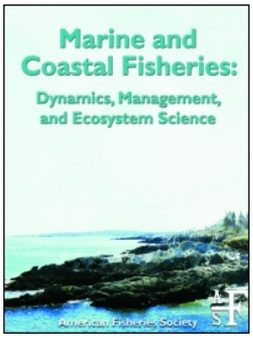

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ARTICLE

Trends and Factors Influencing the Length, Compensatory Growth, and Size-Selective Mortality of Juvenile Bristol Bay, Alaska, Sockeye Salmon at Sea

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Abstract

The productivity of Bristol Bay, Alaska, Sockeye Salmon *Oncorhynchus nerka* increased during the mid-1970s. This increase is believed to be partially due to an increase in early marine growth associated with the 1976–1977 cool-to-warm shift in summer sea surface temperature (SST). The body size of juvenile salmon during their first year at sea is believed to regulate their ability to survive over winter. The back-calculated smolt length, first-year ocean growth, and total juvenile length of Sockeye Salmon from five Bristol Bay river systems (Egegik, Kvichak, Naknek, Ugashik, and Wood) and two smolt ages were used to examine trends and factors influencing total juvenile length, compensatory growth, and size-selective mortality in the first year in the ocean from 1962 to 2007. Juvenile length increased in relation to summer sea temperature, the 1977–2001 and 2002–2007 warm temperature regimes, smolt length, and compensatory growth. Compensatory growth—an inverse relationship between first-year ocean growth and smolt size—increased over time as well as after the 1976–1977 climate regime shift, was more common in age-1.0 fish than in age-2.0 juveniles, and was important in determining the length of juvenile Sockeye Salmon from the Wood River (the shorter fish among rivers and smolt ages). The coefficient of variation in length did not change with SST, suggesting that size-selective mortality occurred prior to the end of the first year at sea for all 10 fish groups. The predictor variables that were significant in the models varied among river systems and smolt ages. This study demonstrated that the frequency of compensatory growth and the total lengths of juvenile Sockeye Salmon during their first year at sea increased with summer SST (range, 7.5–10.5°C) in the eastern Bering Sea, a possible mechanism for the increased productivity of Bristol Bay Sockeye Salmon associated with warmer sea temperatures.

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Bristol Bay, Alaska, supports the world's largest Sockeye Salmon *Oncorhynchus nerka* fishery, contributing from 30% to 60% of the annual global harvest of Sockeye Salmon (FAO 2015). Harvest and escapement of Sockeye Salmon to Bristol Bay is highly variable, ranging from 3 to 65 million annually (Figure 1). Following the 1976–1977 cool-to-warm climate regime change, the productivity of Bristol Bay Sockeye Salmon increased and was generally higher during the warm climate regime, possibly due to higher growth rate potential as juveniles (during the first year at sea) and greater available of prey in the ocean (Farley et al. 2009). The size of juvenile salmon during their first year at sea is believed to be an important factor in determining their marine survival.

The critical-size and critical-period hypothesis states that juvenile salmon need to reach an optimum size in order to survive their first winter at sea (Beamish and Mahnken 2001; Beamish et al. 2004; Farley et al. 2007a). The marine survival of juvenile salmon is believed to be regulated by two factors: predation in the first few months at sea (Parker 1968; Pearcy 1992) and their size and metabolic demands during periods of low prey availability, such as during the first winter at sea (Beamish et al. 2004; Farley et al. 2011). In the eastern Bering Sea, larger body size and higher energetic status in late summer were associated with higher marine survival in juvenile Sockeye Salmon (Farley et al. 2007c, 2011). If juvenile size is important in determining marine survival, then understanding the factors that influence the size of juvenile salmon during their first year at sea is important to understanding the mechanisms driving variations in marine survival.

Climate can influence the growth and size of juvenile Sockeye Salmon in the eastern Bering Sea. The productivity (r = 0.45) and first-year ocean growth (r = 0.37) of Bristol Bay Sockeye Salmon were positively correlated with sea surface temperature (SST) prior to ocean entry (January–April) in the eastern Bering Sea (55–57°N, 165–157°W; Ruggerone et al. 2007). Juvenile Sockeye Salmon collected at sea were more abundant, more widely distributed on the eastern Bering Sea shelf, and had higher growth rate potential during warm years (2002–2005) than in cold years (2000, 2001, and 2006) (Farley and Trudel 2009). The density of their prey was positively correlated with mean May SST in the eastern Bering Sea (P = 0.02), indicating a bottom-up control on growth (Farley and Trudel 2009). We hypothesized that the length of juvenile Sockeye Salmon would increase with ocean warming.

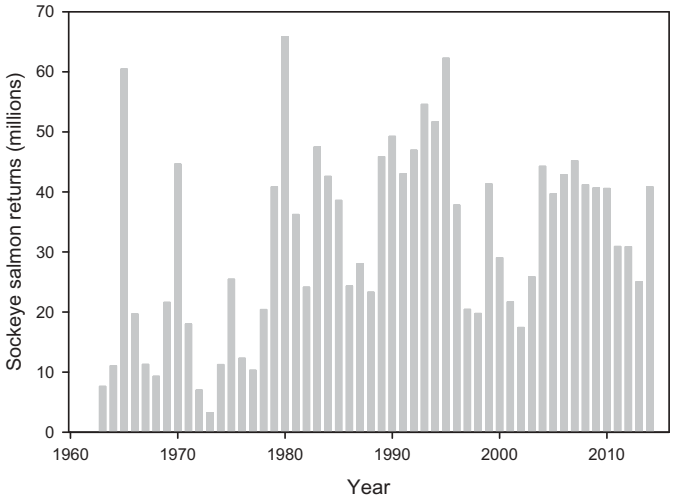

FIGURE 1. Sockeye Salmon returns to Bristol Bay, 1964–2014. The 2014 data are preliminary. The data were provided by the Alaska Department of Fish and Game.

Compensatory or "catch-up" growth may be an important mechanism that juvenile Sockeye Salmon use to reach a critical size prior to winter (Farley et al. 2007a, 2007c; Ruggerone et al. 2007). Compensatory growth entails a period of accelerated growth after a period of depressed growth and is used by fish to increase their size after experiencing poor growing conditions (Sogard 1997). Compensatory growth has been documented in over 20 fish family taxa in laboratory experiments and in natural populations of Atlantic Salmon *Salmo salar*, Atlantic Herring *Clupea harengus*, Common Carp *Cyprinus carpio*, Atlantic Cod *Gadus morhua*, and Pacific Cutlassfish *Trichiurus lepturus* (Ali et al. 2003). In the eastern Bering Sea, smaller age-1.0 Sockeye Salmon feed at higher rates than larger age-2.0 juvenile Sockeye Salmon (Farley et al. 2007b), providing initial evidence for compensatory growth. For Bristol Bay Sockeye Salmon, we hypothesized that smaller and younger smolts at ocean entry would exhibit faster growth during their first year at sea as a means of obtaining a critical size for survival.

Size-selective mortality—the removal of smaller fish from the population—has been documented for salmon at sea using several methods (Sogard 1997). Several authors have used scale pattern and length frequency distributions for specific life history stages over time to examine whether smaller fish were removed from the population (Holtby et al. 1990; Beamish and Mahnken 2001; Beamish et al. 2004; Moss et al. 2005; Farley et al. 2011). The lack of a significant correlation between the back-calculated lengths of salmon during their juvenile life stage using adult scales (i.e., from survivors) and survival indices was interpreted as evidence for size-selective mortality in Sockeye Salmon because smaller fish presumably died at a higher rate than larger fish (Farley et al. 2007b; Martinson et al. 2009a). The length of the scale radius to the first marine annulus had a coefficient of variation of less than 4% for Bristol Bay Sockeye Salmon (Farley et al. 2007a, 2007c), and the authors speculated that this low variability was due to size-selective mortality during the first year at sea. We hypothesized that there would be relatively little variation in body length if juvenile Sockeye Salmon underwent size-selective mortality. In addition, we expected that variability in length would not be correlated with SST because smaller fish would presumably grow more slowly during

colder years and thus be more vulnerable to predation and starvation, which would increase the average size of the survivors in a cold year.

The goal of this study was to understand the factors influencing the size of Bristol Bay Sockeye Salmon during their first year at sea, a critical time in determining their survival. A retrospective approach was used to (1) determine the factors influencing total juvenile length by examining growth characteristics derived from scales of adult salmon (the survivors in the population), (2) detect compensatory growth, and (3) evaluate size-selective mortality. We hypothesized that (1) juvenile size would increase with SST, smolt length, and compensatory growth; (2) compensatory growth would increase with SST and mean annual smolt size and occur in populations with smaller smolts; and (3) the coefficient of variation in juvenile size would not change over time, thereby supporting size-selective mortality.

METHODS

Study Site

Bristol Bay is located off the coast of western Alaska in the southern portion of the eastern Bering Sea. There are nine Sockeye Salmon–producing rivers in the Bristol Bay region. Growth data were analyzed for five major river systems (Egegik, Kvichak, Naknek, Ugashik, and Wood; Figure 2). Bristol Bay Sockeye Salmon leave freshwater from late May to early August, spend the summer as juveniles in the waters of the southeastern Bering Sea shelf, and then overwinter south of the Aleutian Islands and the Alaska Peninsula (Farley et al. 2005; Seeb et al. 2011).

Adult Scale Collection

Scales collected from adult Sockeye Salmon that returned to the study rivers to spawn were used to characterize smolt

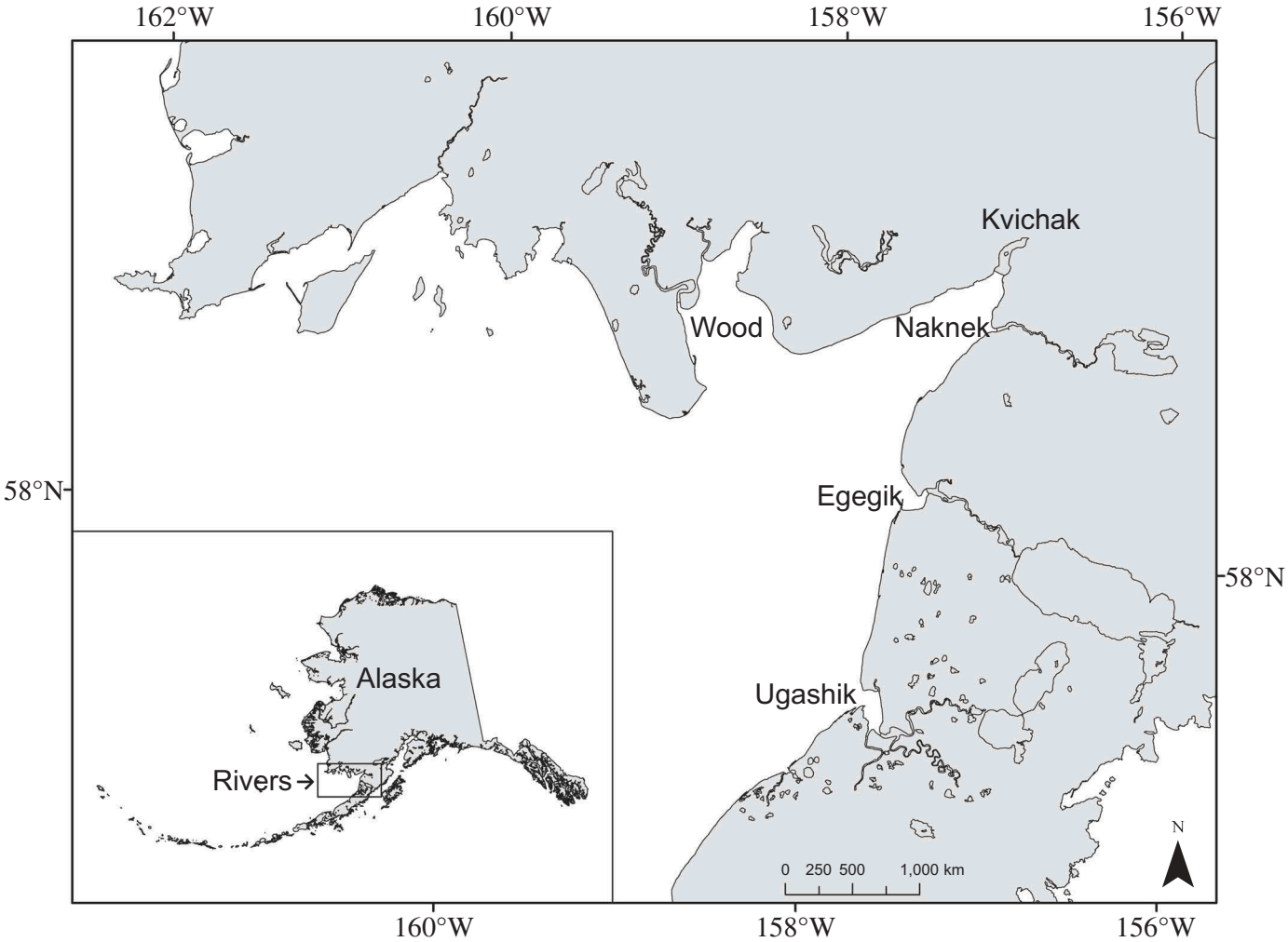

FIGURE 2. Map of the eastern Bering Sea showing the locations of the five river systems included in the study.

length, first-year ocean growth, and total juvenile length for Sockeye Salmon that survived to adulthood. Scale measurements for ocean entry years from 1962 to 2007 (n = 46) were obtained from adult Sockeye Salmon from the five study rivers by the Alaska Department of Fish and Game. Age was designated by the European system of notation, that is, $a.b$, where a is the number of winters spent in freshwater after spending one winter in the gravel and prior to going to sea and b is the number of winters spent in the ocean (Koo 1962). Juveniles spend the first year at sea at different freshwater ages and were referred to as age-1.0 and age-2.0 juveniles based on the number of years spent in freshwater.

Scale collections from adult Sockeye Salmon were available for the dominant freshwater and ocean age groups (1.2, 1.3, 2.2, and 2.3). Not all rivers had both ocean ages in each year. Typically, 100 scales were measured per ocean entry year for each river (25 for each sex and age-group), but sample sizes varied from 4 to 100 in a group. Up to 900 Bristol Bay Sockeye Salmon scales per year (all rivers and age-groups) were available for 46 years; 33,893 scales were from adult Sockeye Salmon from the Egegik (n = 6,162), Kvichak (7,582), Naknek (7,930), Ugashik (6,110), and Wood (6,109) rivers. Missing data included those for age-1.0 juveniles from the Egegik and Ugashik rivers in 1972 and 1966, respectively, and those for age-2.0 juveniles from the Kvichak River in 2006, the Ugashik River in 1966 and 2006, and the Wood River in 1971 and 1999.

Scales from adult Sockeye Salmon were measured following procedures described by Hagen et al. (2001) and Ruggerone et al. (2005). The scale measurement axis was a perpendicular line drawn from a line intersecting each end of the first saltwater annulus (Figure 3). Scales were measured from the focus to the end of the freshwater growth zone (FW) and from the end of the freshwater zone to the outer edge of the first marine annulus (SW1) (Figure 3). Freshwater growth included the annual growth in freshwater (i.e., FW1) and the "plus" growth (FWPL), i.e., growth that likely occurred in freshwater or the estuary during the spring of out-migration (Figure 3).

Length and Growth Indices

Smolt and juvenile lengths (mm) at the end of the first year at sea were back-calculated for each fish using a linear regression relationship between fish length and scale radius that we derived from data for Sockeye Salmon smolts that out-migrated from the five major watersheds in Bristol Bay. There were no apparent differences in this relationship among stocks, so we estimated the following equation from the combined data:

$$\text{length} = 24 + 165 \times \text{scale radius}; \quad R^2 = 0.98, P < 0.001. \tag{1}$$

Equation (1) was used to estimate smolt length (FW_j) and juvenile length ($L1_j$) for individual fish (j) by substituting the measurement of scale radius (i.e., from the focus to the end of last freshwater annulus [FWSR = FW1 + FWPL] and from the focus to the end of first marine annulus [L1SR= FW1 + FWPL + SW1]; Figure 3) into the equation. This relationship is based on data from five Bristol Bay Sockeye Salmon stocks over 5 years, with 10 smolts per 10-mm interval per stock and year. The back-calculated lengths and growth indices were treated as real observations, i.e., as not being subject to error. Not accounting for the errors may influence our results.

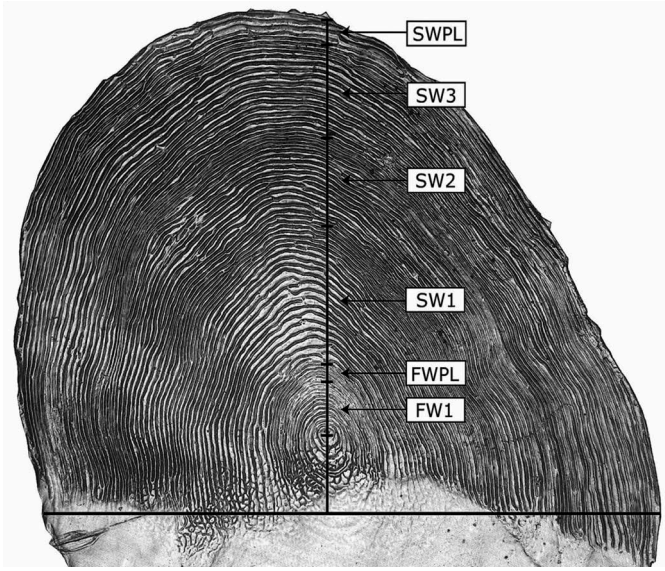

FIGURE 3. Scale image from an age-1.3 Sockeye Salmon showing the reference line used to measure growth and growth zones. The growth indices used in the analysis include the freshwater scale radius (FWSR = FW1 + FWPL) and the scale radius to the end of the first year at sea (L1SR = FW1 + FWPL + SW1).

The growth of individual fish in their first year at sea was computed as the difference between the estimated juvenile length and the smolt length ($SW1_j = L1_j - FW_j$). Means were calculated for smolt length ($\overline{FW}_{i,a,t}$), juvenile length ($\overline{L1}_{i,a,t}$), and first-year ocean growth ($\overline{SW1}_{i,a,t}$) by river system (i = 1 [Egegik], 2 [Kvichak], 3 [Naknek], 4 [Ugashik], and 5 [Wood]), smolt age (a = 1, 2), and ocean entry year (t). Means for years without data were estimated using a 3-year centered average.

Juvenile Abundance Index

An index of the abundance of juvenile Sockeye Salmon from Bristol Bay was back-calculated using harvest, escapement, and age data from the Alaska Department of Fish and Game. We assumed that Sockeye Salmon returns from an ocean entry year were representative of the abundance of juveniles from that year, though the back-calculated abundance index was likely less variable than the observed abundance of juvenile Sockeye Salmon at sea. The abundance of juvenile Sockeye Salmon from Bristol Bay rivers was derived from the equation

$$\text{Abundance}_t = \sum_{i=1}^{5} \text{returns}_{age-x.i,t+i}, \quad (2)$$

where returns is the number of adult Sockeye Salmon (catch and escapement), x is the freshwater age (number of freshwater annuli on the scale [0–3]), i is the saltwater age (number of ocean annuli on the scale [1–5]), and t is the year. Information on the number of returns of Sockeye Salmon to the study rivers by age was provided by the Alaska Department of Fish and Game.

Sea Surface Temperature Indices

Sea surface temperature data for the southeastern Bering Sea shelf (54.3°–58.1°N, 159.4–170.6°E) were used to represent the conditions experienced by juvenile Sockeye Salmon (Figure 4). Monthly mean values of SST produced from ship, buoy, and satellite data were obtained from National Center for Environmental Prediction Reanalysis Derived data provided by NOAA's Earth Science Research Laboratories, Boulder, Colorado (http://www.esrl.noaa.gov/psd/) (Kalnay et al. 1996). Summer SSTs were estimated as the averages of the mean monthly SSTs for July–September, the warmest months of the year and the primary growing season during a fish's first year at sea. Climate regime shifts were identified by an analysis of the summer SST time series using a regime shift detection tool (Rodionov 2004). The method developed by Rodionov (2004) is based on a sequential t-test analysis of adding years one step ahead in a time series that detects a shift and monitors the magnitude of the shift over time. Positive shifts in SSTs were detected in 1976–1977 and 2001–2002 (Figure 4). We therefore designated the years 1962–1976, 1977–2001, and 2002–2007 as having different climate regimes.

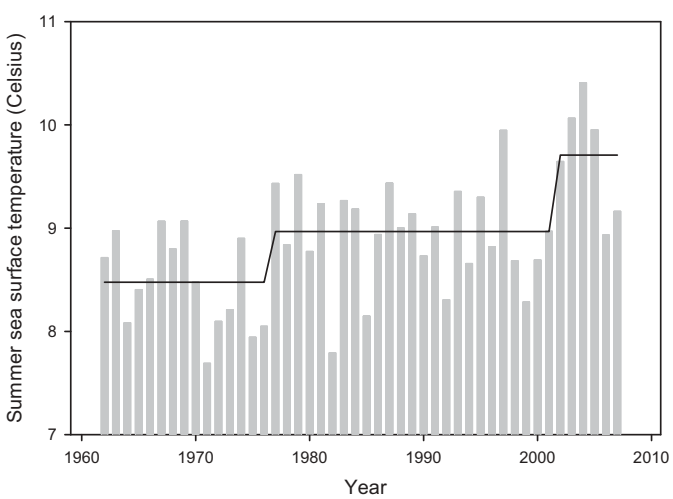

FIGURE 4. Mean summer (July–September) sea surface temperatures in the eastern Bering Sea, 1962–2007. The serrated portions of the dark line show the statistical shifts in temperature in 1976–1977 and 2001–2002 identified using the Rodionov (2004) regime shift algorithm; the horizontal portions show the mean temperatures for the different climate regimes.

Compensatory Growth

Compensatory growth ($CG_{i,a,t}$) was identified from the relationship between individual observations of $SW1_{i,a,t}$ and $FW_{i,a,t}$ within each ocean entry year by river and freshwater age. Prior to model estimation, each data set ($SW1_{i,a,t}$ and $FW_{i,a,t}$) was scaled by subtracting the mean and dividing by the SD of the mean within each year to allow for comparison of coefficients over time. Compensatory growth was indexed by the slope coefficient $\alpha_{1,i,a,t}$ in the linear regression

$$SW1_{i,a,t} = \alpha_{1,i,a,t} FW_{i,a,t} + \varepsilon_{i,a,t}. \quad (3)$$

Compensatory growth was indicated by statistically significant negative coefficients for given ocean entry year, river system, and smolt age combinations.

The frequency of statistically significant negative slope coefficients was used to evaluate the frequency of compensatory growth (FCG). Significant compensatory growth was represented with a value of 1 and insignificant compensatory growth by a value of 0. This binary index was used to compare the frequency of compensatory growth among river systems and freshwater ages.

Size-Selective Mortality

To detect size-selective mortality, we examined the trends in the annual coefficients of variation for the total juvenile length of survivors. This coefficient represented the standardized variability in total juvenile length while accounting for an increase in variance with an increase in mean length and a decrease in variance with a decrease in mean length. The equation was

$$L1cv_{i,a,t} = \frac{SD(L1_{i,a,t})}{\overline{L1}_{i,a,t}}, \quad (4)$$

where SD is the standard deviation of the sampling distribution for juvenile length. Time series of $L1cv_{i,a,t}$ by ocean entry year were estimated for each river system and smolt age combination.

Data Analysis

Statistical and graphic analyses were primarily conducted using the R software program (R Foundation for Statistical Computing, version 3.0.3, Vienna). To determine the timing of climate regime shifts in the SST time series we used a regime shift detection algorithm in Excel (Rodionov 2004). Shifts in the mean SST over time occurred in 1976–1977 and 2001–2002. These shifts were used to designate dummy variables for regime in the time series regression models.

Time series plots were used to examine trends in mean ± SE juvenile length, the coefficients of variation in juvenile length, and the CG slope indices by smolt age and river system (10 fish groups). To show the low-frequency trends

in each time series, a smooth line was fit to the time series using the fitted values of a generalized additive model. This analysis was conducted using the gam function in the gam package (version 1.12) in R.

To test for a difference in juvenile length, compensatory growth, and the coefficient of variation in juvenile length among smolt ages, rivers, and climate regimes, we used a three-factor ANOVA test. This analysis was conducted using the aov function in the stats package (version 3.0.3) in R. The frequency of compensatory growth was not tested using ANOVA due to its being represented by binomial data. A Tukey's honestly significant difference, multiple-comparison test for unequal sample sizes was used to compare the means of the biological variables among fish groups using the HSD. test function in the agricolae package (version 1.2.1) in R.

For the time series regression models, the tseries (version 1.00-32) and forecast (version 5.8) packages were used. The forecast package allowed joint estimation of the structural relationship and the autoregression model for the errors. The models were tested for assumptions associated with time series and regression. That is, we tested for heteroscedasticity of the residuals (plot of absolute residuals versus fitted values; Goldfeld–Quandt test), normality of the residuals (quantile–quantile plots; Shapiro test), serial correlation of the residuals (autocorrelation test), and multicollinearity among predictor variables (variance inflation factor). The best-fit model was selected using the Bayesian information criterion (BIC) and Bonferroni correction factor (Schwarz 1978). The BIC was used to choose the best predictors in the models. The Bonferroni correction factor ($P < \alpha$/number of predictor variables) was used to impose a penalty on the t-values of significant predictor variables to account for the number of possible predictor variables in the model at a 95% significance level ($\alpha = 0.05$).

Evaluation of Parameters

Juvenile length.—To evaluate the factors influencing the juvenile length of survivors, we modeled mean juvenile length at the end of the first year at sea as a function of climate regime, summer SST, mean smolt length, juvenile abundance, CG slope index, and underlying cycles in total juvenile length using the following time series regression model:

$$\begin{aligned}\overline{\mathrm{L1}}_{i,a,t} &= \beta_0 + \beta_1\mathrm{regime}_{1976-1977} + \beta_2\mathrm{regime}_{2001-2002} \\ &\quad + \beta_3\mathrm{SST}_t + \beta_4\overline{\mathrm{FW}}_{i,a,t} + \beta_5\mathrm{abundance}_{i,a,t} + \beta_6\mathrm{CG}_{i,a,t} \\ &\quad + +\phi_{i,a,t-x}\overline{\mathrm{L1}}_{i,a,t-x} + \varepsilon_{i,a,t}.\end{aligned} \tag{5}$$

The autocorrelation parameter (φ) was used to capture variability in the time series not explained by the predictor variables in the model. Lags included 1–4 years.

Compensatory growth.—To evaluate the factors influencing compensatory growth, we modeled the CG slope index as a function of climate regime, summer SST, mean smolt length, juvenile abundance, and underlying cycles using the following time series regression model:

$$\begin{aligned}\mathrm{CG}_{i,a,t} &= \beta_0 + \beta_1\mathrm{regime}_{1976-1977} + \beta_2\mathrm{regime}_{2001-2002} \\ &\quad + \beta_3\mathrm{SST}_t + \beta_4\overline{\mathrm{FW}}_{i,a,t} + \beta_5\mathrm{abundance}_t \\ &\quad + \phi_{i,a,t-x}\mathrm{CG}_{i,a,t-x} + \varepsilon_{i,a,t}.\end{aligned} \tag{6}$$

Size-selective mortality.—To evaluate size-selective mortality, we modeled the coefficient of variation of juvenile length as a function of SST and climate regime. The linear regression equation was expressed as

$$\begin{aligned}\mathrm{L1cv}_{i,a,t} &= \beta_0 + \beta_1\mathrm{regime}_{1976-1977} + \beta_2\mathrm{regime}_{2001-2002} \\ &\quad + \beta 3\mathrm{SST}_t + \varepsilon_t.\end{aligned} \tag{7}$$

If size-selective mortality exists, then the coefficient of variation in juvenile length should be constant over time and not correlated with either climate regime or SST. As noted above, in one study the length of the scale radius to the end of the first marine annulus had a coefficient of variation of less than 4% for Bristol Bay Sockeye Salmon and the authors speculated that this low variability was due to size-selective mortality during the first year at sea (Farley et al. 2007a, 2007c).

RESULTS

Juvenile Length

Trends in the annual mean lengths of juvenile Sockeye Salmon from the five Bristol Bay river systems at the end of their first year at sea were similar among smolt ages and rivers, except for Naknek River Sockeye Salmon (Figures 5, 6). For the Egegik, Kvichak, Ugashik, and Wood River Sockeye Salmon, juvenile length increased from the early 1960s to the late 1970s, was variable but had no upward or downward trend from the late 1970s to the late 1990s, and then increased in the 2000s. In contrast, Naknek River juvenile Sockeye Salmon were longer prior to the mid-1970s.

There were significant differences in the annual mean lengths of juvenile Sockeye Salmon between smolt ages, among rivers, and among climate regimes (ANOVA; all $P < 0.001$; Table 1). Age-1.0 juveniles were on average 16 mm shorter than age-2.0 juveniles for the five river systems combined. The differences in the mean lengths of age-1.0 and age-2.0 juveniles were statistically significant within each river system (Tukey's test; all $P < 0.01$)—18 mm for Egegik River fish, 17 mm for Kvichak River fish, 12 mm for Naknek River fish, 25 mm for Ugashik River fish, and 8 mm for Wood River fish. Egegik River Sockeye Salmon were the longest, while Wood River Sockeye Salmon were typically the shortest (age-1.0 juveniles from the Ugashik River were statistically as short as those from the Wood River; Table 2). Among rivers, lengths were similar for age-1.0 juveniles from the Kvichak and Naknek rivers, age-1.0 juveniles from the

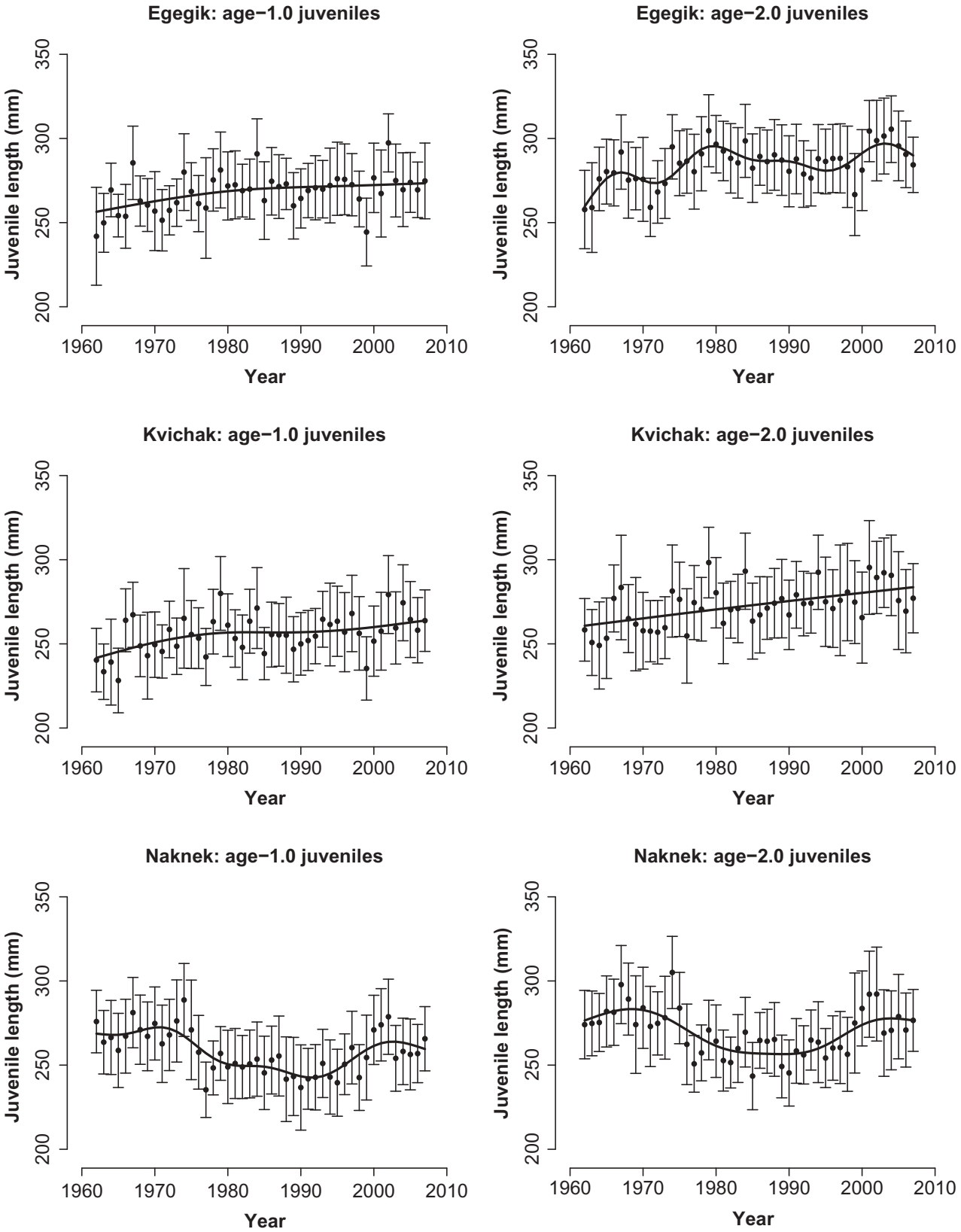

FIGURE 5. Time series of mean back-calculated lengths of age-1.0 and age-2.0 Sockeye Salmon from the Egegik, Kvichak, and Naknek rivers after their first year at sea. The error bars are SDs.

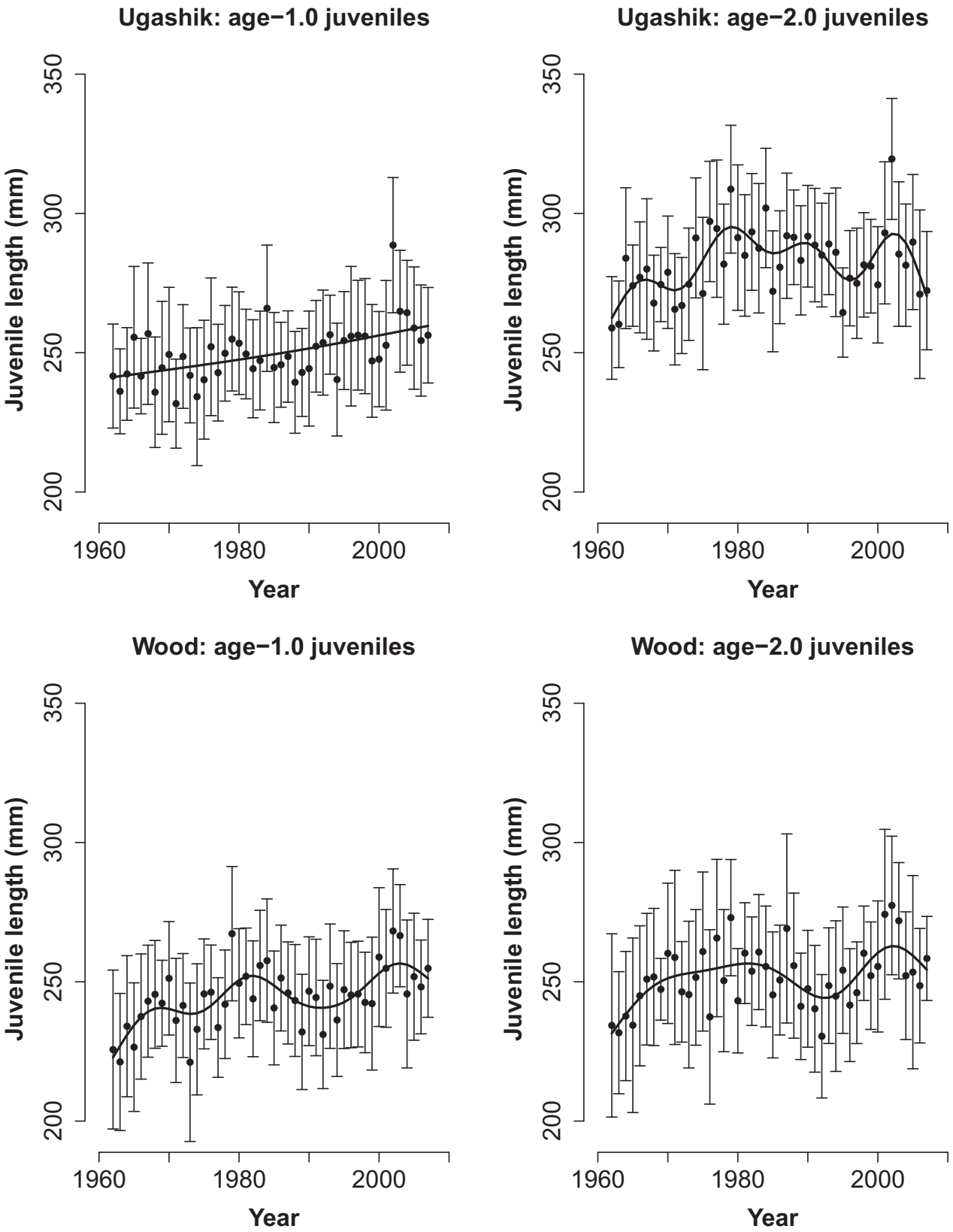

FIGURE 6. Time series of mean back-calculated lengths of age-1.0 and age-2.0 Sockeye Salmon from the Ugashik and Wood rivers after their first year at sea. The error bars are SDs.

TABLE 1. Results of ANOVA of the effects of smolt age, river, and climate regime on the mean length of age-1.0 and age-2.0 Sockeye Salmon from the Egegik, Kvichak, Naknek, Ugashik, and Wood rivers in Bristol Bay, western Alaska. Climate regimes are represented by the periods 1962–1976, 1977–2001, and 2002–2007. Abbreviations are as follows: SS = sum of squares, MS = mean square.

Variable	df	SS	MS	*F*	*P*
Smolt age	1	29,258	29,258	217.01	<0.001
River	4	39,704	9,926	73.62	<0.001
Regime	2	6,635	3,318	24.61	<0.001
Smolt age × river	4	4,314	1,078	10.93	<0.001
Smolt age × regime	2	206	103	1.04	0.35
River × regime	8	13,216	1,652	16.74	<0.001
Smolt age × river × regime	8	764	96	0.97	0.46
Residuals	430	42,440	99		

Ugashik and Wood rivers, and age-2.0 juveniles from the Kvichak, Naknek, and Ugashik rivers (Table 2).

The effects of climate regime on juvenile length were more frequent for Bristol Bay Sockeye Salmon stocks during the 1977–2001 climate regime than during the 2002–2007 climate regime (Table 3). During the 1977–2001 climate regime, average juvenile lengths increased for age-1.0 juvenile Sockeye Salmon from the Egegik, Ugashik, and Wood rivers and for age-2.0 juvenile Sockeye Salmon from the Egegik and Kvichak rivers (Table 3) but decreased for age-1.0 and age-2.0 juveniles from the Naknek River. Juvenile length increased during the 2002–2007 climate regime for age-1.0 juveniles from Ugashik River. All groups of juvenile Sockeye Salmon were longer during the 2002–2007 climate regime than the 1962–1976 climate regime, except for Naknek River fish.

In the time series regression models, the mean length of juvenile Sockeye Salmon at the end of their first year at sea was related to one or more of the following variables: summer SST in the eastern Bering Sea, the 2002–2007 climate regime, compensatory growth, smolt length, and an underlying cycle (Table 4). Overall, the results varied among rivers. Juvenile length was not correlated with the estimated abundance of juvenile Sockeye Salmon from Bristol Bay. Summer SST was a significant, positively correlated predictor of the length of age-1.0 Sockeye Salmon from the Egegik, Kvichak, Naknek, and Wood rivers and the length of age-2.0 Sockeye Salmon from Egegik, Kvichak, and Wood rivers. The influence of climate regime on juvenile length was statistically significant and positive for age-1.0 Sockeye Salmon from the Ugashik River during 2002–2007. The effect of the 1977–2001 climate regime was not statistically significant, possibly due to the greater influence of interannual variability in SST on length. Compensatory growth showed a statistically significant relationship with the length of age-1.0 Sockeye Salmon from the Wood River (the shortest group).

Compensatory Growth

Compensatory growth was indicated by statistically significant, negative slope coefficients for the relationship between SW1 and FW, which was calculated for each smolt age, river,

TABLE 2. Results of Tukey's honestly significant difference familywise comparison tests of the effect of river system on mean total length (Lmean [mm]), the coefficient of variation of total length (Lcv), compensatory growth (CG), and the frequency of compensatory growth (FCG) for age-1.0 and age-2.0 juvenile Sockeye Salmon from Bristol Bay. Within age-groups, means with the same letter were not significantly different at the 95% familywise confidence level.

River	Lmean	Lcv	CG	FCG
		Age-1.0 juveniles		
Egegik	275 z	0.073 x	0.104 z	0.109 y
Kvichak	264 y	0.077 yx	–0.153 y	0.435 z
Naknek	265 y	0.082 zy	–0.155 y	0.457 z
Ugashik	257 x	0.078 yx	–0.126 y	0.326 zy
Wood	251 x	0.086 z	–0.199 y	0.587 z
		Age-2.0 juveniles		
Egegik	293 z	0.072 x	0.244 z	0.000 z
Kvichak	281 y	0.083 y	0.125 y	0.065 z
Naknek	277 y	0.078 yx	0.122 y	0.000 z
Ugashik	282 y	0.074 x	0.082 y	0.043 z
Wood	259 x	0.093 z	0.128 y	0.000 z

TABLE 3. Results of Tukey's honestly significant difference familywise comparison tests for the effect of climate regime on mean length, compensatory growth, and the frequency of compensatory growth for age-1.0 and age-2.0 Sockeye Salmon from Bristol Bay. Within rivers, means with the same letter were not significantly different at the 95% familywise confidence level.

		Age-1.0 juveniles			Age-2.0 juveniles		
River	Regime	Lmean	CG	FCG	Lmean	CG	FCG
Egegik	1962–1976	268 z	0.155 z	0.07 z	284 z	0.320 y	0.000 z
	1977–2001	278 y	0.107 z	0.08 z	295 y	0.200 z	0.000 z
	2002–2007	284 y	–0.032 z	0.33 z	304 y	0.244 zy	0.000 z
Kvichak	1962–1976	260 z	0.006 y	0.13 zy	272 z	0.250 y	0.000 z
	1977–2001	264 zy	–0.236 z	0.56 y	284 y	0.066 z	0.120 z
	2002–2007	274 y	–0.209 zy	0.67 y	290 y	0.060 z	0.000 z
Naknek	1962–1976	278 y	0.029 y	0.13 zy	289 y	0.206 y	0.000 z
	1977–2001	257 z	–0.243 z	0.60 y	269 z	0.081 z	0.000 z
	2002–2007	269 zy	–0.251 z	0.67 y	284 y	0.081 z	0.000 z
Ugashik	1962–1976	250 z	–0.036 z	0.20 z	275 z	0.059 z	0.067 z
	1977–2001	257 y	–0.172 z	0.33 z	286 zy	0.081 z	0.040 z
	2002–2007	272 x	–0.164 z	0.40 z	287 y	0.141 y	0.000 z
Wood	1962–1976	243 z	–0.041 y	0.20 z	253 z	0.223 y	0.000 z
	1977–2001	253 y	–0.263 y	0.80 y	260 zy	0.086 z	0.000 z
	2002–2006	263 y	–0.331 z	0.67 zy	268 y	0.069 z	0.000 z

and ocean entry year. The CG slope index decreased over time (Figures 7, 8), indicating that compensatory growth became more frequent over time. The CG slope index differed between smolt ages as well as among rivers and climate regimes (all $P < 0.001$; Table 5). In all five river systems, the index was significantly lower for age-1.0 juveniles and negative (indicating compensatory growth), in contrast to the positive CG slope index for age-2.0 juveniles. For both age-1.0 and age-2.0 juveniles, the index was significantly lower for Sockeye Salmon from the Kvichak, Naknek, Ugashik, and Wood rivers than for those from the Egegik River (Table 2). In terms of climate regime, the CG slope index was significantly lower (and negative) during the 1977–2001 climate regime than during the 1962–1976 regime for age-1.0 juveniles from the Kvichak, Naknek, and Wood rivers (Table 3). For age-2.0 juveniles, the index was significantly lower (though positive) for Egegik, Kvichak, Naknek, and Wood River Sockeye Salmon during the 1977–2001 climate regime (Table 3). There were no significant differences in the mean CG slope index between the 1977–2001 and 2002–2007 climate regimes.

The relationship between compensatory growth and smolt length varied among rivers, with CG increasing with smolt length among Sockeye Salmon in all but the Naknek River (Table 6). In the time series regression models, the CG slope index was influenced by smolt length and an underlying cycle but not summer SST (except in the case of age-1.0 Sockeye Salmon from the Wood River), climate regime, or juvenile abundance (Table 6). For the age-1.0 Wood River fish, the magnitude of compensatory growth increased in years with warmer sea surface conditions. Contrary to our hypothesis, compensatory growth in age-1.0 juveniles from the Kvichak and Wood rivers and age-2.0 juveniles from the Egegik River occurred more often in years when smolts were larger. In contrast, compensatory growth in age-1.0 juveniles from the Naknek River occurred in years when smolts were smaller. The compensatory growth of age-1.0 Sockeye Salmon from the Ugashik River and age-2.0 juveniles from the Kvichak, Ugashik, and Wood rivers was not significantly related to SST or smolt length. Compensatory growth increased with an increase in juvenile salmon abundance for age-1.0 Naknek, Ugashik, and Wood River Sockeye Salmon, but juvenile abundance was not the best predictor of compensatory growth in these models.

The frequency of compensatory growth was higher for age-1.0 Sockeye Salmon than for age-2.0 juveniles for all five river systems (Tukey's test; all $P < 0.01$). The FCG index differed among rivers for age-1.0 but not age-2.0 fish (Table 2). The index ranged from 11% to 59% for age-1.0 fish among river systems. It was higher for the Kvichak, Naknek, and Wood rivers than for the Egegik River; by contrast, the index for the Ugashik River was similar to that for all of the other rivers (Table 2).

Climate regimes influenced FCG for age-1.0 but not age-2.0 fish (Table 3). For age-1.0 fish from the Kvichak and Naknek rivers, FCG was higher during the 2002–2007 climate regime in than during the 1962–1976 climate regime. The largest change in FCG was for Wood River Sockeye Salmon,

TABLE 4. Results of the time series regression models for the mean length of age-1.0 and age-2.0 Sockeye Salmon returning to the Egegik, Kvichak, Naknek, Ugashik, and Wood rivers in Bristol Bay in relation to climate regime, summer sea surface temperature (SST), compensatory growth, juvenile abundance, and a first-order autoregressive parameter (φ_1) for the years 1962–2007.

	Coefficient statistics				Model statistics		
River	Variable	Estimate	t	P	R^2	F	P
		Age-1.0 juveniles					
Egegik	SST	0.46	3.43	0.001	0.21	11.77	0.001
Kvichak	SST	0.40	3.34	<0.001	0.51	22.70	<0.001
	Smolt length	0.47	4.27	0.001			
Naknek	SST	0.21	2.79	<0.001	0.79	80.81	< 0.001
	Smolt length	0.94	12.61	<0.001			
Ugashik	Climate regime (2002–2007)	1.50	4.38	<0.001	0.30	19.18	<0.001
Wood	SST	0.33	3.18	<0.001	0.60	23.73	<0.001
	Smolt length	0.49	4.76	<0.001			
	CG	–0.30	–2.73	<0.001			
		Age-2.0 juveniles					
Egegik	SST	0.40	4.29	<0.001	0.63	39.57	<0.001
	Smolt length	0.60	6.45	<0.001			
Kvichak	SST	0.44	4.16	<0.001	0.51	24.95	<0.001
	Smolt length	0.50	4.78	<0.001			
Naknek	Smolt length	0.84	6.95	< 0.001	0.69	48.65	<0.001
	φ_1	0.43	2.97	0.004			
Ugashik	Smolt length	0.61	5.10	<0.001	0.35	26.02	<0.001
Wood	SST	0.37	3.40	0.001	0.50	14.20	<0.001
	Smolt length	0.53	4.64	<0.001			
	φ_1	0.43	3.23	0.002			

which rose from 20% during the 1962–1976 climate regime to 80% during the 1977–2001 climate regime.

Size-Selective Mortality

The trends in the annual CVs of the back-calculated lengths of juvenile Sockeye Salmon were constant over time (Figures 9, 10). In the ANOVA test, Lcv differed among rivers but not between smolt ages or among climate regimes. There were significant interactions between river and smolt age and regime and smolt age. Within rivers, Lcv was greater for age-2.0 than age-1.0 Sockeye Salmon from the Kvichak and Wood River systems (Tukey's test; both $P < 0.01$) but not statistically different for those from the Egegik, Naknek, and Ugashik rivers. For age-1.0 fish, Lcv was lower for those from the Egegik, Kvichak, and Ugashik rivers and higher for those from the Naknek and Wood rivers (Table 2). For age-2.0 fish, Lcv was low for those from the Egegik and Ugashik rivers, intermediate for those from the Kvichak River, and high for those from the Wood River. The Lcv for age-2.0 Naknek River Sockeye Salmon was similar to those for all other stocks except that in the Wood River. The lack of a significant relationship between Lcv and SST or climate regime in the time series regression models provides evidence for size-selective mortality in all Bristol Bay Sockeye Salmon groups.

DISCUSSION

Factors Influencing Juvenile Length

For the Sockeye Salmon from the five Bristol Bay river systems analyzed in this study, juvenile length was influenced by climate regime, summer sea temperature, smolt length, and compensatory growth. Compensatory growth increased over time, occurring more frequently in age-1.0 than age-2.0 juveniles and after the 1976–1977 climate regime shift, and was an important factor in determining the length of juvenile Sockeye Salmon from the Wood River. Size-selective mortality was detected in Sockeye Salmon from all five rivers.

The lengths of age-1.0 and age-2.0 Sockeye Salmon from the five Bristol Bay river systems increased with mean summer SST (range, 7.5–10.5°C) in the eastern Bering Sea, except for age-2.0 fish from the Naknek and Ugashik rivers. These findings are consistent with those of other studies of the growth of juvenile Sockeye Salmon in the Gulf of Alaska and the Bering Sea (Martinson 2004; Martinson et al. 2009b; Ruggerone et al. 2007). Year-round sea surface temperatures in the southeastern Bering Sea are expected to increase 1 ± 2° C by 2050 and 3 ± 2°C by 2100 (Wang et al. 2012). The marine scale growth of juvenile Sockeye Salmon from the Karluk River on Kodiak Island (in the Gulf of Alaska) was

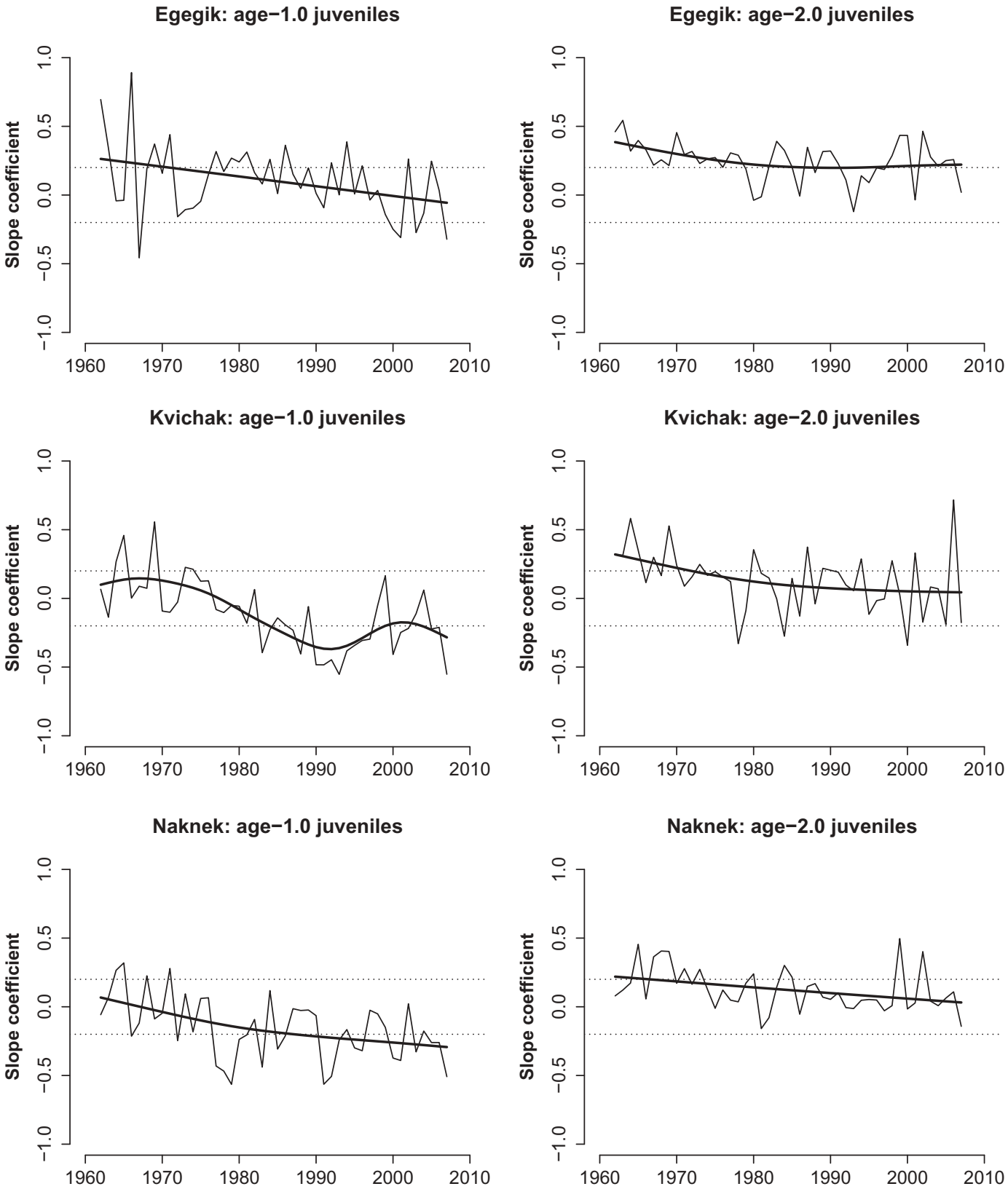

FIGURE 7. Compensatory growth slope coefficients for age-1.0 and age-2.0 Sockeye Salmon from the Egegik, Kvichak, and Naknek rivers from linear regression models relating first-year ocean growth and freshwater growth within a year. Significant negative (positive) coefficients are represented by values below (above) the lower and upper dotted lines, respectively.

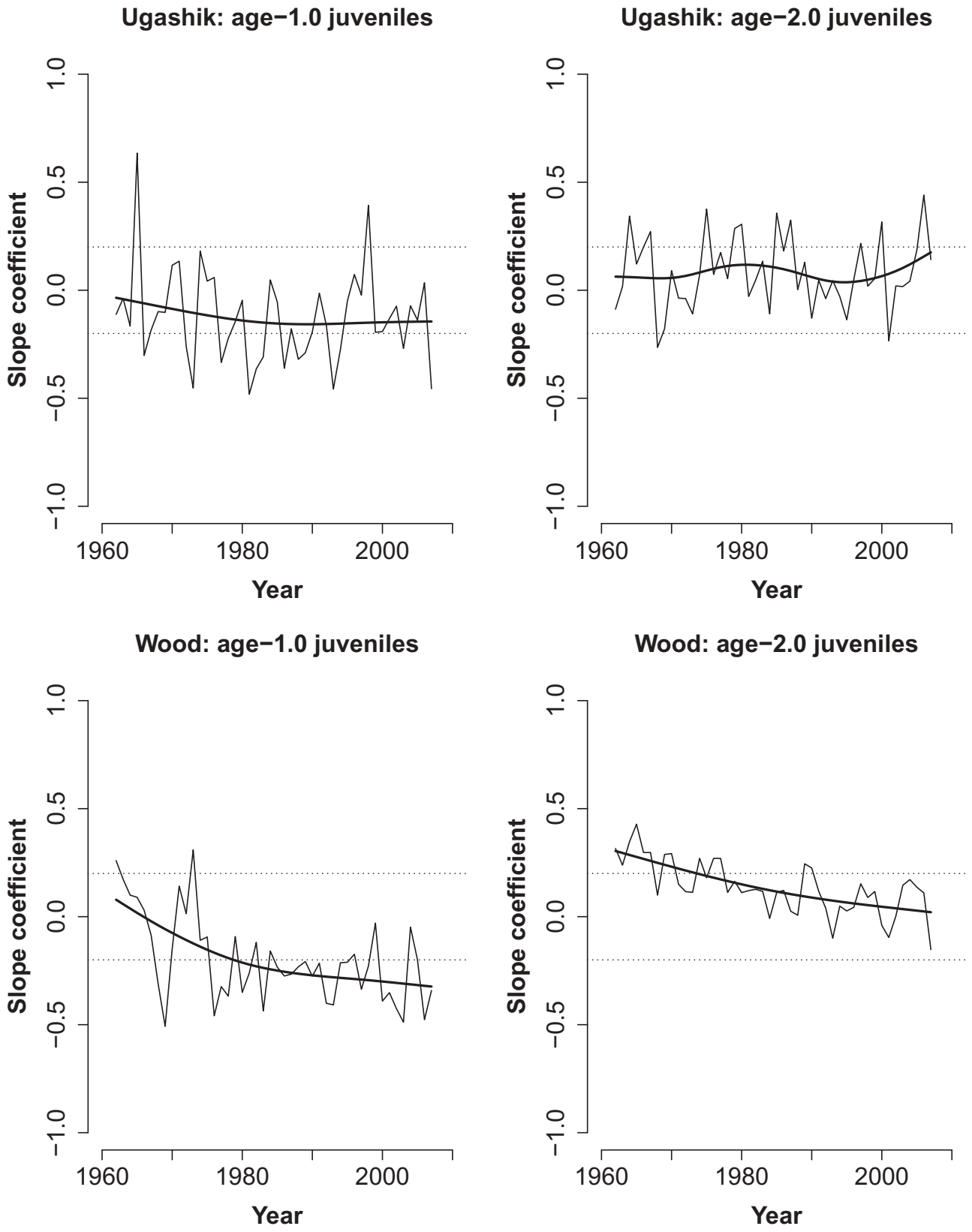

FIGURE 8. Compensatory growth slope coefficients for age-1.0 and age-2.0 Sockeye Salmon from the Ugashik and Wood rivers. See Figure 7 for additional details.

TABLE 5. Results of ANOVA of the effects of smolt age, river, and climate regime on the compensatory growth of age-1.0 and age-2.0 Sockeye Salmon from the Egegik, Kvichak, Naknek, Ugashik, and Wood rivers in Bristol Bay. See Table 1 for additional details.

Variable	df	SS	MS	*F*	*P*
Smolt age	1	6.972	6.972	205.266	<0.001
River	4	2.863	0.716	21.071	<0.001
Regime	2	2.229	1.114	32.808	<0.001
Smolt age × river	4	0.493	0.123	3.626	0.006
Smolt age × regime	2	0.215	0.108	3.168	0.043
River × regime	8	0.464	0.058	1.708	0.095
Smolt age × river × regime	8	0.200	0.025	0.735	0.661
Residuals	430	14.605	0.034		

found to be positively correlated with the average monthly June–August SST values (range, 8.2–12.0°C; $r = 0.49$, $P < 0.01$, $n = 40$) from 1950 to 1998 (Martinson 2004). These fish also had SST-related shifts in juvenile length associated with the 1957–1958 El Niño, the 1988–1989 warm-to-cool shift, and in 1974 preceding the cool-to-warm shift in 1976–1977 in the North Pacific Ocean (Martinson et al. 2009b). In the Bering Sea, the first- and second-year scale growth of Bristol Bay (Kvichak and Egegik rivers) Sockeye Salmon and the number of returns per spawner increased in response to the 1977–2001 warm climate regime (Ruggerone et al. 2007). These authors hypothesized that greater marine growth contributed to the increase in survival (Ruggerone et al. 2007). A similar positive response was seen in the influence of SST on the growth and size of juvenile Sockeye Salmon from Bristol Bay in this study and for juvenile Sockeye Salmon in the eastern Bering Sea and Gulf of Alaska.

There are several mechanisms by which length might relate positively to sea surface temperatures in the eastern Bering Sea, including changes in physiology and food availability (Portner and Peck 2010). In ectotherms, growth rates increase over a mid-range of temperatures and decline at temperatures above growth tolerance limits (Neuheimer et al. 2011). For yearling Sockeye Salmon studied in the laboratory, 15°C was the optimum water temperature for meeting metabolic demands (Brett 1964; Brett et al. 1964). In the eastern Bering Sea, the diets of juvenile Sockeye Salmon consisted of age-0 Walleye Pollock *Gadus chalcogrammus* during warm years (2002–2003) and Pacific Sand Lance *Ammodytes hexapterus* during cold years (2000–2001) (Farley et al. 2007b). During this survey, the catch per unit effort of age-0 Walleye Pollock was an order of magnitude higher than that of Pacific Sand Lances, indicating that prey were more abundant during the warm years (Farley et al. 2007b). Farley and Trudel (2009) also found that juvenile Sockeye Salmon were larger and had higher growth rate potential during warm years than during cold years on the eastern Bering Sea shelf. In addition, the densities of juvenile Sockeye Salmon prey were positively related to spring SST on the eastern Bering Sea shelf (Farley and Trudel 2009). The benefits of greater size include enhanced resistance to starvation, less vulnerability to predators, and greater tolerance of changes in the environment (Sograd 1997). We hypothesize that the length of juvenile Sockeye Salmon from Bristol Bay will continue to increase with continued warming in the southeastern Bering Sea but will decrease at a particular threshold when temperature tolerance limits are reached and juvenile Sockeye Salmon have increased metabolic demands.

In addition to the length of the fish, physiological factors are important in determining the marine survival of Sockeye Salmon. The energetic status (kJ/g wet weight) of juvenile Sockeye Salmon in the eastern Bering Sea during autumn was positively associated with marine survival in 2003–2007 but not related to sea surface temperature (Farley et al. 2007c, 2011). The mechanisms by which higher energy status might increase survival in salmon include reductions in predation risk, starvation, and competition, although these mechanisms are still poorly understood (Farley et al. 2011). Hunt et al. (2011) found evidence that crustacean zooplankton were less lipid rich during warm years and that this negatively impacted Walleye Pollock recruitment. Farley et al. (2013) hypothesized that increases in SST that lead to lipid-poor prey during warm years could reduce the energy status of juvenile Sockeye Salmon and their marine survival. We hypothesize that there is a trade-off between increased length and reduced girth in warming climate regimes and that this will have an effect on survival.

No density-dependent effect entailing higher juvenile abundance and reduced length was observed for the Sockeye Salmon in our study. In the Gulf of Alaska, growth during the first year at sea estimated from the scales of adult Sockeye Salmon from the Karluk River on Kodiak Island was negatively associated with the juvenile Sockeye Salmon abundance index and positively associated with the 1976–1977 regime shift (Martinson et al. 2008). Density-dependent effects on growth are often observed among salmon after their first year at sea. For example, the growth of age-2.3 Sockeye Salmon from the Kvichak River during their second year at

TABLE 6. Results of the time series regression model of compensatory growth of Sockeye Salmon that returned to the Egegik, Kvichak, Naknek, Ugashik, and Wood rivers in Bristol Bay in relation to climate regime, summer sea surface temperature, smolt length, juvenile abundance, and a first-order autoregressive parameter for the years 1962–2007.

			Coefficient statistics			Model statistics	
River	Variable	Estimate	t	P	R^2	F	P
			Age-1.0 juveniles				
Egegik	None						
Kvichak	Smolt length	–0.37	–3.35	0.0002	0.32	10.3	<0.001
	φ_1	0.56	4.71	0.00004			
Naknek	Smolt length	0.43	3.23	0.002	0.18	10.4	0.002
Ugashik	None						
Wood	Smolt length	–0.38	–3.0	0.005	0.26	8.9	<0.001
	SST	–0.38	–3.0	0.005			
			Age-2.0 juveniles				
Egegik	Smolt length	–0.51	–3.95	0.0003	0.26	15.6	<0.001
Kvichak	None						
Naknek	Smolt length	0.39	2.84	0.007	0.13	8.08	0.007
Ugashik	None						
Wood	None						

sea and the size of age-1.3 adult fish were negatively related to the returns of eastern Kamchatka Pink Salmon *Oncorhynchus gorbuscha* (Ruggerone et al. 2002). Other factors that were not investigated in this study may also influence the size of juvenile fish. For example, changes in the size of the parental cohort influenced the body lengths of 4-year-old Atlantic Cod, in part owing to a genetic response to size-selective mortality in the wild (Swain et al. 2007). Density-dependent growth is probably easier to detect in later life stages because the growth-related mortality is likely to be less.

Compensatory Growth

In our study, the compensatory growth of Bristol Bay Sockeye Salmon increased over time, occurred more frequently in age-1.0 than in age-2.0 fish as well as after the 1976–1977 climate regime shift, was an important factor in determining the length of juvenile Sockeye Salmon from the Wood River, and was more common in years when the fish had more freshwater growth. For juvenile Sockeye Salmon captured in the eastern Bering Sea, the smaller age-1.0 fish had more food in their stomachs and were in better condition than the larger age-2.0 juveniles during years in which ocean productivity appeared to be high (Farley et al. 2007c). Compensatory growth occurred more frequently after the 1976–1977 climate regime shift, and it is likely that during years when the marine environment is favorable for growth more fish are able to reach the critical size for overwinter survival. The advantage of reaching the critical size is that it increases fecundity and feeding and reduces mortality (Ali et al. 2003). However, the costs of rapid growth include riskier feeding behavior among predators, reduced growth, lower reproductive potential, poorer swimming performance, and lower lipid reserves (Ali et al. 2003).

One caveat of using adult scales is not knowing whether the observed compensatory growth simply reflects higher mortality of the smallest age-1.0 smolts or lower mortality of the largest age-2.0 smolts. In other words, when compensatory growth is observed, perhaps only the fastest-growing small smolts survived. After 1977, Kvichak River Sockeye Salmon exhibited an increase in size-selective mortality at sea (Ruggerone et al. 2013). This needs to be investigated further to determine the influence of compensatory growth on survival.

Size-Selective Mortality

Size-selective mortality was evident in all five Bristol Bay Sockeye Salmon populations over the 46 years of our study based on the lack of trends in Lcv at the end of the first year at sea and the lack of a relationship between Lcv, annual summer sea surface temperature, and climate regime. These results are supported by other studies of Bristol Bay Sockeye Salmon (Farley et al. 2011; Ruggerone et al. 2013). A comparison of the length frequency distributions of juvenile Sockeye Salmon in the eastern Bering Sea before winter in 2008 and south of the Aleutian Islands after winter in 2009 showed more truncated distributions after winter, indicating that smaller juvenile fish had been removed from the population (Farley et al. 2011). Ruggerone et al. (2013) compared observed and back-calculated smolt lengths of Sockeye Salmon from the Kvichak River from 1955 to 2008 and found (1) stronger size-selective mortality in

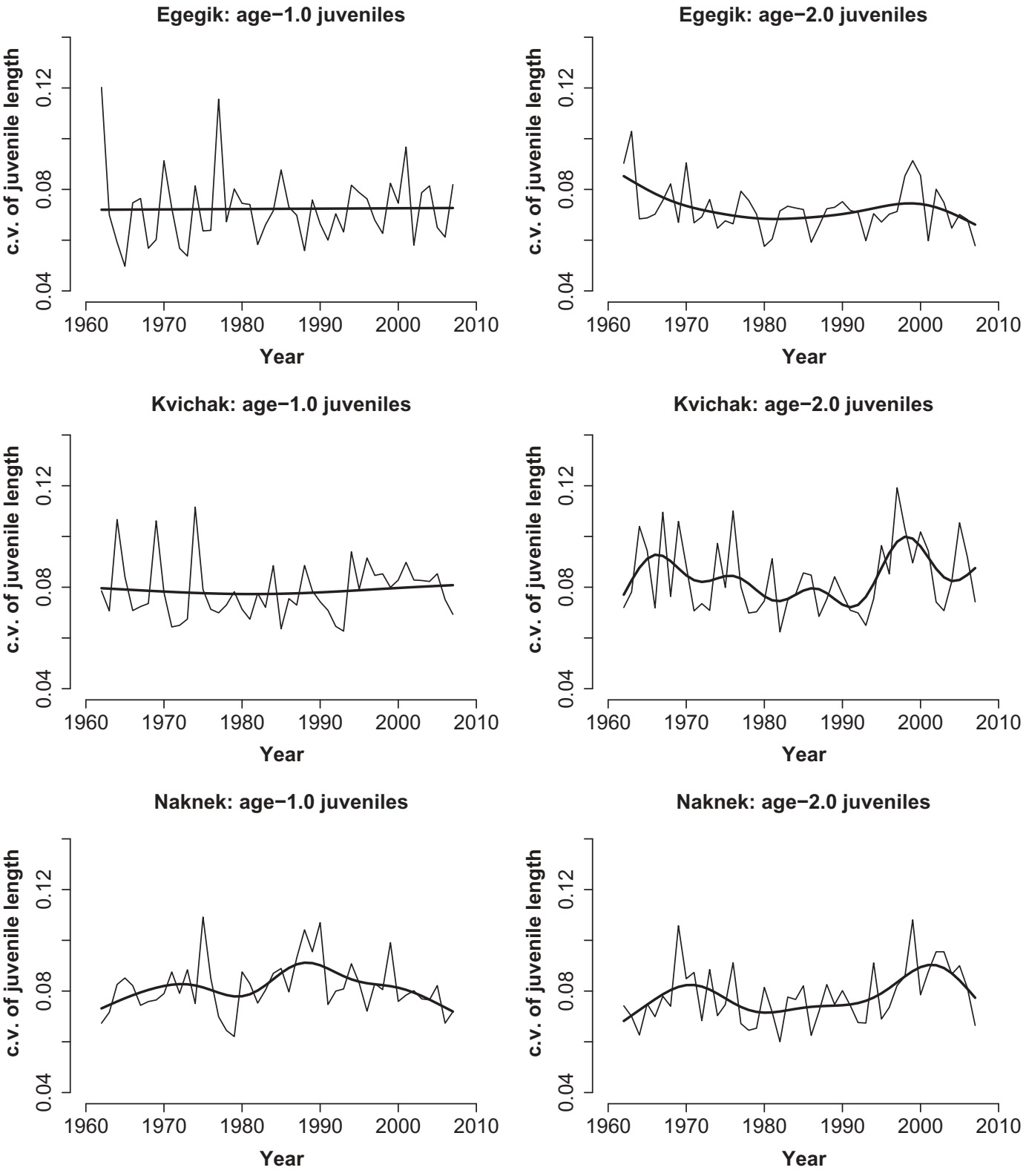

FIGURE 9. Coefficients of variation of the lengths of age-1.0 and age-2.0 Sockeye Salmon from the Egegik, Kvichak, and Naknek rivers after their first year at sea.

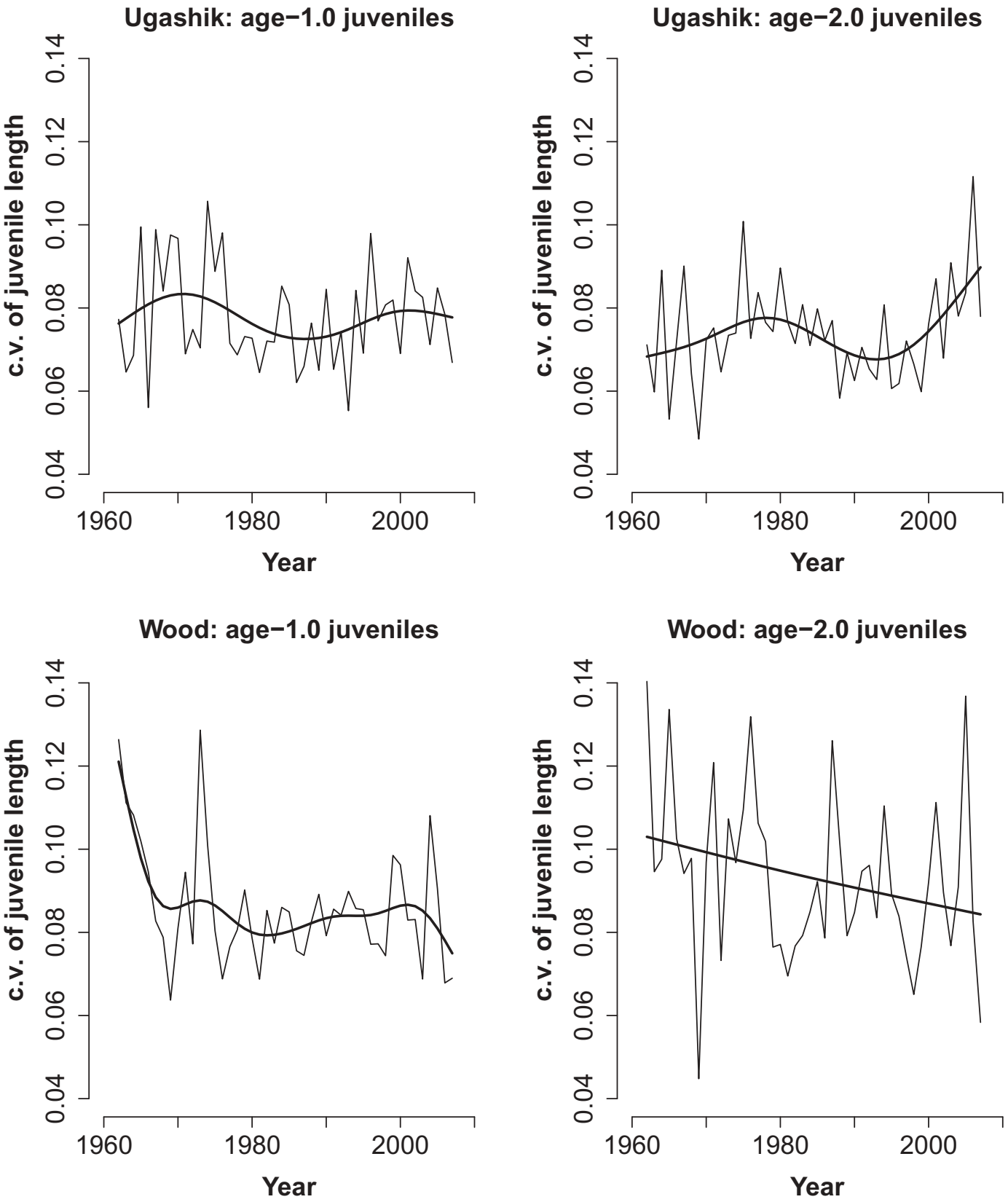

FIGURE 10. Coefficients of variation of the lengths of age-1.0 and age-2.0 Sockeye Salmon from the Ugashik and Wood rivers after their first year at sea.

age-1.0 smolts than in age-2.0 smolts, (2) higher size-selective mortality in years when smolts were smaller, and (3) an increase in size-selective mortality after the 1976–1977 climate regime shift. Possible mechanisms by which smaller juvenile fish might be selected against include starvation, low tolerance of extreme environmental conditions, and predation (Sogard 1997). Our size-adjusted estimate of the variance in the back-calculated lengths of juvenile Sockeye Salmon suggests that there is selection against the smaller fish in a cohort, but we did not assess the variability in size-selective mortality over time. Ruggerone et al. (2013) found a reduction in size-selective mortality after adjusting for size. The Lcv was more highly variable for the Wood River Sockeye Salmon, indicating that there was more variability in size-selective mortality in that stock than in the other stocks.

Our results supplement the understanding of the marine ecology of Bristol Bay Sockeye Salmon. Based on the findings of this and other studies, increases in SSTs in the Bering Sea are expected to lead to increases in the length of juvenile Sockeye Salmon; the frequency of compensatory growth; size-selective mortality; and overall survival (to the point where the greater metabolic demands on the juvenile Sockeye Salmon reduce their overwinter survival). Future studies should address the importance of climate-related changes in juvenile length, compensatory growth, and size-selective mortality on the overall survival of Bristol Bay Sockeye Salmon stocks.

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