Growth and survival of sockeye salmon (*Oncorhynchus nerka*) from Karluk Lake and River, Alaska, in relation to climatic and oceanic regimes and indices, 1922–2000

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Abstract—We examined whether the relationship between climate and salmon production was linked through the effect of climate on the growth of sockeye salmon (*Oncorhynchus nerka*) at sea. Smolt length and juvenile, immature, and maturing growth rates were estimated from increments on scales of adult sockeye salmon that returned to the Karluk River and Lake system on Kodiak Island, Alaska, over 77 years, 1924–2000. Survival was higher during the warm climate regimes and lower during the cool regime. Growth was not correlated with survival, as estimated from the residuals of the Ricker stock-recruitment model. Juvenile growth was correlated with an atmospheric forcing index and immature growth was correlated with the amount of coastal precipitation, but the magnitude of winter and spring coastal downwelling in the Gulf of Alaska and the Pacific Northwest atmospheric patterns that influence the directional bifurcation of the Pacific Current were not related to the growth of Karluk sockeye salmon. However, indices of sea surface temperature, coastal precipitation, and atmospheric circulation in the eastern North Pacific were correlated with the survival of Karluk sockeye salmon. Winter and spring precipitation and atmospheric circulation are possible processes linking survival to climate variation in Karluk sockeye salmon.

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Fish stocks and fisheries in the Gulf of Alaska are strongly influenced by climatic and oceanic (C-O) conditions (Francis and Hare, 1994; Hare and Francis, 1995). In the past century C-O conditions in the North Pacific Ocean and Gulf of Alaska (GOA) have shifted from a warm regime and higher salmon (*Oncorhynchus* spp.) production (1927–46) to a cool regime and low salmon production (1947–76) and back to a warm regime and higher salmon production (1977–2000) (Francis and Hare, 1994; Hare and Francis, 1995).

Changes in C-O conditions, either annually or over longer regime periods, may affect salmon smolt-to-adult survival rates by affecting the growth rate of smolts after they enter the ocean. For example, higher survival rates of Alaska sockeye (*O. nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon have been associated with warmer coastal sea-surface temperatures (SST) during the first year that young salmon spend in the ocean (Mueter et al., 2002a). Relationships have been found between faster early marine growth and higher survival in chum salmon (Healey, 1982), pink salmon (Moss et al., 2005), and coho salmon (*O. kisutch*) (Beamish and Mahnken, 2001). The influence of C-O indices and regime shifts in the GOA on the survival of south central Alaska sockeye salmon has yet to be specifically linked to changes in marine growth rates of fish.

If marine growth influences sockeye salmon survival, then relating marine growth to specific C-O indices over an extended time period would provide insight into environmental factors leading to variation in year-class strength. Although direct information on fish growth (e.g., growth rates of smolts and postsmolts at standard times and locations) is not available, measurements from archived scales can be used to indirectly estimate the freshwater and marine growth rates of age 2.2[1] sockeye salmon that

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[1] In expressing age of salmon in this article, numbers before the decimal refer to numbers of freshwater annuli, numbers after the decimal refer to numbers of marine annuli (Koo, 1962).

returned to Karluk River and Lake system on Kodiak Island, Alaska, from 1922 to 2000, with the exception of seven years for which data were missing. Hereafter, we refer to these fish as Karluk sockeye salmon. The objectives of this study were 1) to describe how mean freshwater and marine growth rates of Karluk sockeye salmon varied over multiyear periods in relation to warm and cold C-O regimes in the North Pacific Ocean; 2) to describe how marine growth rates varied annually in relation to annual variations in regional C-O indices; and 3) to describe the interrelationships among annual growth rates, annual C-O indices, and annual survival.

Historically, the production of sockeye salmon in the Karluk system declined 90% from 1894 to the 1950s and then increased 30% during the 1990s. Proposed causes for the decline include the following: initial overharvesting of the entire run which led to declines in the spawning population (Barnaby 1944); overharvesting of the middle part of the salmon run (Thompson[2]); intense predation on juvenile salmon by Dolly Varden (*Salvelinus malma*) and charr (*Salvelinus alpinus*) in freshwater (Rounsefell, 1958); loss of marine-derived nutrients in the lake (Rounsefell, 1958); increased population size of threespine stickleback (*Gasterosteus aculeatus*), a freshwater competitor (McIntyre[3]); asynchrony of the plankton bloom and fry emergence (Koenings and Burkett, 1987); and ocean climate change (Finney et al., 2000). The analysis of salmon-derived nitrogen levels in lake sediment cores revealed that from 1752 to 1993, nitrogen levels oscillated in synchrony with Gulf of Alaska sea surface temperatures reconstructed from tree ring widths (Finney et al., 2000). In our study, we found that Karluk sockeye salmon abundance had undergone significant fluctuations in association with C-O conditions and regimes.

Study area

The Karluk Lake and River system is located on the west side of Kodiak Island in the northern Gulf of Alaska (Fig. 1). Karluk River is about 36 km long and from 18 to 165 m wide. Karluk Lake is 19 km long and has an average depth of 48 m. Sockeye salmon spawn in the river and the lake, and their tributaries. The early-run (June 1–July 21) sockeye salmon spawn mostly in tributaries of the lake. Scales were collected from adult sockeye salmon returning from the ocean and were sampled at the weir located on the river. The weir was located near the mouth of the river from 1921 to 1941, 20 km upriver from the mouth from 1942 to 1944, and 300 m below the lake from 1942 to 2000. The average annual escapement was 421,146 sockeye salmon, 233,779 Chinook salmon (*O. tshawytscha*), 630,176 pink salmon, 12,867 coho salmon, 51 chum salmon, and 1,800 steelhead trout (*O. mykiss*), for the years 2006–2008 (ADF&G, 2009).

Northeastern Pacific salmon distribute and migrate primarily in the GOA and central North Pacific Ocean (Myers et al., 1996). The GOA continental shelf waters encompass an area of 37,000,000 km^2 (Burrell, 1986). The GOA is dominated by counterclockwise current systems in offshore waters (i.e., Alaska Current) and on the continental shelf (i.e., Alaska Coastal Current). Water moves parallel to shore at speeds of 13 to 133 cm/s (Reed and Schumacher, 1986).

Hypotheses and possible mechanisms that affect growth and survival

To explain mechanisms for climate regime conditions to affect growth and survival we hypothesized that 1) faster growth and higher-than-average brood-year survival was expected as a consequence of the warm C-O regimes from 1922 to 1946 and from 1977 to 2000, and slower growth and lower-than-average brood survival was expected as a consequence of the cool C-O regime from 1947 to 1976; 2) annual growth and variation in brood survival were expected to correlate positively with sea surface temperature, precipitation, and atmospheric circulation (Atmospheric Forcing Index), and to correlate negatively with upwelling and the bifurcation of the Pacific Current (Northern Oscillation Index); and 3) annual growth was expected to correlate positively with annual variations in brood survival for Karluk sockeye salmon.

Mechanisms were proposed for the influence of C-O indices on increased marine growth and brood survival of salmon. Sea surface warming during the spring initiates thermal stratification of the water column and an algal bloom in the Gulf of Alaska, food for the zooplankton that salmon feed on. Therefore, warmer sea surface temperatures in the spring were expected to increase the growth and survival of salmon. Annual primary productivity in the GOA is also limited by inorganic nitrogen, phosphorus, and silicon (Martin and Gordon, 1988). Winter and spring precipitation runoff from land to sea brings terrestrial silicon and iron into the GOA (Burrell, 1986). Precipitation also accelerates the Alaska Coastal Current (ACC) and draws nutrients in the GOA from the southern waters (Royer, 1979). Winter and spring downwelling aids in deep-mixing of inorganic nutrients into the euphotic zone to enhance the bloom of phytoplankton during the spring. The Atmospheric Forcing Index (AFI) and the Northern Oscillation Index (NOI) represent two additional pathways for nutrient input into the GOA. A positive

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[2] Thompson, W. 1950. Some salmon research problems in Alaska. Presented at Alaskan Science conference of the National Academy of Science, National Research Council, Washington, 9–11 Novemeber, 1950. University of Washington, Fisheries Research Institute, Seattle, WA, 39 p.

[3] McIntyre, J. 1980. Further consideration of causes for decline of Karluk sockeye salmon. Unpubl. report, 29 p. .S. Fish and Wildlife Service, National Fisheries Research Center, Seattle, WA.

AFI is a measure of increased offshore upwelling of nutrient-rich, cool water in the central North Pacific, more frequent and intense storms passing through the GOA, increased frequency of westerly and southwesterly winds, and warmer coastal waters in the eastern North Pacific Ocean (McFarlane et al., 2000). The NOI describes the pattern of wind and atmospheric circulation between the North Pacific High (35°N, 130°W) and Darwin, Australia (10°S, 130°E) (Schwing et al., 2002). A more negative NOI is associated with a stronger northward projection of the Pacific Current along the Canada and southeast Alaska coasts that increases the speed of the ACC and draws nutrients and warmer waters from southern to northern coastal waters of Alaska.

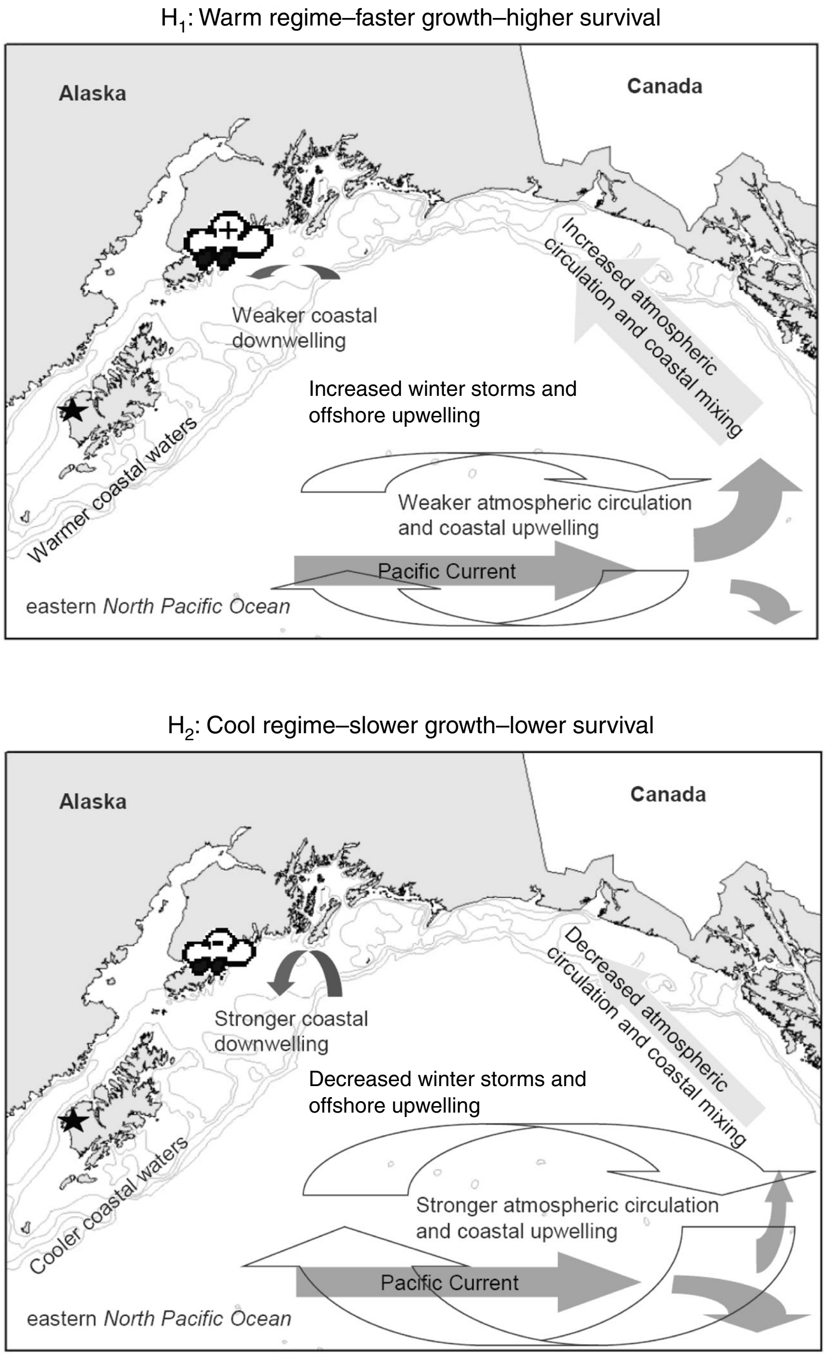

Figure 1

Schematics of the ocean-regime hypotheses (H_1 and H_2) for the effect of climate on the growth and survival of sockeye salmon from the Karluk system during warm and cool climatic and oceanic (C-O) regimes in the eastern North Pacific Ocean. A star marks the location of the Karluk River and Karluk Lake on Kodiak Island. The + sign represents higher precipitation amounts and – sign represent lower precipitation amounts.

Material and methods

Data, sample sizes, and assumptions

Measurements from scales from age-2.2 sockeye salmon were used to indirectly estimate the freshwater and marine growth rates of smolts and postsmolts. The age-2.2 adult fish had returned to the Karluk system during the early run spawning migration from May 1 to July 21 from 1924 to 2000. Seven years of data were unavailable (1945, 1947, 1958, 1965, 1966, and 1979). Scales were systematically selected from the archived collection of scales from the early-run of each year. The scales had been mounted on gum cards in the field. In the laboratory, impressions of the scales were made on plastic acetate cards (Arnold, 1951). Scale impressions were viewed with an Indus microfiche reader, model 4601-11 (Indus, West Salem, WI) with a 24× objective lens. Scale images were copied from the reader screen with a Screenscan Microfiche PC high-resolution scanner (Indus, West Salem, WI) and saved as tiff files by using ScreenScan Application software, vers. 1.00.0.8 (Indus, West Salem, WI). Images were then imported into the Optimate image analysis program (Media Cybernetics, Bathesda, MD) for measurement.

One scale was measured per fish, and 30–50 scales were measured from each year (n=70 years) for a total of 3167 scales read. Scales with evidence of resorption or regeneration were not measured. Measurements were taken along a consistent reference line drawn from the focus to the edge of the scale along the longest anterior radial axis to reduce the amount of variation in measurements at different radial axes (Martinson et al., 2000). Marks were made along the reference line at the center of the scale focus, between the last freshwater circulus and the first marine circulus, at the outer edge of the first marine annulus, at the outer edge of the second marine annulus, and the outer edge of the scale. Scales were measured to the nearest 0.0001 mm.

Growth indices

Four growth rates in body length were estimated from the scale measurements. Body length at the time of entry into saltwater (FW) was estimated as the distance from the focus to the end of the last freshwater annulus or the end of the plus growth. First-year marine (M1) scale growth was estimated as the distance from the center of the space between the last freshwater and first marine circulus to the outer edge of the first marine annulus. Second marine-year scale growth (M2) was estimated as the distance from the outer edge of the first marine annulus and the outer edge of the second marine annulus. Third marine-year (M3) scale growth was estimated as the distance from the outer edge of the second marine annulus to the outer edge of the scale. Means were calculated for each growth variable by brood year. Growth along the radius of the scale was assumed to be proportional to the growth in length of the fish, where the distance from each annulus on the scale provides an estimate of the total annual increase in body length for each year at sea (Dahl, 1909).

Climate and oceanic indices

Five climatic and oceanic indices (C-O indices) were used in the analysis. Three coastal indices of the northern GOA included sea-surface temperature (SST), precipitation (PREC), and the Upwelling Index (UI). Two North Pacific Ocean wide indices were used: the Atmospheric Forcing Index (AFI) and the Northern Oscillation Index (NOI). Because of the shorter time series of the coastal indices, we used two periods for the correlation analysis (1922–2000 and 1951–2000).

Sea-surface temperature Sea-surface temperature (SST) was represented by the Reynolds reconstructed sea surface temperatures in waters off the continental shelf at a point 150 nmi south of the west end of Kodiak Island (55°N, 155°W), the general direction of migration of juvenile salmon. Data were accessed from the NOAA Pacific Fisheries Environmental Laboratory (PFEL), National Marine Fisheries Service, at the Southwest Fisheries Science Center, Pacific Grove, California (http://www.pfeg.noaa.gov, accessed June 2004). An average annual spring SST index was estimated as the average monthly (Mar–May) temperature (°C) for years from 1951 to 2000 (n=50 years).

Precipitation Precipitation (PREC) amounts (cm) near Kodiak, Alaska, were accessed from the NOAA Western Regional Climate Center homepage (http://www.wrcc.dri.edu, accessed June 2004). Daily records taken at the Kodiak Naval Air Station were available for the years 1951 to 1969 (n=19 years), data taken at the National Weather Service Office on the U.S. Coast Guard Kodiak Base were available for the years 1970 to 1972 (n=3 years), and data from the the Kodiak Airport were available for the years 1973 to 2000 (n=28 years). The PREC index was calculated as the cumulative winter and spring precipitation amounts from December 1 through May 31.

Upwelling Index The coastal upwelling index (UI) east of Kodiak Island (60°N, 149°W) from 1951 to 2000 (n=50 years) were obtained from the PFEL homepage (http://www.pfeg.noaa.gov, accessed June 2004). Upwelling indices to the east were correlated with the one used in our study. The UI values (m^3/s/100 m coastline) were derived from wind stress and resulting mass transport of the surface water from subsurface layers. Mass transport was determined by the wind stress divided by the Coriolis parameter (a function of the rotation and latitude of the earth). Positive UI values indicated upwelling and negative UI values indicated downwelling. Cumulative winter and spring coastal upwelling east of Kodiak Island were calculated as the sums of monthly values from December 1 to March 31.

Atmospheric Forcing Index The Atmospheric Forcing Index (AFI) was accessed from the Fisheries and Oceans of Canada fisheries climatology webpage (http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/climate/clm_indx_afi.htm, accessed June 2004). The AFI values are the standardized scores of the first principle component of the winter (December through March) Aleutian Low Pressure Index, the Pacific Decadal Oscillation Index, and the Pacific Circulation Index (McFarlane et al., 2000). We used AFI winter values from 1922 to 2000 (n=79 years).

Northern Oscillation Index The Northern Oscillation Index (NOI) values were obtained from the PFEL homepage (http://www.pfeg.noaa.gov, accessed June 2004). The NOI is calculated as the difference between the monthly sea level pressure anomaly at the North Pacific High and the monthly sea level pressure anomaly at Darwin, Australia. The NOI was calculated as the average of the December through February from 1949 through 2000 (n=52 years).

Survival index

Direct estimates of marine survival of Karluk sockeye were not available; therefore indirect survival estimates were obtained from residuals of the stock-recruitment curve (Ricker, 1975). Stock size was estimated as the escapement counts of sockeye made at the Karluk weir from 1924 to 1996 (n=72 years), and recruitment was estimated as the number of offspring from the spawning population that returned from the ocean to the

Karluk commercial fishery and Karluk weir. Harvest, escapement, and age composition were available from the National Archives in Anchorage, the Alaska Department of Fish and Game, the National Marine Fisheries Service, and the Fishery Research Institute at the University of Washington.

With this approach, residuals (ε_i) of the fitted Ricker curve represented survival in the form of the annual deviation from the expected numbers of recruits based on the numbers of parents (escapement). The linear form of the survival model is given as

$$\ln\left[R_{t+r} / E_t\right] = \alpha + \beta E_t + \varepsilon, \tag{1}$$

where E = number of sockeye salmon counted at the Karluk weir during the spawning migration in year t;
R = number of sockeye salmon counted at Karluk weir and caught in the fishery in years r from brood year t;
α = density-independent parameter;
β = density-dependent parameter; and
ε = residuals, the survival index.

The survival index was lagged to match each of the three years of data of marine residence (i.e., juvenile, immature, and maturing stages) for the age 2.2 fish in the brood and was related to annual scale growth measurements and C-O indices.

The residual method is unfortunately less reliable than direct measurements of marine survival and requires several assumptions. One assumption is that the survival variability of the brood represents the survival of age 2.2 fish, a dominant age class in the brood. Also, because the recruitment estimate is based on the number of salmon counted at the Karluk weir and the number of salmon captured in the commercial fishery near the mouth of the Karluk River during the early and late run, it was assumed that there was equal fishing effort, minimal catch of non-Karluk sockeye salmon, and limited size selectivity of the fishing gear between runs and among years. It was also assumed that the fitted curve accurately reflected the overall density-dependent response of a stock at a given environmental state.

Analytical techniques

Ocean regime trends and comparison of regimes To describe and visually assess the low-frequency fluctuation in growth, climate indices, and survival in relation to the three ocean regimes, we fitted a loess regression line to the annual values using SigmaPlot software (Systat Software, Inc., Chicago, IL). The loess method of smoothing is based on tricube weighting and polynomial regression (Cleveland and Devlin, 1988). The loess regression method uses a variant of the local regression algorithm to approximate a nonlinear surface. Assume a series x_i for i=l, n. . The basic idea involves estimating a smoothed series y_i

$$y_i = g(x_i) + \varepsilon_i, \tag{2}$$

where points in the near neighbor of (y_i, x_i) have more weight than points further away.

In contrast use of an ordinary least-squares regression method, all points are equally weighted. In the analysis it is assumed that 30% of data points are used to compute each smoothed value and a 1° polynomial is then estimated. To determine the differences among regimes, an analysis of variance (ANOVA) was used to compare an average of the annual means of growth among C-O regimes. When a difference occurred we used the Tukey and Dunn pairwise comparison test to determine the regimes that differed.

Correlation analyses To describe the relationships among the scale growth, the C-O indices, and survival, we used the Pearson product moment correlation method. The null hypotheses of no associations among indices (H_0: ρ=0) was tested against the alternative hypotheses that growth, climate, and survival were positively (H_a: ρ>0) or negatively (H_a: ρ<0) related at a 5% level of significance (α=0.05). A Bonferonni correction factor was used to adjust the critical P-value for the number of correlations = 0.05/ the number of correlations. Correlations among growth variables within broods were used to determine the dependence of growth on growth in the previous year.

Results

Influence of C-O regimes on mean sockeye salmon growth

Juvenile (M1) growth and immature (M2) growth were lower during the cool regime and higher during the recent warm regime, whereas maturing growth (M3) was lower during the early warm regime and higher during the cool and recent regime (Fig. 2). Growth varied over time by 14% for FW, 10% for M1, 15% for M2, and 46% for M3. FW declined 12% during the early warm regime, was relatively constant during the cool regime, increased 8% from 1970 to 1980, and decreased 8% from 1980 to 1998. M1 decreased during the early warm regime, increased 7% from the later part of the early warm regime to mid-cool regime, increased 5% from 1970 to 1980, and decreased 2% from 1980 to 1998. M2 was low and constant during the early warm and cool regimes and increased 15% from the early 1970s to the mid 1980s. M3 increased 40% from the mid 1920s to the mid-cool regime period and decreased 18% in the mid-1980s.

For all four growth variables, at least one mean or median value was significantly different (ANOVA: P<0.002) among periods (Table 1). Mean M1 and M2 were significantly higher (Tukey test: P<0.05) during the 1977–2000 warm C-O regime than during the 1922–46 warm and 1947–76 cool regimes. Mean FW

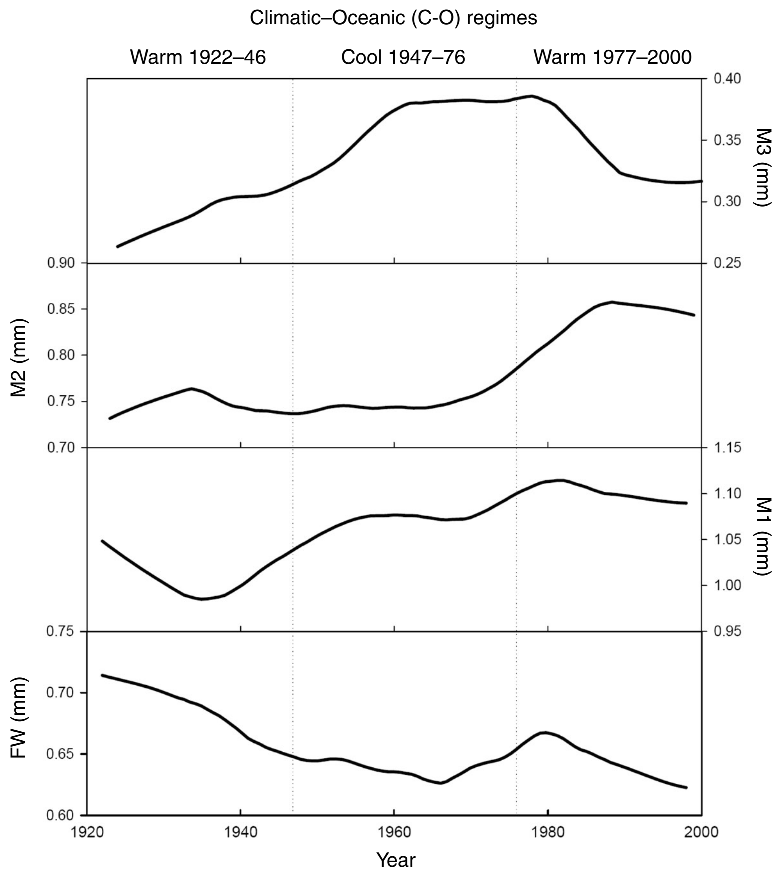

Figure 2

Trends in annual freshwater (FW) and annual (first year through third year, M1–M3) marine growth for the 1922–46 warm, 1947–76 cool, and 1977–2000 warm regimes represented by loess regression lines. Scale measurements are estimates of growth rates for age 2.2 sockeye salmon (*Oncorhynchus nerka*) that returned to Karluk River during the early run spawning migration from 1924 to 2000.

Table 1

Comparison of freshwater and oceanic growth rates of sockeye salmon (*Oncorhynchus nerka*) that returned to the Karluk lake and river system, Alaska, from years 1924 to 2000. Smolt length (freshwater, FW), and juvenile (first-year marine, M1), immature (second-year marine, M2), and maturing (third-year marine, M3) growth were estimated from measurement on the scales of age-2.2 sockeye salmon that returned to the Karluk system, Kodiak Island, Alaska. "Yes" indicates normal distribution and equal variances of the growth variables. Significance differences occurred at $P \leq 0.05$ for normality, variance, ANOVA, and multiple comparison tests.

	Assumption test		ANOVA		Tukey and Dunn pairwise test mean or median and statistical differences				
Growth variable	Normal	Equal variance	Test statistic	*P*-value	1922–1946 Warm regime		1947–1976 Cool regime		1977–2000 Warm regime
FW	Yes	Yes	6.624	0.002	0.687	>	0.640	=	0.644
M1	Yes	Yes	28.753	<0.001	1.006	<	1.072	<	1.104
M2	Yes	Yes	24.625	<0.001	0.745	=	0.752	<	0.841
M3	Yes	No	26.055	<0.001	0.293	<	0.366	=	0.353

was significantly higher ($P \leq 0.05$) during the 1922–46 warm regime than during the 1947–76 cool, and 1977–2000 warm regimes. Mean M3 was significantly higher (25%; Dunn's test, nonparametric test; $P \leq 0.05$) during the 1947–76 cool regime than during the 1922–46 warm regime but not significantly higher ($P > 0.05$) than the mean M3 during the 1977–2000 warm regime. Growth variables within a brood were not significantly correlated (Table 2).

Table 2

Correlation coefficients (r) and P-values among growth variables for broods of age-2.2 sockeye (*Oncorhynchus nerka*) that returned as adults to the Karluk River weir during the early run. Scales were used for measurements. Smolt length (freshwater, FW), and juvenile (first-year marine, M1), immature (second-year marine, M2), and maturing (third-year marine, M3) growth were estimated from measurements of the scales of age-2.2 sockeye salmon that returned to the Karluk system, Kodiak Island, Alaska. There were no significant relationships between any pair of variables in the correlation table at 5% ($P < 0.008 = 0.05/6$) and 1% ($P < 0.002 = 0.01/6$).

Brood year	Growth variables		M1	M2	M3
1919–95					
n=71	FW	r	−0.150	−0.079	−0.214
		P	0.212	0.512	0.073
	M1	r		0.24	0.253
		P		0.060	0.033
	M2	r			0.009
		P			0.940
1948–95					
n=48	FW	r	0.287	0.055	0.065
		P	0.051	0.722	0.675
	M1	r		0.138	−0.098
		P		0.372	0.527
	M2	r			−0.291
		P			0.050

The regional C-O indices in the North Pacific varied in association with the warm (1922–46), cool (1947–76), and warm (1977–2000) C-O regimes (Fig. 3). Compared to the 1947–76 cool regime, the 1977–2000 warm regime had 1°C higher SST, a 54% higher PREC, weaker coastal downwelling near Prince William Sound, 42% higher AFI, and 61% lower NOI. Compared to the 1947–76 cool regime, the 1922–46 warm regime had a 27% higher PREC and a 47% higher AFI.

Influence of regional C-O conditions on mean sockeye salmon growth

Regional C-O indices correlated significantly with juvenile (M1) and immature (M2) scale growth, but not with maturing growth (M3) (Table 3). Growth was correlated with C-O indices for the 1951–2000 period, but not with C-O indices for the 1922–2000 period. Growth indices were correlated with two of the five C-O indices. M1 had a significant positive association with AFI ($r=0.40$; $P=0.005$). M2 had a strong positive relationship with the PREC ($r=0.39$; $P=0.005$). FW and M3 did not correlate with the five C-O indices.

Interrelationships among regional C-O conditions, mean growth, and annual survival of sockeye salmon

Survival, as indicated by the residuals from the stock-recruitment model, was higher than expected during warm regimes and lower than expected during the cool regime (Fig. 4), and there was a brief high from 1959 to 1965. The linear regression model of the logarithm of the recruits per spawner [$\ln(R/E)$] as a function of spawners (E) was

$$\ln(R_{t+r} / E_t) = -0.48039 \times 10^{-7} \bullet E + 0.7668. \tag{3}$$

A reduction in the number of recruits per escapement at higher escapement levels is characteristic of strong density-dependence at high stock levels ($r^2=0.1035$; $P=0007$). Residuals of the model were used as an index for survival.

Survival was not significantly correlated with growth (Table 4), but it was significantly correlated with four of the five C-O indices and with C-O indices during all marine life stages (Table 5). For the 1921–89 broods, survival was correlated positively with SST (0.409, 0.567, 0.536) and AFI (0.314, 0.307, 0.364) during the M1, M2, and M3 years spent at sea by the age-2.2 fish in the brood (Table 5). For the 1948–89 brood years, survival correlated positively with SST (0.409, 0.607), PREC (0.397, 0.349), and AFI (0.447, 0.477) during the first and second year at sea. A significant negative correlation of 0.421 occurred between UI and survival in the final year at sea.

Discussion

Influence of C-O regimes on mean sockeye salmon growth

The synchronous patterns between sockeye salmon mean M1 and M2 growth indices and the two most recent ocean regimes may indicate that changes in C-O conditions in the North Pacific Ocean influenced the marine growth of sockeye salmon from Karluk River and Karluk Lake. The increase in juvenile and immature growth and the reduction of maturing growth in the final year at sea of sockeye salmon from the northern Gulf of Alaska after the 1976–77 regime shift is distinct from the growth pattern seen in sockeye salmon stocks from the Bering Sea off western Alaska. For western Alaska, the M1 of Bristol Bay sockeye salmon and M1 and M2 of Chignik sockeye salmon tended to increase soon after the 1976–1977 climate shift (Ruggerone et al. 2007). However, for

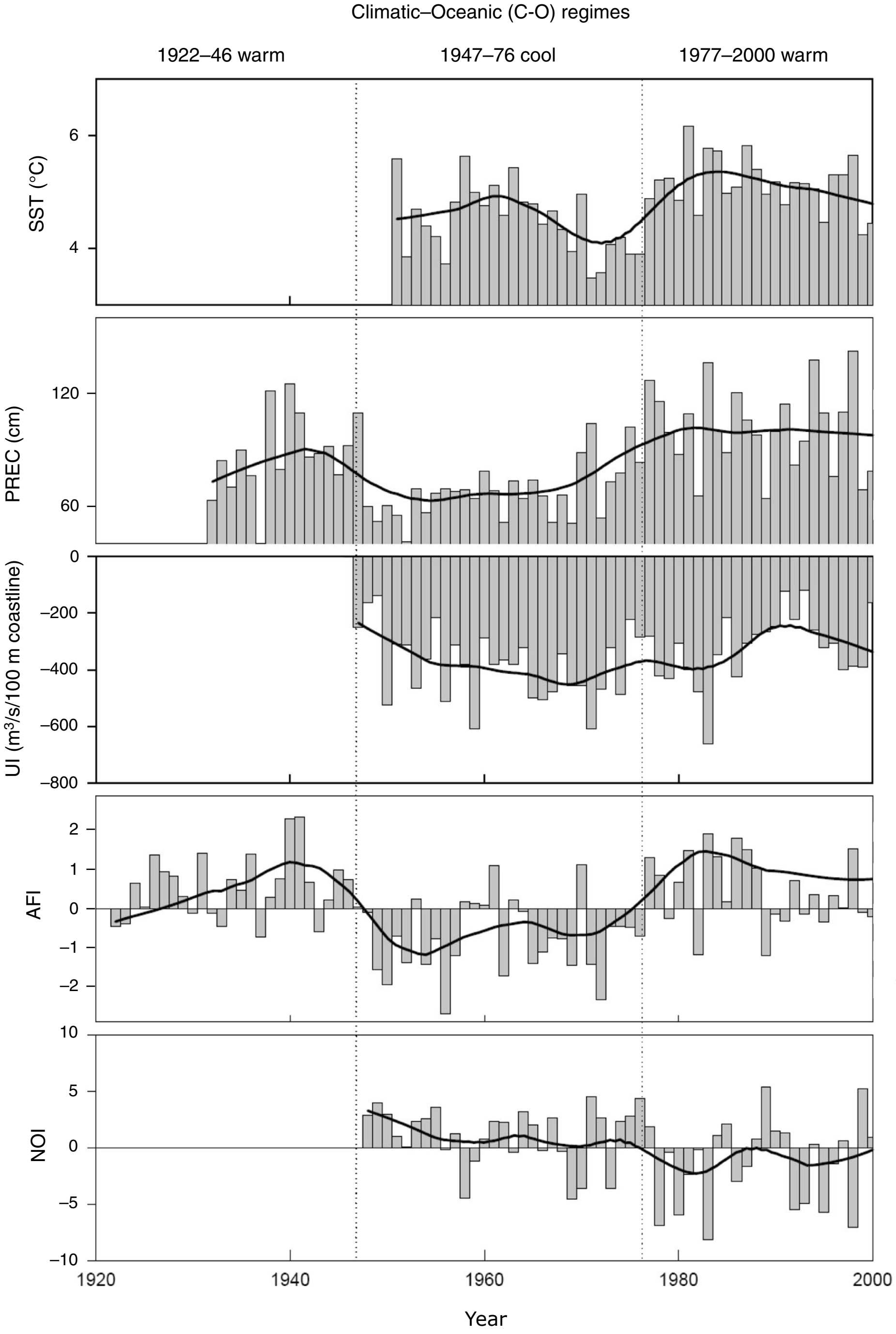

Figure 3

Trends in climate and ocean conditions as represented by five climatic and oceanic (C-O) indices in the eastern North Pacific Ocean from 1922 to 2000. C-O indices comprise the average spring (Mar–May) coastal sea-surface temperature (SST), cumulative amounts of winter and spring (Dec–May) coastal precipitation (PREC), cumulative winter (Dec–Mar) coastal Upwelling Index (UI), average winter (Dec–Mar) Atmospheric Forcing Index (AFI), and the average winter (Dec–Feb) Northern Oscillation Index (NOI). Lines are the loess regression line. Bars are the annual means.

age 2.2 sockeye salmon from Kvichak River in western Alaska from 1920 to 1997, a positive warm-regime effect occurred for M1, but not for M2 (Isakov et al., 2000). For ocean age-3 sockeye salmon from Bristol Bay from 1955 through 2000, scale growth increased after 1977 (following entry into saltwater and later in the year for M1, after the peak summer growing season for M2, and during the peak growing season for M3 (Ruggerone et al., 2005). Such long-term patterns may continue to persist over a period of years during which C-O regime conditions remain relatively stable or warm.

Several mechanisms could explain the lower than expected M1 and M2 growth during the 1922–46 warm regime. First, growth rates derived from the scales of returning adult salmon, a small subset of the original smolts entering the ocean, may not accurately reflect the actual growth rate of the population of juvenile and immature salmon as a whole. However, the decline in freshwater scale growth in the mid 1940s corresponds with the reduced freshwater productivity in Karluk Lake over the period 1940s through 1993, as indicated by salmon-derived nitrogen levels in lake sediment cores from 1752 to 1993 (Gregory-Eaves et al., 2004), and the decline in scale growth supports the use of adult scales to estimate the past growth life history of the fish. Second, higher marine survival of smaller size classes indicate a larger proportion of slower growing fish in the surviving population that was sampled. Alternatively, an increase in inter- and intra-specific competition for food led to slower M1 and M2 growth during the 1922–46 warm regime. Finally, a change in the scale sampling method in the 1950s indicated a lower precision and accuracy of growth measurement in the years before the 1950s. Before the 1950s, a scraping method was used to remove scales

Table 3

Correlation coefficients (*r*), *P*-values, and sample sizes (*n*) relating the growth of early run age-2.2 sockeye (*Oncorhynchus nerka*) from the Karluk system to climatic and oceanic (C-O) indices in the North Pacific Ocean. C-O indices include the average spring (Mar–May) coastal sea-surface temperature (SST), cumulative winter and spring (Dec–May) coastal precipitation amounts (PREC), cumulative winter (Dec–Mar) coastal upwelling (UI), average winter (Dec–Mar) Atmospheric Forcing Index (AFI), and the average winter (Dec–Feb) Northern Oscillation Index (NOI). Smolt length (freshwater, FW), and juvenile (first-year marine, M1), immature (second-year marine M2), and maturing (third-year marine, M3) growth were estimated from measurement on the scales of age-2.2 sockeye salmon. Relationships between variables in the correlation table are significant at 5% ($P<0.01=0.05/5$) indicated by *.

Year	Growth variable	C-O indices for the North Pacific Ocean				
		SST	PREC	UI	AFI	NOI
1922–2000						
FW	*r*	0.245	0.070	−0.101	0.224	0.025
	P	0.109	0.590	0.493	0.061	0.870
	n	44	61	48	71	47
M1	*r*	0.303	0.158	0.115	−0.074	−0.089
	P	0.047	0.223	0.438	0.538	0.552
	n	44	61	48	71	47
M2	*r*	0.194	0.283	0.269	0.151	−0.269
	P	0.201	0.026	0.061	0.209	0.064
	n	45	62	49	71	48
M3	*r*	−0.193	−0.151	−0.176	−0.222	0.017
	P	0.200	0.237	0.225	0.056	0.908
	n	46	63	49	71	49
1951–2000						
FW	*r*	0.245	0.120	−0.118	0.206	−0.001
	P	0.109	0.439	0.444	0.181	0.994
	n	44	44	44	44	44
M1	*r*	0.303	0.269	0.210	0.380*	−0.060
	P	0.047	0.079	0.171	0.011	0.700
	n	44	44	44	44	44
M2	*r*	0.194	0.392*	0.250	0.308	−0.251
	P	0.201	0.008	0.097	0.039	0.096
	n	45	45	45	45	45
M3	*r*	−0.193	−0.248	−0.214	−0.104	0.077
	P	0.200	0.097	0.153	0.490	0.612
	n	46	46	46	46	46

from a fish and involved a wider area of the body of a fish than the more localized sampling with forceps done after the 1950s.

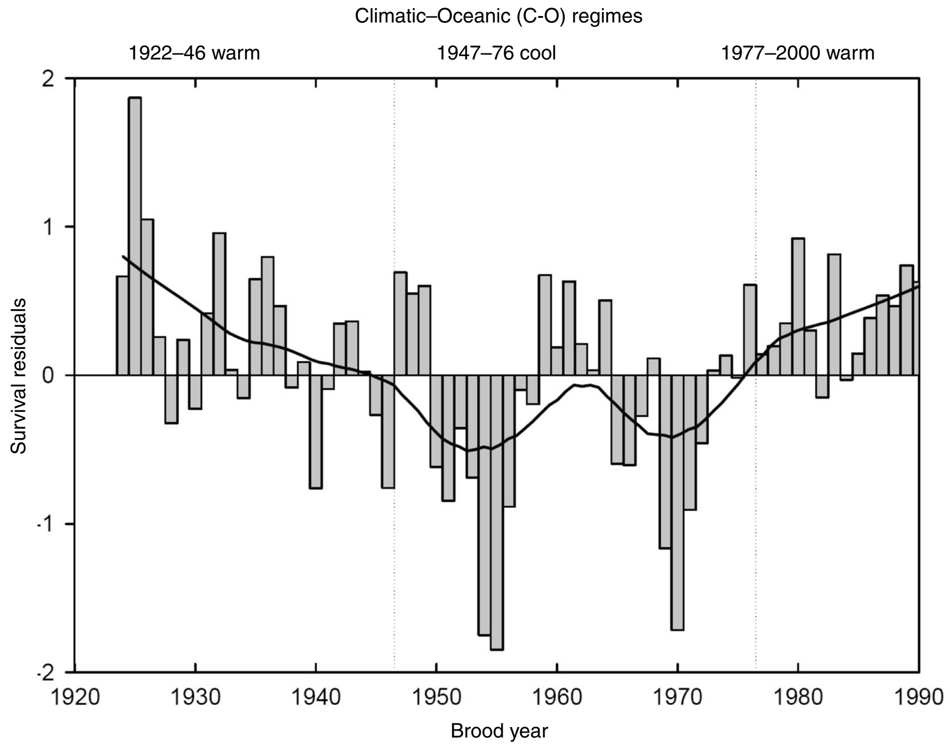

Figure 4

Annual survival as indicated by residuals from a stock-recruitment curve ($\ln[R_{t+r}/E_t]=\alpha+\beta E_t$) for sockeye salmon (*Oncorhynchus nerka*), from Karluk Lake, Alaska, 1924 to 1989. The line is the loess regression line. Bars are the annual values.

The inverse relationship between the regime pattern and M3 is consistent with the idea that a density-dependent effect on growth occurred during the final year at sea. For example, mean body weights of pink, chum, and sockeye salmon stocks in commercial fisheries ranging from Washington to western Alaska were negatively related to increased salmon production from the mid-1970s to the mid-1990s (Bigler et al., 1996; Helle et al., 2008). Declines in size of chum salmon were also documented for carcasses sampled at Fish Creek, Hyder, Alaska, and Quilcene National Fish Hatchery in Hood Canal, Washington (Helle and Hoffman, 1995). Authors speculated that a greater number of fish in the ocean led to increased competition for food and in turn decreased the marine growth and size at maturity of salmon.

Influence of regional C-O conditions on mean sockeye salmon growth

Juvenile growth was correlated with atmospheric circulation during the winter and spring and weakly correlated with sea surface temperature and amount of coastal precipitation, whereas immature growth was correlated with coastal precipitation and weakly correlated with sea surface temperature and atmospheric circulation. Results are similar to those from other studies. For sockeye salmon that returned to the Kvichak River in western Alaska, M1 was positively correlated with SST in Bristol Bay and near the Aleutian Islands in the eastern Bering Sea (Isakov et al., 2000). Similarly, Helle (1979) found a significant relationship (r=0.64; P<0.01) between the mean number of circuli formed during the first year of marine growth on the scales of age-0.3 chum salmon from Olsen Bay in Prince William Sound, Alaska, and the mean summer and fall SST, but not air temperature, cloud cover, PREC, atmospheric pressure, or seawater density, in the GOA from 1957 to 1975. For the same Karluk sockeye salmon time series, the early juvenile growth, as indicated by the distance from between the last freshwater and first marine circulus to the end of the 9th circulus, was negatively correlated with the numbers of juvenile pink salmon fry (r=–0.77; P=0.002) released from hatcheries in Prince William Sound, Cook Inlet, and Kodiak, and the distance from the 9th circulus to the end of the first marine annulus within M1 was positively correlated with summer SST in the GOA (r=0.49; P<0.01) (Martinson, 2004). A stronger density-dependent effect on early marine growth indicates a masked influence of C-O conditions on growth (Martinson et al., 2008).

Interrelationships among regional C-O conditions, mean growth, and annual survival of sockeye salmon

The higher survival during the warm regimes and lower survival during the cool regime indicate that marine climate influenced the production of sockeye salmon from Karluk Lake. Results are consistent with other studies showing a strong relationship between various C-O indices and salmon survival. Regional scale covariation in survival rates of pink, chum, and sockeye salmon were more closely related to coastal SST during the first summer at sea than surface salinity or upwelling

(Mueter et al., 2002b). In addition, coastal SST during the first year at sea for sockeye salmon and within 400 km of the point of ocean entry associated positively with survival rates of 19 stocks ranging from western Alaska to northern British Columbia and negatively with survival rates of 18 stocks in central British Columbia and Washington (Mueter et al., 2002a). Warmer winter SST (Nov–Feb) in offshore waters in the Gulf of Alaska were related to increases in total annual adult catch plus escapement of major B.C. and Alaska stocks (Pyper and Peterman, 1999). For the Karluk sockeye salmon, survival was correlated with spring coastal sea surface temperatures, winter and spring precipitation, and the more stormy winters before and following the juvenile stage, indicating two important marine periods in determining the survival of Karluk sockeye salmon. This result is consistent with the hypotheses that climatic and oceanic conditions during the first few months at sea (Parker, 1971) and the first winter at sea (Beamish and Mahnken, 2001) are important in determining mortality rates.

Climatic processes influencing salmon in the Pacific Northwest were not consistent with processes affecting Karluk sockeye salmon from Alaska. For example, water column mixing, as indicated by the Upwelling Index, did not correlate positively with faster growth or higher survival of Karluk sockeye salmon except in the winter and spring before the year of maturity. In the coastal waters off Oregon, by contrast, upwelling during the first year at sea of age-1 coho salmon was positively correlated with commercial catch of coho salmon from 1947 to 1962 (Scarnecchia, 1981). The Northern Oscillation Index that is associated with a stronger trade winds, stronger coastal upwelling off Washington and Oregon, cooler surface and subsurface sea temperatures in waters off Washington, and higher Oregon hatchery salmon production (Schwing et al., 2002) was not correlated with the growth and survival of Karluk sockeye salmon.

The lack of a correlation between survival and growth of the age-2.2 sockeye salmon is similar to the findings of other studies where growth was determined from the scales of adult sockeye salmon. For example, M1 on the scales of adult sockeye salmon that returned to Egegik and Kvichak rivers in Bristol Bay, Alaska, was not correlated with variations in brood survival estimated from residuals of the Ricker model (Farley et al., 2007). From 1977 to 1997, growth on the scales of adult sockeye salmon from Bristol Bay showed reduced M2 and M3 growth and there was a smaller size-at-age for adults and lower smolt-to-adult survival rates for the even-year migrating smolts (Ruggerone et al., 2003). Alternatively, the size of juvenile sockeye salmon in Bristol Bay was positively correlated with survival rates of Bristol Bay sockeye salmon (Farley et al., 2007). The difference in results of correlating juvenile size with survival and with correlating adult scale growth with survival is likely due to size-selective mortality on the smaller fish during the juvenile stage (Farley et al., 2007; Moss et al., 2005) and a reduced detection of growth-survival relationships based on adult scales.

Table 4

Correlation coefficients (*r*), *P*-values, and sample sizes (*n*) relating survival to growth of sockeye salmon from Karluk River and Karluk Lake, Kodiak Island, Alaska. Survival is the residuals of the Ricker spawner-recruitment curve for Karluk sockeye salmon (*Oncorhynchus nerka*). Smolt length (freshwater, FW), and juvenile (first-year marine, M1), immature (second-year marine, M2), and maturing (third-year marine, M3) growth were estimated from measurement on the scales of age-2.2 sockeye salmon. No relationships between any pair of variables are significant at 5% ($P<0.0125=0.05/4$) indicated by *.

Brood year		Growth variable			
		FW	M1	M2	M3
1921–89		0.073	0.005	0.136	−0.290
Survival	*r*	0.035	0.315	0.301	−0.106
	P	0.573	0.967	0.294	0.022
	n	62	62	62	62
1948–89					
Survival	*r*	0.035	0.315	0.301	−0.106
	P	0.835	0.058	0.070	0.531
	n	37	37	37	37

Conclusion

The first-, second-, and third-year marine scale growth, a proxy for the change in growth rate, of Karluk sockeye salmon was not detected as a link between climate and survival for Karluk sockeye salmon. If the growth on the scales of adult sockeye salmon represents only a subset of the survivors (possibly fewer smaller and slower growing fish when mortality is high), then the weaker climate-growth-survival relationships recognized from adult scales provides insight into possible growth-climate-survival relationships. The growth-climate relationships and the mechanism for these relationships should further be assessed by relating the size and growth of juvenile salmon with physical and biological conditions measured at sea.

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Table 5

Correlation coefficients (*r*), *P*-values, and sample sizes (*n*) relating survival to climatic and oceanic (C-O) conditions of the North Pacific Ocean experienced by the age-2.2 sockeye salmon (*Oncorhynchus nerka*) from Karluk River and Karluk Lake during their juvenile, immature, and maturing stages at sea. Survival is the residuals of the Ricker spawner-recruitment curve of Karluk sockeye. C-O indices comprise the average spring (Mar–May) coastal sea-surface temperature (SST), cumulative winter and spring (Dec–May) coastal precipitation amounts (PREC), cumulative winter (Dec–Mar) coastal upwelling (UI), average winter (Dec–Mar) Atmospheric Forcing Index (AFI), and the average winter (Dec–Feb) Northern Oscillation Index (NOI). Relationships between any pair of variables in the correlation table are significant at 5% ($P<0.010=0.05/5$) and 1% ($P<0.002=0.01/5$), indicated by * and **, respectively.

Marine life stage		C-O indices for the North Pacific Ocean				
		SST	PREC	UI	AFI	NOI
1921–89 brood years						
juvenile	*r*	0.409*	0.214	0.300	0.314*	–0.140
	P	0.007	0.098	0.043	0.009	0.360
	n	42	61	46	69	45
immature	*r*	0.567**	0.154	0.349	0.307*	–0.112
	P	0.00007	0.234	0.016	0.010	0.458
	n	43	62	47	69	46
maturing	*r*	0.536**	0.240	0.258	0.364**	–0.138
	P	0.0002	0.059	0.077	0.002	0.357
	n	44	63	48	69	47
1948–89 brood years						
juvenile	*r*	0.409*	0.397*	0.215	0.447*	–0.175
	P	0.007	0.009	0.172	0.003	0.267
	n	42	42	42	42	42
immature	*r*	0.607**	0.349*	0.386	0.477**	–0.180
	P	0.00002	0.024	0.012	0.001	0.253
	n	42	42	42	42	42
maturing	*r*	–0.195	–0.178	–0.421*	–0.107	0.117
	P	0.189	0.232	0.003	0.474	0.435
	n	42	42	42	42	42

Literature cited

Arnold, E., Jr.
1951. An impression method for preparing fish scales for age and growth analysis. Prog. Fish-Cult. 13:11–16.

Barnaby, J.
1944. Fluctuations in abundance of red salmon, *Oncorhynchus nerka* (Walbaum), of the Karluk Lake, Alaska. Fish. Bull. 50:237–295.

Beamish, R., and C. Mahnken.
2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog. Oceanogr. 49:423–437.

Bigler, B., D. Welch, and J. Helle.
1996. A review of size trends among North Pacific salmon *Oncorhynchus* spp. Can. J. Fish. Aquat. Sci. 53:455–465.

Burrell, D.
1986. Physical oceanography. *In* The Gulf of Alaska: physical environment and biological resource (D. W. Hood, and S. T. Zimmerman, eds.), p. 57–76. U.S. Dep. Commerce, Washington, D.C.

Cleveland, W., and S. Devlin.
1988. Locally weighted regression: an approach to regression analysis by local fitting. J. Am. Stat. Assoc. 83:596–610.

Dahl, K.
1909. The assessment of age and growth in fish. Int. Rev. Geophys. Hydro. Bull. 2, p. 758–769.

Farley, E., J. Murphy, M. Adkison, L. Eisner, J. Helle, J. Moss, J. Nielsen.
2007. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). Fish. Bull. 105:121–130.

Finney, B., I. Gregory-Eaves, J. Sweetman, M. Douglas, and J. Smol.
2000. Impacts of climate change and fishing on Pacific salmon abundance over the past 300 years. Science 290:795–799.

Francis, R., and S. Hare.
1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. Fish. Oceanogr. 3:279–291.

Gregory-Eaves, I., B. Finney, M. Douglas, and J. Smol.
2004. Inferring sockeye salmon (*Oncorhynchus nerka*) population dynamics and water quality changes in a stained nursery lake of the past ~500 years. Can. J. Fish. Aquat. Sci. 61:1235–1246.

Hare, S., and R. Francis.
1995. Climate change and salmon production in the north-

east Pacific Ocean. *In* Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. (R. J. Beamish, ed.), p. 357–372.

Healey, M.
1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon *Oncorhynchus keta* during early sea life. Can. J. Fish. Aquat. Sci. 39:952–957.

Helle, J.
1979. Influences of marine environment on age and size at maturity, growth, and abundance of chum salmon *Oncorhynchus keta* (Walbaum), from Olsen Creek, Prince William Sound, Alaska. Ph.D. diss., 118 p. Oregon State Univ., Corvallis, OR.

Helle, J., and M. Hoffman.
1995. Size decline and older age at maturity of two chum salmon *Oncorhynchus keta* stocks in western North America, 1972–92. *In* Climate change and northern fish populations (R. J. Beamish, ed.), p. 245–260. Can. Spec. Publ. Fish. Aquat. Sci. 121

Helle, J., E. Martinson, D. Eggers, and O. Gritsenko.
2008. Influence of salmon abundance and ocean conditions on body size of Pacific salmon. N. Pac. Anadr. Fish Comm. Bull. 4:289–298.

Isakov, A., O. Mathisen, S. Ignell, and T. Quinn II.
2000. Ocean growth of sockeye salmon from the Kvichak River, Bristol Bay based on scale analysis. N. Pac. Anadr. Fish Comm. Bull. 2:233–245.

Koenings, J., and R. Burkett.
1987. An aquatic Rubic's cube: Restoration of the Karluk Lake sockeye salmon (*Oncorhynchus nerka*). *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. (H. D. Smith, L. Margolis, and C.C. Wood, eds.), 419–434.

Koo, T.
1962. Age designation in salmon. *In* Studies of Alaska salmon, vol. 1 (T. S. Koo, ed.), p. 37–48. Univ. Washington Press, Seattle.

Martin, J., and R. Gordon.
1988. Northeast Pacific iron distribution in relation to primary productivity. Deep-Sea Res. 35:188–196.

Martinson, E.
2004. Influence of three north Pacific Ocean regime shifts on the early growth and survival of sockeye salmon from Karluk Lake, Alaska. M.S. thesis, 152 p. Univ. Idaho, Moscow, ID.

Martinson, E., J. Helle, D. Scarnecchia, and H. Stokes.
2008. Density-dependent growth of Alaska sockeye salmon *Oncorhynchus nerka* in relation to climate–oceanic regimes, population abundance, and body size, 1925 to 1998. Mar. Ecol. Prog. Ser. 370:1–18.

Martinson, E., M. Masuda, and J. Helle.
2000. Back-calculated fish lengths, percentages of scale growth, and scale measurements for two scale measurement methods used in studies of salmon growth. N. Pac. Anadr. Fish Comm. Bull. 2:331–336.

McFarlane, G., J. King, and R. Beamish.
2000. Have there been recent changes in climate? Ask the fish. Oceanogr. 47:147–169.

Moss, J., D. Beucham, A. Cross, K. Myers, E. Farley, J. Murphy, and J. Helle.
2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans. Am. Fish. Soc. 134:1313–1322.

Mueter, F., R. Peterman, and B. Pyper.
2002b. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Can. J. Fish. Aquat. Sci. 59:456–463.

Mueter, F., D. Ware, and R. Peterman.
2002a. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific. Fish. Oceanogr. 11:205–218.

Myers, K., K. Aydin, R. Walker, S. Fowler, and M. Dahlberg.
1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1995. N. Pac. Anadr. Fish Comm. Doc. 192, 228 p.

Parker, R.
1971. Size selective predation among juvenile salmonid fishes in British Columbia inlet. J. Fish. Res. Board Can. 28:1503–1510.

Pyper, B., and R. Peterman.
1999. Relationship among body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon *Oncorhynchus nerka*, 1967–1997. Can. J. Fish. Aquat. Sci. 56:1716–1720.

Reed, R., and J. Schumacher.
1986. Physical oceanography. *In* The Gulf of Alaska: physical environment and biological resource (D. W. Hood, and S. T. Zimmerman, eds.), p. 57–75. U.S. Dep. Commerce, Washington, D.C.

Ricker, W.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can., p. 265–296.

Rounsefell, G.A.
1958. Factors causing the decline in sockeye salmon of Karluk River, Alaska. Fish. Bull. 130:1–58.

Royer, J.
1979. On the effect of precipitation and runoff on coastal circulation in the Gulf of Alaska. J. Phys. Oceanogr. 9:555–563.

Ruggerone, G., 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. Fish. Bull. 103:355–370.
2007. Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002. Deep-Sea Res. II. 54:2776–2793.

Ruggerone, G., M. Zimmerman, K. Myers, J. Nielsen, and D. Rogers.
2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. Fish. Oceanogr. 12:209–219.

Scarnecchia, D.
1981. Effects of streamflow and upwelling on yield of wild coho salmon *Oncorhynchus kisutch* in Oregon. Can. J. Fish. Aquat. Sci. 38:471–475.

Schwing, F., T. Murphree, and P. Green.
2002. The Northern Oscillation Index (NOI): a new climate index for the Northeast Pacific. Prog. Oceanogr. 53:115–139.