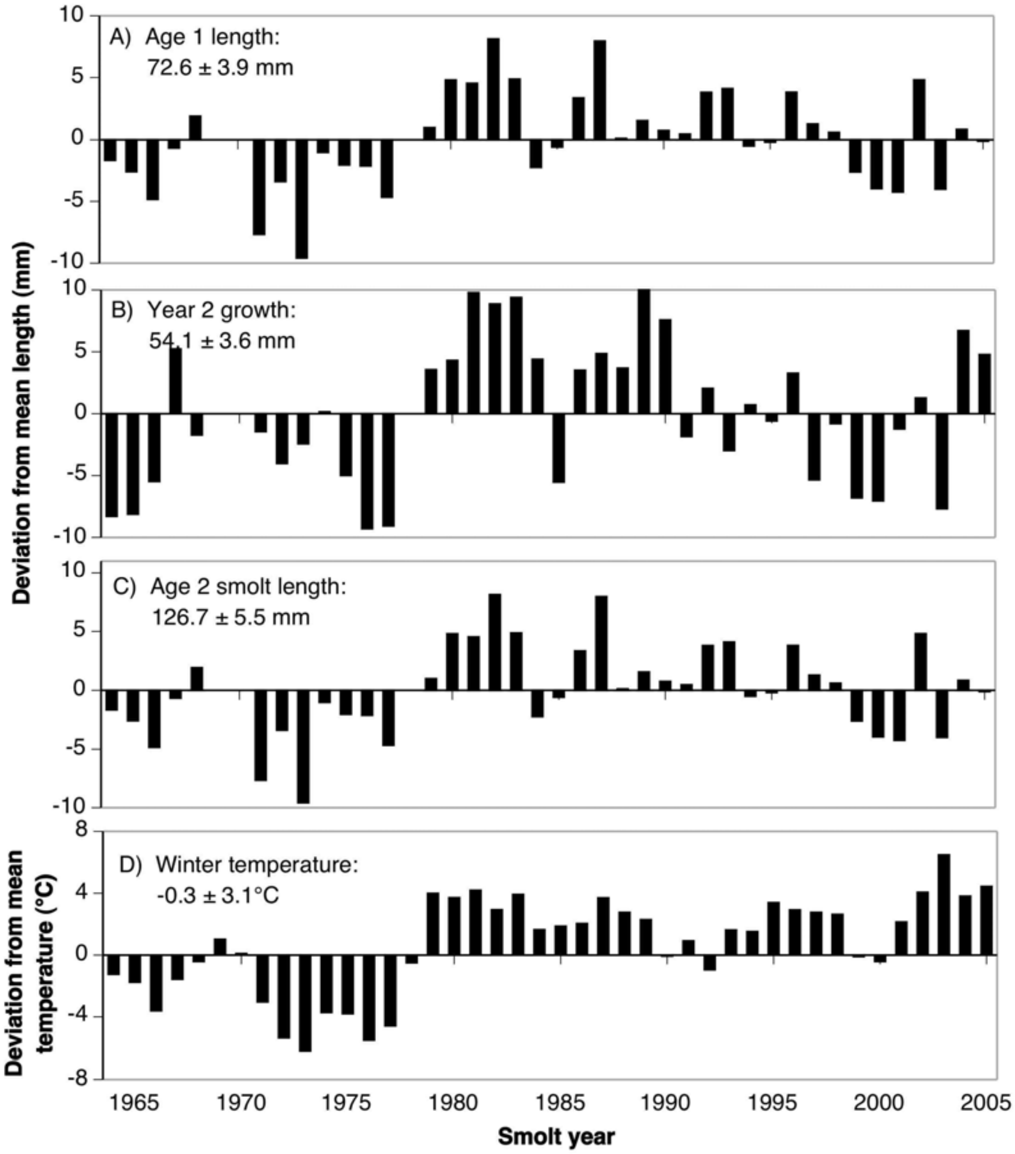

Fig. 5 Mean live length of juvenile coho salmon originating from the Kuskokwim River at the end of the first (A) and second growing seasons (C), the incremental growth during the second season (B), and mean winter air temperature (December to April) at Bethel Airport during three years prior to smolt migration. Length values were back calculated from adult scales collected from coho salmon sampled near Bethel, 1965-2006. No data for 1969,1970, and 1978.

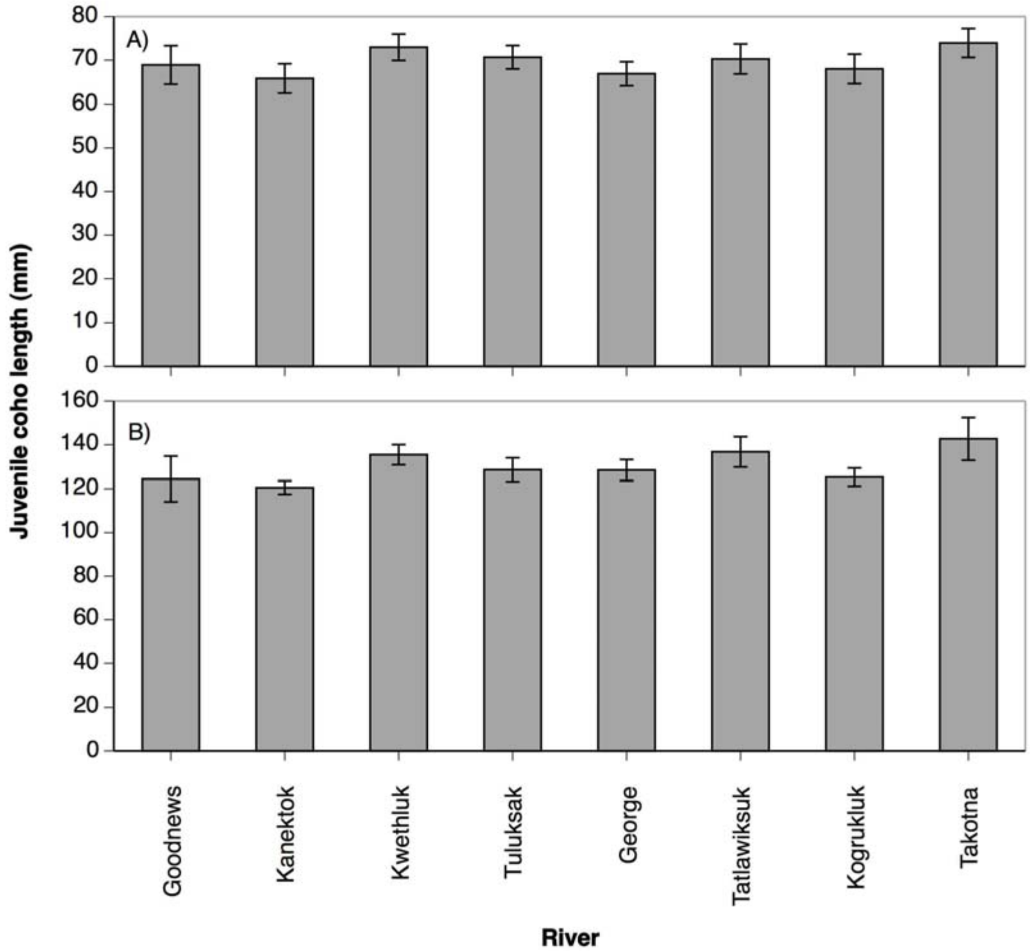

Fig. 6. Mean length (± 1 SD) of juvenile coho salmon originating from Kuskokwim area watersheds at the end of the first growing season (A) and as age-2 smolts (B). Distance of rivers from the mouth of the Kuskokwim River increases from left to right. Goodnews and Kanektok rivers discharge into Kuskokwim Bay. Values back-calculated from adult scales collected from fish in each watershed, 2003-2007 (smolt years 2002-2006).

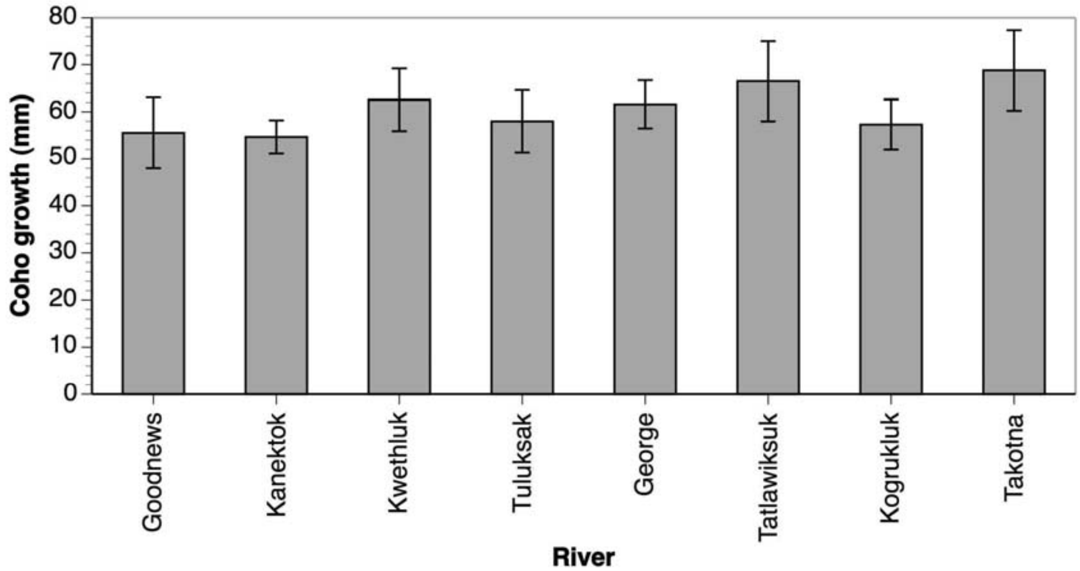

Fig. 7. Mean growth (± 1 SD) of juvenile coho salmon originating from Kuskokwim area watersheds during the second growing season (FW2). Values back calculated from adult scales collected from fish in each watershed, 2003-2007 (smolt years 2002-2006).

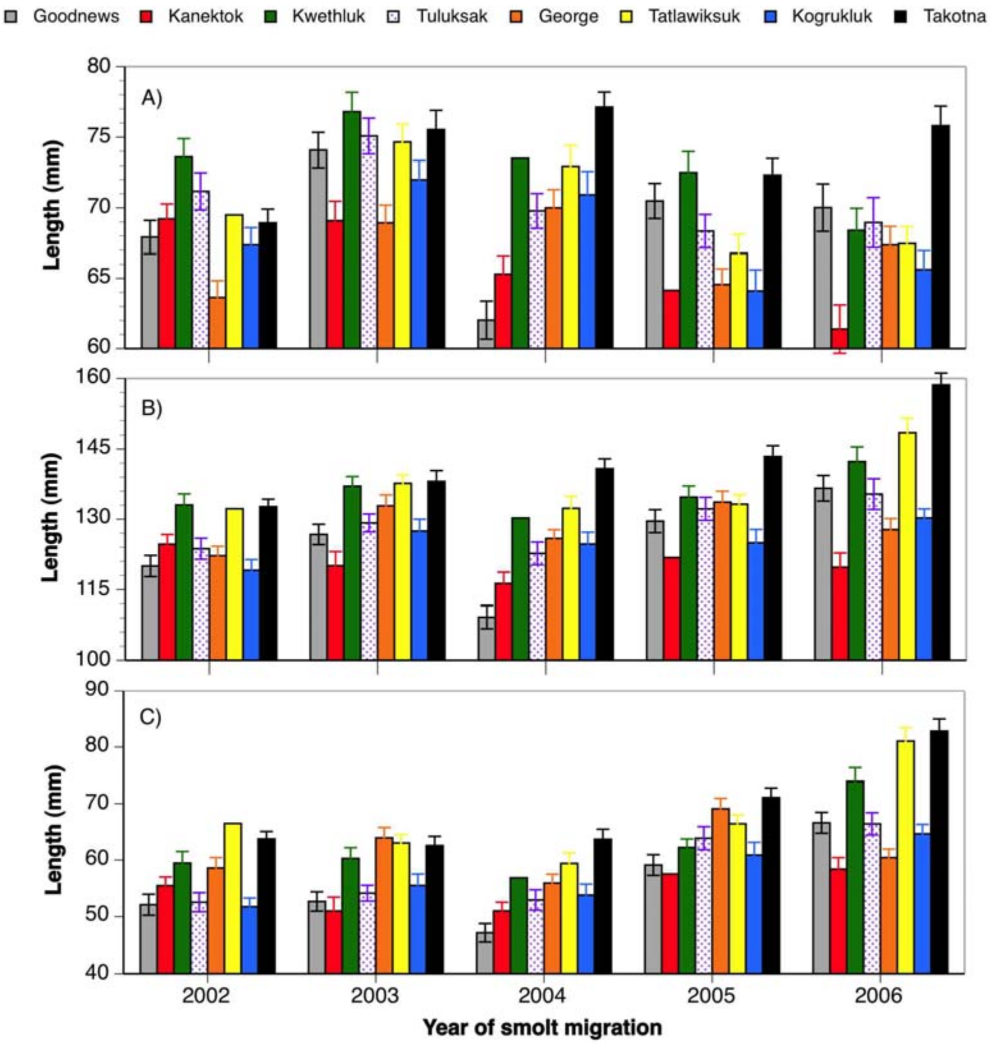

Fig. 8. Mean annual length (± 1 SE) of juvenile coho salmon originating from each Kuskokwim area watershed after A) the first season, B) the combined first and second seasons, and C) within the second season only. Values back-calculated from adult scales collected from fish in each watershed, 2003-2007 (smolt years 2002-2006). Three missing length values were estimated and shown here without error bars. Stock order (left to right) reflects distance from mouth of Kuskokwim River.

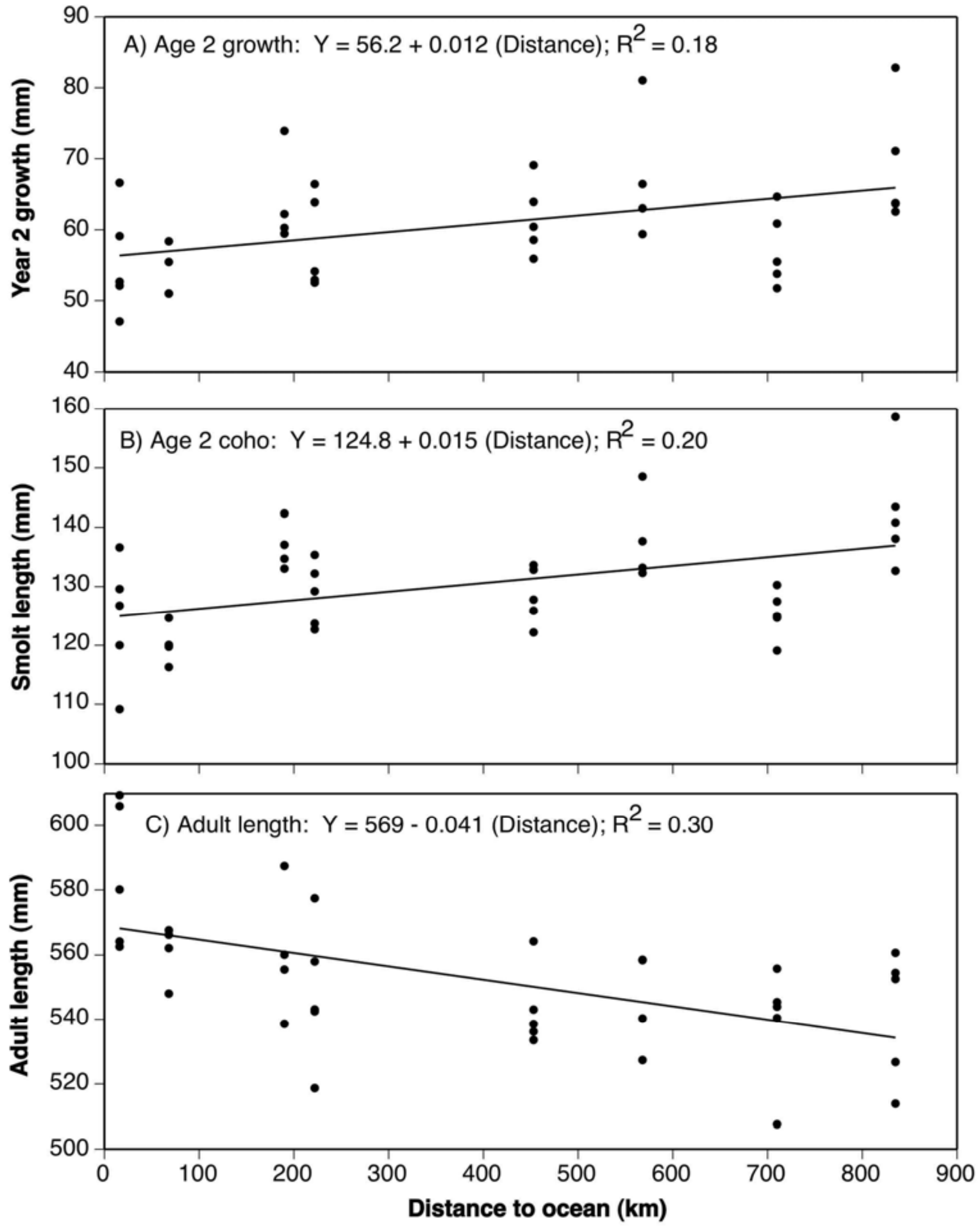

Fig. 9. Relationship between A) coho growth during the second year in freshwater, B) length of age-2 coho smolts, C) adult length (age-2.1) and the distance of each stock from the ocean. Distance is based on the location of weirs in which adult coho salmon were sampled for scales and adult length. Each value is the annual mean of approximately 50 coho salmon during 2003-2007.

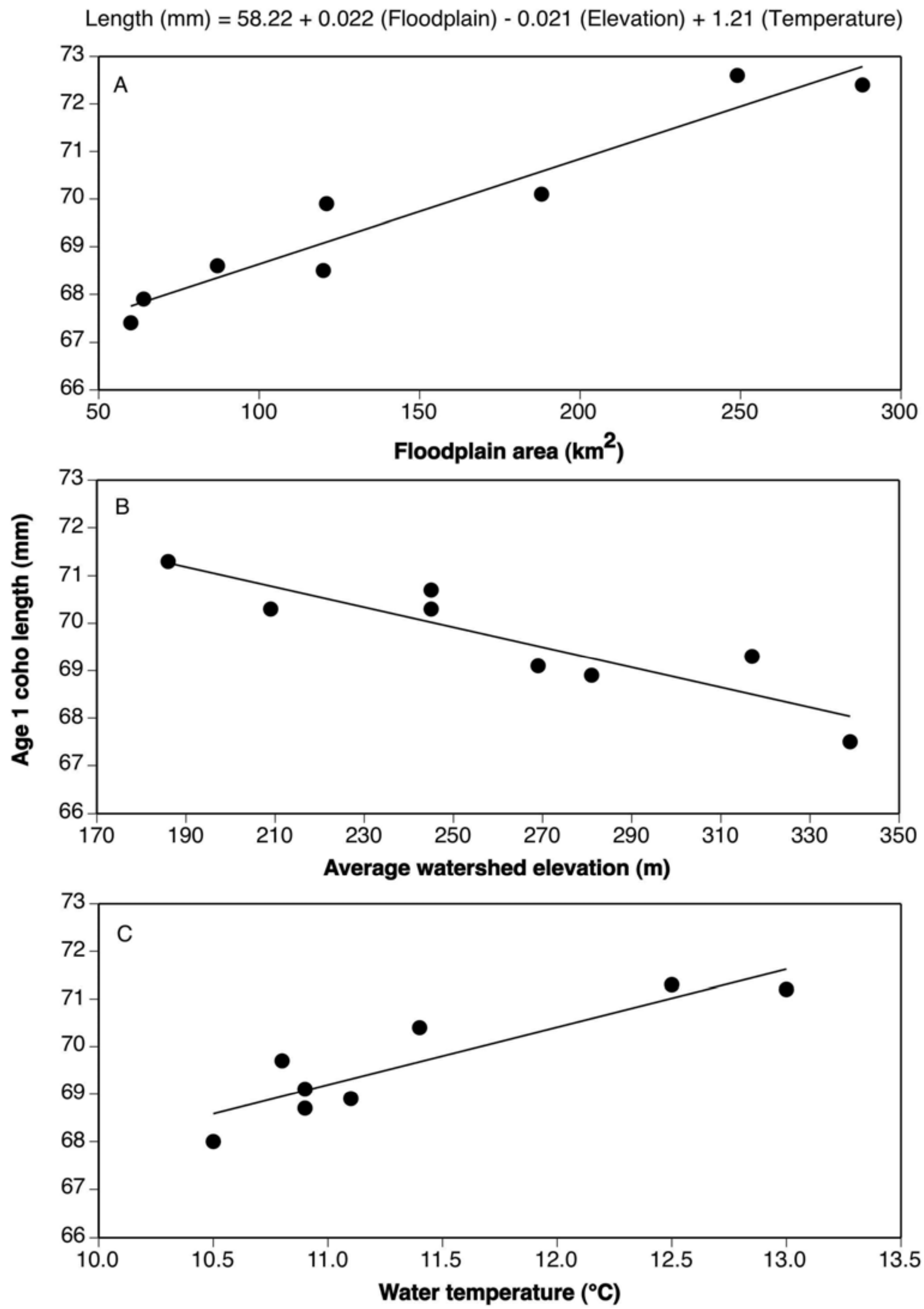

Fig. 10. Multivariate relationship between annual mean length of juvenile coho salmon after one year in freshwater and the following watershed characteristics: A) floodplain habitat area, B) average elevation, and C) average summer water temperature. Length values were calculated from the mean of back-calculated lengths for each of eight watersheds. The plots are based on partial residual analysis, which shows the influence of each independent variable while incorporating other variables in the model.

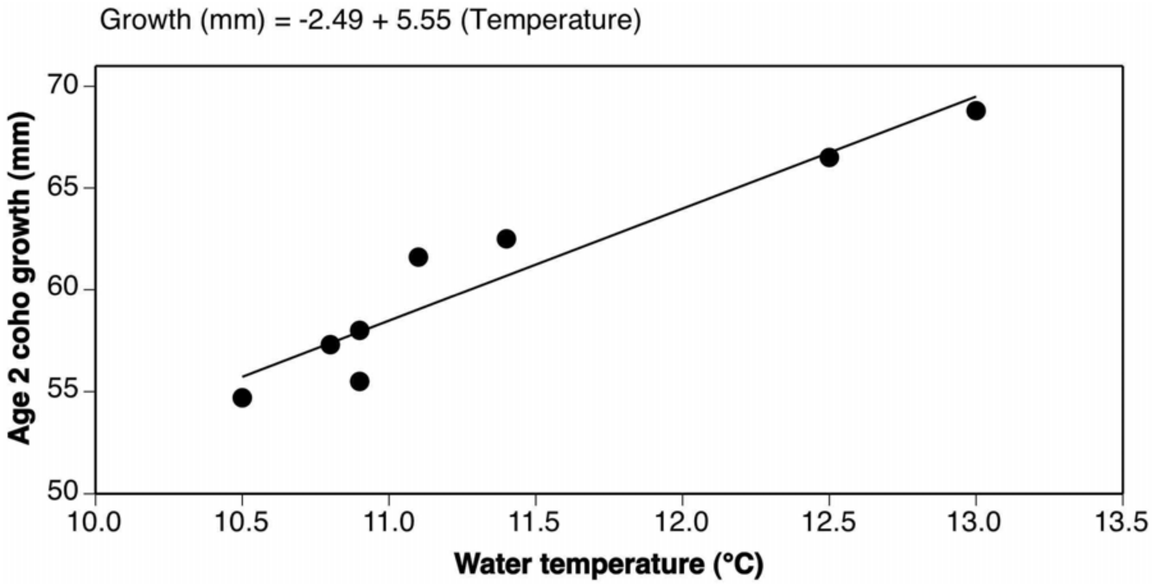

Fig. 11. Relationship between mean annual coho salmon growth during the second year in freshwater and average summer water temperature in each of the eight watersheds where coho were sampled. Length values were calculated from the mean of back-calculated lengths for each watershed.

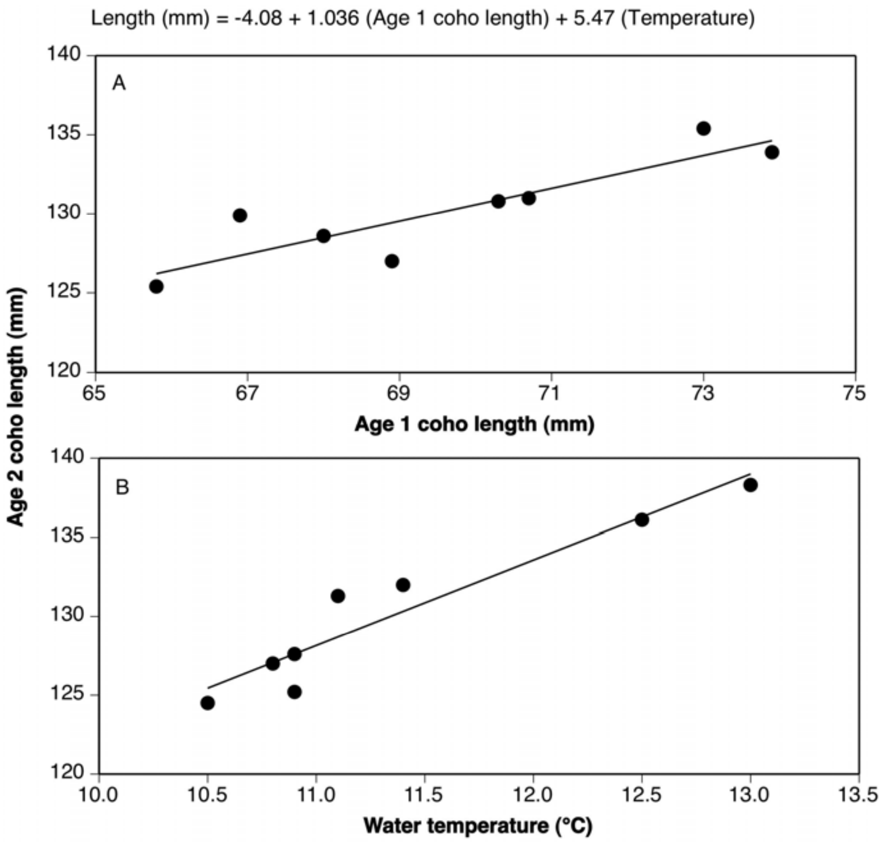

Fig. 12. Multivariate relationship between annual mean length of juvenile coho salmon after two years in freshwater and A) length of coho salmon after one year in freshwater, and B) average summer water temperature in the Kuskokwim River Area watershed. Length values were calculated from the mean of back-calculated lengths for each of eight watersheds. The plots are based on partial residual analysis, which shows the influence of each independent variable while incorporating other variables in the model.