

Abstract—We tested the hypothesis that larger juvenile sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska, have higher marine-stage survival rates than smaller juvenile salmon. We used scales from returning adults (33 years of data) and trawl samples of juveniles ($n=3572$) collected along the eastern Bering Sea shelf during August through September 2000–02. The size of juvenile sockeye salmon mirrored indices of their marine-stage survival rate (e.g., smaller fish had lower indices of marine-stage survival rate). However, there was no relationship between the size of sockeye salmon after their first year at sea, as estimated from archived scales, and brood-year survival size was relatively uniform over the time series, possibly indicating size-selective mortality on smaller individuals during their marine residence. Variation in size, relative abundance, and marine-stage survival rate of juvenile sockeye salmon is likely related to ocean conditions affecting their early marine migratory pathways along the eastern Bering Sea shelf.

Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*)

Edward V. Farley Jr¹

James M. Murphy¹

Milo D. Adkison²

Lisa B. Eisner¹

John H. Helle¹

Jamal H. Moss¹

Jennifer Nielsen³

Email address for E. V. Farley: Ed.Farley@noaa.gov

¹ NOAA, Auke Bay Laboratory
National Marine Fisheries Service, NOAA
11305 Glacier Highway
Juneau, Alaska 99801

² Juneau Center, School of Fisheries and Ocean Sciences,
University of Alaska Fairbanks
11120 Glacier Highway
Juneau, Alaska 99801

³ U.S. Geological Survey, Alaska Science Center
1011 East Tudor Road
Anchorage, Alaska 99503

Pacific salmon (*Oncorhynchus* spp.) experience relatively high mortality rates during the first few months at sea (Hartt, 1980), and it is believed that size plays an important role in survival (Parker, 1968; Pearcy, 1992). Size-dependent mortality of juvenile salmon may be concentrated during two specific life-history stages. The first stage is thought to occur just after juvenile salmon enter the marine environment, where smaller individuals are believed to experience higher size-selective predation (Parker, 1968; Willette et al., 1999). The second stage is thought to occur after the first summer at sea, when smaller individuals may not have sufficient energy reserves to survive late fall and winter (Beamish and Mahnken, 2001). Thus, larger individuals likely have a higher probability of survival during both of these stages, and size and growth while salmon reside in the estuary and during their first summer at sea may be important for survival.

Previous studies indicate that scale radius length is proportional to fish body length (Francis, 1990; Ricker,

1992) and, in particular, incremental increases in sockeye salmon (*O. nerka*) scale radius are strongly correlated with somatic growth (Fukuwaka and Kaeriyama, 1997). In our study, scales from adult Bristol Bay sockeye salmon were examined to determine the relationship between size after their first year at sea and survival to adulthood. We compared the time series (1965–97) of brood-year returns per spawner with scale growth measurements taken from adult sockeye salmon returning to the Egegik and Kvichak River systems in Bristol Bay, Alaska.

Juvenile sockeye salmon enter the marine waters of the eastern Bering Sea during May and June (Burgner, 1991) and migrate through Bristol Bay to the Bering Sea and North Pacific during the summer and early fall months (Straty, 1981; Farley et al., 2005). Two differing models of seaward migration are believed to exist for juvenile Bristol Bay sockeye salmon: in some years juvenile sockeye salmon migrate along the coastal waters of the eastern Bering Sea near the Alaska Peninsula, and in other

Manuscript submitted 27 March 2006
to the Scientific Editor.

Manuscript approved for publication
5 July by the Scientific Editor.

Fish. Bull. 105:121–130 (2007).

years their migration is farther offshore (Farley et al., 2005). We also compared the size of juvenile Bristol Bay sockeye salmon collected during late summer and early fall (2000–02) trawl surveys along the eastern Bering Sea shelf with indices of their abundance, marine stage survival rate after our survey, and returns per spawner from these cohorts. Interannual differences in the size and growth rates of juvenile sockeye salmon were also compared to their early marine distribution and ocean conditions. The specific objectives of this study were to determine whether larger, presumably faster growing, juvenile sockeye salmon in fact had higher survival rates than smaller, presumably slower growing individuals, and what aspects of the marine environment might influence these growth rates.

Materials and methods

Data

Our research focused on Bristol Bay sockeye salmon because this region has the largest returns and commercial harvest of sockeye salmon in the world. Scales from adult sockeye salmon, their fork lengths, and data on brood-year return per spawner for the Egegik and Kvichak Rivers in Bristol Bay, Alaska, as well as annual totals of the number of adult Bristol Bay sockeye salmon returns and spawners, were obtained from the Alaska Department of Fish and Game (ADF&G). Salmon scales are collected annually by ADF&G to estimate the age composition of adult sockeye salmon for fishery management. Age was designated by the European notation, i.e., $a.b$, where a = the number of winters spent in freshwater prior to going to sea and b = the number of winters spent in the ocean (Koo, 1962a). Salmon scale collections and brood year return per spawner data were available for the dominant freshwater and ocean age groups of sockeye salmon sampled in the Kvichak River (brood year returns for ages 1.2, 1.3, 2.2, 2.3; 1965–97) and the Egegik River (brood year returns for ages 1.3, 2.2, 2.3; 1965–97).

Scales were selected for measurement by following the procedures described in Ruggerone et al. (2005). Briefly, scales were selected when our age determination matched that previously made by ADF&G, the shape of the scale indicated that the scale was from the “preferred area” (below the dorsal fin and above the lateral line—see Koo, 1962b), and the circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis. The number of scale samples for each river system and age group are provided in Table 1.

Scales from adult sockeye salmon were digitized following procedures described by Hagen et al.¹ and Rug-

Table 1

The total number of scale samples for sockeye salmon (*Oncorhynchus nerka*) for brood years 1965–97 from the Egegik and Kvichak River systems in Bristol Bay, Alaska. Age groups are 1.2, 1.3, 2.2, and 2.3.

River	Age group			
	1.2	1.3	2.2	2.3
Egegik	0	1265	1592	1581
Kvichak	1563	1441	1582	1246

gerone et al. (2005). The scale measurement axis was determined by a perpendicular line drawn from a line intersecting each end of the first saltwater annulus. Distance (mm) between the focus and the outer edge of the scale was designated as the total scale length. The relationship between total scale length and adult fork length was linear for both the Egegik River (F -test, $P < 0.001$; $r^2 = 0.41$) and Kvichak River (F -test, $P < 0.001$; $r^2 = 0.36$) sockeye salmon samples. For an index of total growth through the first year at sea, we measured the distance from the focus to the outer edge of the first saltwater growth zone for each fish. A time series of annual means of the individual growth during the first year at sea ($MSWI_{i,a,t}$) estimated for each adult freshwater age group (a represents 1 or 2) within a river system (i represents Egegik, Kvichak) was used as an index of size that sockeye salmon would have attained after their first year (t) at sea.

The total number of fish caught and the fork lengths (mm) of juvenile sockeye salmon within each trawl haul were recorded during the Bering-Aleutian Salmon International Survey (BASIS) research cruises along the eastern Bering Sea shelf during fall (August–September) 2000 to 2002 (Fig. 1). The surveys were conducted over a broad area of the shelf and over major oceanographic domains (coastal and middle domains; Kinder and Schumacher, 1981) along the eastern Bering Sea shelf. In addition, the surveys were designed to sample the entire population of juvenile sockeye salmon from Bristol Bay lake systems to reduce the chance of sample variability that could affect one’s ability to interpret results from these samples. Recent descriptions of juvenile salmon migration pathways along the eastern Bering Sea shelf (Farley et al., 2005) and genetic stock composition indicate that juvenile sockeye salmon collected during the surveys were primarily from Bristol Bay.

Fish were collected by using a mid water rope trawl (see Farley et al., 2005 for description) rigged to sample the top 15 m of the water column. We attempted to collect scales from juvenile sockeye salmon during all three years of the survey; however, sample sizes of scales (from the preferred location on fish) were too small for statistical analyses because of descaling of the juvenile salmon by our mid-water rope trawl. Data

¹ Hagen, P. T., D. S. Oxman, and B. A. Agler. 2001. Developing and deploying a high resolution imaging approach for scale analysis. Doc. 567, p. 11. North Pacific Anadromous Fish Commission, 889 Pender Street, Vancouver, Canada.

collected during each trawl included the trawl speed obtained with a global positioning system and the height and width of the net opening obtained with a Simrad FS900 (Simrad, Lynnwood, WA) net sounder. The mean date of collection of juvenile sockeye salmon sampled for length differed slightly between years (i.e., 26 August during 2000; 5 September during 2001; 1 September during 2002); lengths were adjusted to account for these differences.

Survival and early marine-stage growth rates inferred from adult scales

For each freshwater age group, we calculated an index of survival rate that normalized the data and removed possible density-dependent effects (i.e., Peterman et al., 1998; Mueter et al., 2002). Specifically, our index of survival rate was the time series of residuals from a Ricker model defined by

$$\ln\left(\frac{R_{i,a,2,t+2} + R_{i,a,3,t+3}}{S_{i,t-(a+1)}}\right) = \alpha_{i,a} - \beta_{i,a} S_{i,t-(a+1)} + \varepsilon_{i,a,t}, \tag{1}$$

where t = the first ocean year for sockeye salmon;

S = the total number of spawners within river system i (i represents Egegik or Kvichak);

R = the total return (catch+spawners) for each freshwater age group a (a represents freshwater age 1 or 2) within river system i ;

α and β = model parameters representing the number of recruits per spawner at low numbers of spawners and the level of density dependence (Quinn and Deriso, 1999); and

$\varepsilon_{i,a,t}$ = the normally distributed residuals of the model.

For our analysis, partitioning salmon brood-year productivity by freshwater age group was necessary to directly compare our index of survival with our time series of $MSW1_{i,a,t}$ growth.

Analysis of covariance (ANCOVA) was used to examine the effect of $MSW1_{i,a,t}$ on our indices of survival (see Fig. 2, A–D for scatter plots of $\varepsilon_{i,a,t}$ and $MSW1_{i,a,t}$ and the addition of river system, age group and year were used as factors in the model. The results indicated that the year factor was highly significant (F -test, $P < 0.001$) and that $MSW1_{i,a,t}$ was not significant (F -test,

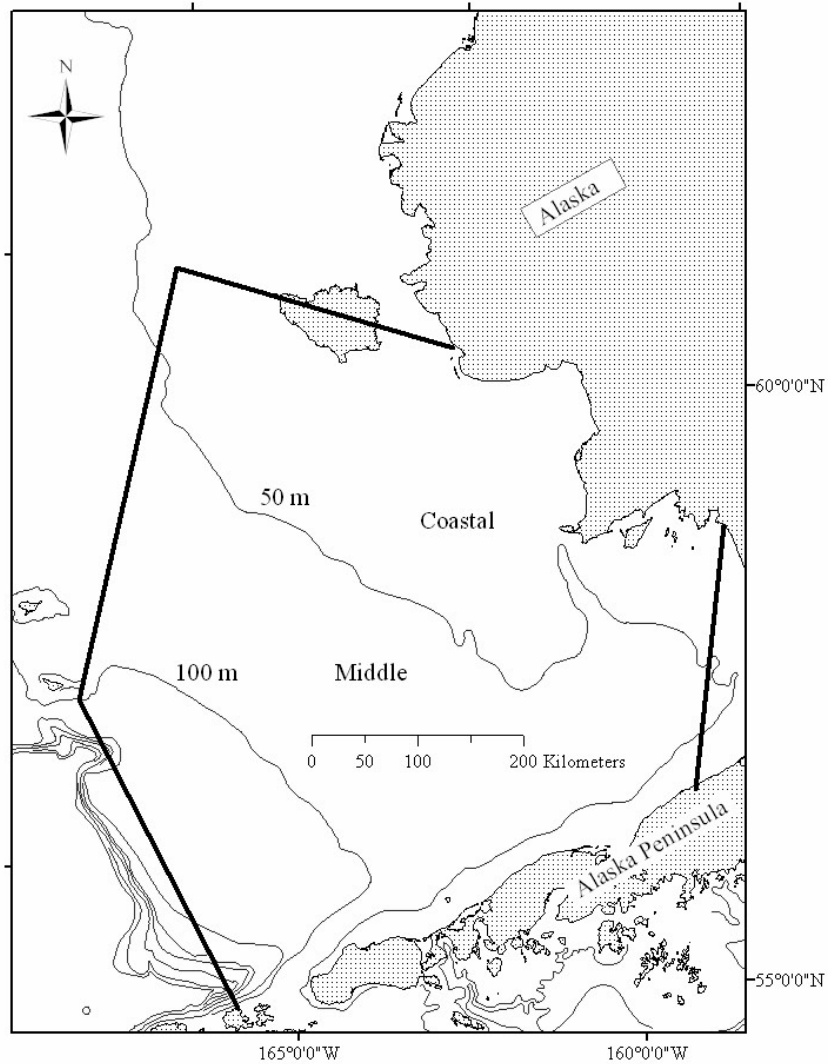
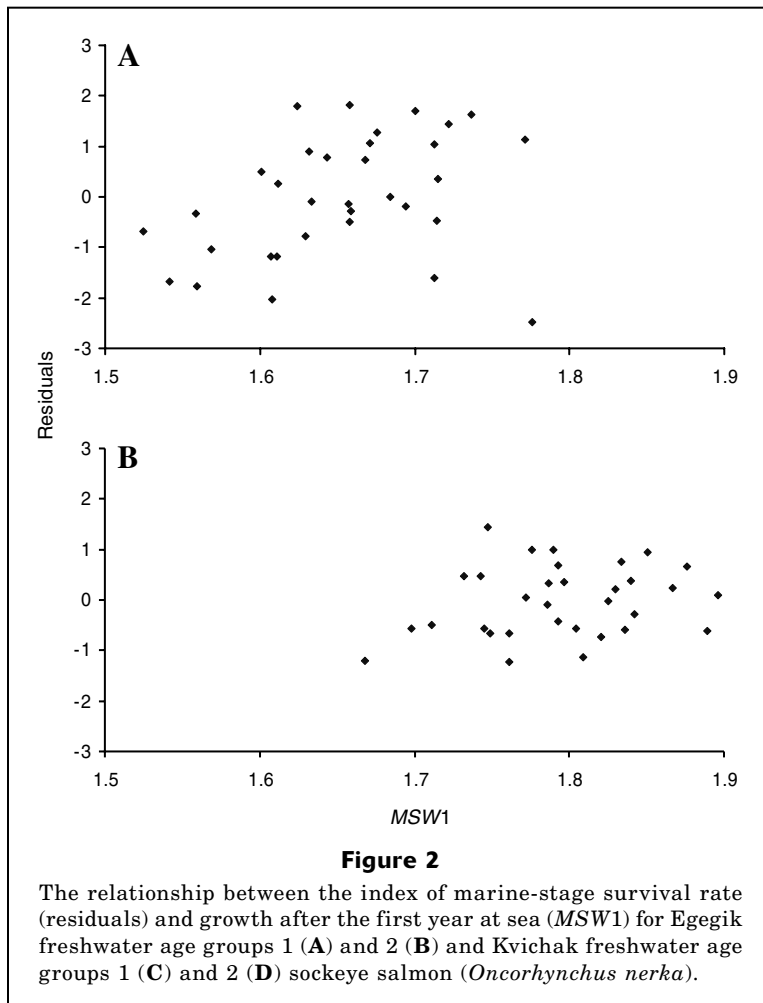


Figure 1

Survey area of the annual August–September (2000–2002) Bering-Aleutian Salmon International Survey (BASIS) within the coastal and middle domains of the eastern Bering Sea.

$P=0.18$). It was possible that during some years all fish could have had excellent growth and attained a large size, but the ANCOVA model would have attributed the large size to the highly significant year factor. However, when we removed the year factor from the ANCOVA model, $MSW1_{i,a,t}$ was less significant (F -test, $P=0.27$). In addition, the residuals from these models contained significant positive autocorrelation.

Because our data contained significant autocorrelation and showed a time series character, we created univariate time series models (Wei, 1990) for both $MSW1_{i,a,t}$ and $\varepsilon_{i,a,t}$ to determine whether autoregressive or moving average components were present. The univariate models were developed by examining the sample autocorrelation and partial autocorrelation functions for each time series. Time series data were considered white noise processes, i.e., uncorrelated random variables



with constant mean and variance, when none of the components of the sample autocorrelation and partial autocorrelation functions differed significantly ($P=0.01$) from zero (Wei, 1990).

Multivariate time series models in the form of linear transfer function (LTF) models (Liu and Hudak, 1992) were developed to describe the relationship between $MSW1_{i,a,t}$ and our index of survival rate for each freshwater age group and river system. All the univariate time series of survival rate indices contained significant positive first-order autoregressive parameters (see Table 2). Therefore, we included the first order autoregressive parameter in the LTF models. The models were defined as

$$\varepsilon_{i,a,t} = c_{i,a} + \lambda_{i,a} MSW1_{i,a,t} + \frac{1}{(1 - \phi_{1,i,a} B)} N_{i,a,t}, \quad (2)$$

where t , i , a are described in Equation 1;

$MSW1$ = the early marine growth index for sockeye salmon during their first year at sea;

ϕ_1 = the autoregressive lag 1 parameter;

B = the symbol for the backshift operator (i.e., $B \times S_t = S_{t-1}$);

$c_{i,a}$ and $\lambda_{i,a}$ = parameters within the model; and
 $N_{i,a,t}$ = a sequence of random errors that are independently and identically distributed with a normal distribution.

Parameters within the univariate and LTF models were deemed significant when their t -value was greater than 2.0 ($P < 0.05$).

Autocorrelation analysis was used to examine whether the model residuals were white noise. Univariate and LTF models were compared by using Schwartz's Bayesian criterion (SBC; Wei, 1990) to determine if the inclusion of $MSW1$ in Equation 2 improved the model fit.

Analyses of data from juveniles collected by trawling

Next, we developed an index of relative survival rate of adult Bristol Bay sockeye salmon for 2000–02, and indices of abundance and marine-stage survival rate of juvenile sockeye salmon collected during 2000–02 to compare with mean lengths of juvenile sockeye salmon collected during those years. Relative survival was defined as the number of returning adult sockeye salmon from brood-year escapements that contributed to the

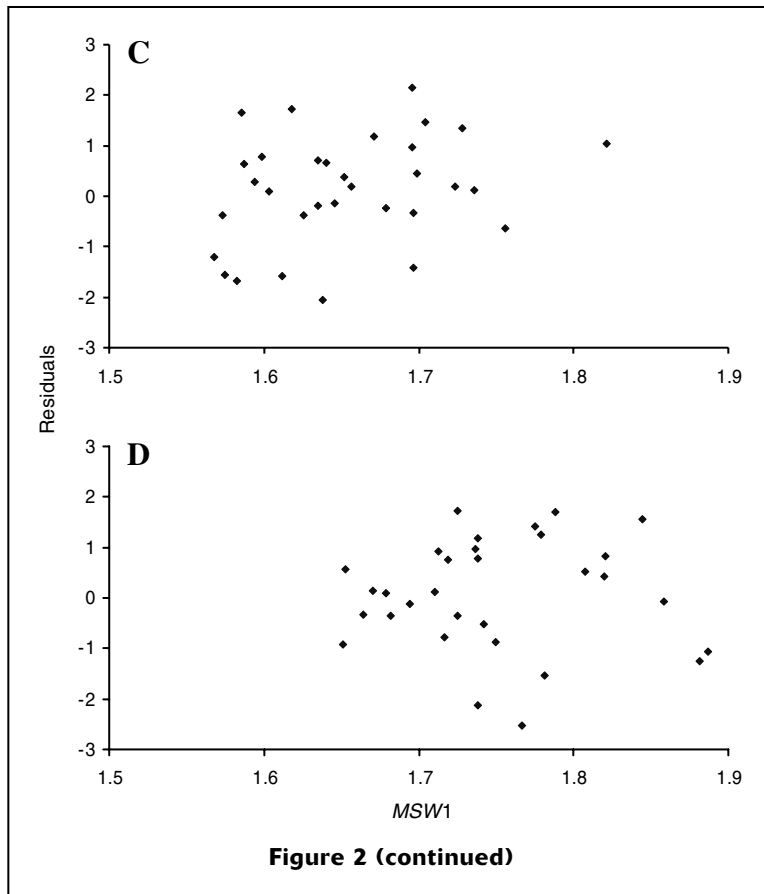


Table 2

Univariate (Univ) and linear transfer function (LTF) models indicating the effect of early marine growth index (*MSW1*) on the index of marine stage survival rates for each freshwater age group of sockeye salmon (*Oncorhynchus nerka*) returning to the Egegik and Kvichak rivers. Other variables include the constant (*Const*) and the autoregressive parameter ϕ_1 . Model statistics included the number of effective observations (*n*), the coefficient of determination (r^2), residual standard error (*RSE*), the number of parameters (*M*), and Schwartz's Bayesian criterion (*SBC*).

River	Age (yr)	Model	<i>n</i>	r^2	<i>RSE</i>	<i>M</i>	<i>SBC</i>	Model coefficients			<i>t</i> -value		
								<i>Const.</i>	<i>MSW1</i>	ϕ_1	<i>Const.</i>	<i>MSW1</i>	ϕ_1
Egegik	1	Univ	32	0.34	0.958	2	4.19	0.13	—	0.48	0.40	—	3.37
		LTF	32	0.41	0.908	3	4.22	-10.38	6.36	0.30	-2.22	2.25	2.07
	2	Univ	32	0.17	0.630	2	-22.64	0.02	—	0.42	0.10	—	2.64
		LTF	32	0.25	0.601	3	-22.19	-6.61	3.69	0.41	-1.74	1.75	2.59
Kvichak	1	Univ	32	0.29	1.075	2	11.56	-0.15	—	0.54	-0.36	—	3.60
		LTF	32	0.29	1.074	3	14.97	1.06	-0.73	0.54	0.21	-0.24	3.62
	2	Univ	32	0.35	0.986	2	6.00	-0.32	—	0.64	-0.64	—	3.99
		LTF	32	0.35	0.985	3	9.43	0.71	-0.59	0.64	0.18	-0.26	3.98

juvenile sockeye salmon in the trawl samples taken during years 2000, 2001, and 2002. For instance, juvenile sockeye salmon contributing to the early marine population during 2000 comprised age-2.0 fish from the

1997 and age-1.0 fish from the 1998 brood-year escapements, and these fish would have returned as adults during 2002 and 2003. Relative marine-stage survival rate (RS) was thus calculated as

$$RS_t = \frac{\sum_{a=1}^2 (R_{a,2,t+2} + R_{a,3,t+3})}{(S_{t-2} + S_{t-3})/2}, \quad (3)$$

where t = the year juvenile sockeye salmon were sampled ($t=2000, 2001, 2002$);

a = the freshwater age (1.0 or 2.0);

R = is the total number of returning adult sockeye salmon to Bristol Bay after year t ; and

S = the total number of spawners in Bristol Bay that contributed to the juvenile salmon population during year t .

For instance, freshwater juvenile sockeye salmon (ages 1.0 and 2.0) sampled during 2000 came from cohorts spawning during 1998 (age 1.0) and 1999 (age 2.0) and returned to Bristol Bay during 2002 as adult salmon at age 1.2 and 2.2 in 2002 and at age 1.3 and 2.3 in 2003. The numbers of returning adult and spawning Bristol Bay sockeye salmon were estimated from brood-year return information provided by ADF&G.

Annual indices of juvenile sockeye salmon abundance (IA) were defined as

$$IA_t = (SA / \overline{ma}) \overline{C}_t, \quad (4)$$

where SA = the estimated survey area (189,000 km²);

\overline{ma} = the mean area sampled by a trawl haul during the survey (distance traveled during the tow multiplied by the width of the net); and

\overline{C}_t = the mean number of juvenile sockeye salmon caught during year t ($t=2000, 2001, 2002$).

This formula would give the abundance of juvenile sockeye salmon in the survey area if we assumed that catchability with our midwater trawl was 1, (i.e., all fish in front of the net were caught). Because this is unlikely, we treat our estimates as an index rather than as actual abundance. In fact, our juvenile sockeye salmon abundance indices were less than the resultant adult returns in some years, indicating that catchability of the net was much less than 1. One study (Shuntov et al., 1993) where larger surface trawl gear was used to sample juvenile salmon indicated that catchability of juvenile salmon was 0.3. We therefore divided our abundance indices by 0.3, although we still considered these values to be indices.

An index of juvenile sockeye salmon marine-stage survival rate (IMS) was estimated by

$$IMS_t = \frac{\sum_{a=1}^2 (R_{a,2,t+2} + R_{a,3,t+3})}{IA_t} \times 100, \quad (5)$$

where R is defined above in Equation 3, IA_t is defined in Equation 4, t is the year juvenile sockeye salmon were

sampled ($t=2000, 2001, 2002$), and a is freshwater age (age 1.0 or 2.0).

These survival rate indices were correlated with the mean length of juvenile fish collected during the corresponding first year at sea. Because the mean date for juvenile sockeye salmon sampled for length differed among years, we adjusted fish lengths to provide a standardized length using September 1 as the standard date. Adjusted mean fish lengths were calculated by assuming three different daily growth rates: 1) 0 mm/day, representing no daily growth at sea; 2) 0.3 mm/day, the lower end of published growth-rate ranges for juvenile Pacific salmon; and 3) 1.7 mm/day, representing the upper end of the ranges (see Fisher and Pearcy, 1988, 1990; Fukuwaka and Kaeriyama, 1994; Orsi et al., 2000 for daily growth-rate ranges for juvenile Pacific salmon).

Results

Analyses of adult scale data

Examination of the autocorrelation and partial autocorrelation functions for Kvichak River freshwater age groups 1 and 2 and the Egegik River freshwater age-group-1 MSW1 univariate time series indicated that these time series had a constant mean and variance. For the Egegik River freshwater age-group-2 MSW1 growth index, the sample autocorrelation and partial autocorrelation functions indicated that a lag-1 autoregressive parameter was appropriate and the estimate of the parameter was significant (t -test, $P < 0.01$). Coefficients of variation were less than 4% for the MSW1 growth-rate indices for each freshwater age group, and thus confirmed the univariate model results that these time series varied little over time. By comparison, the coefficients of variation for the time series of returns per spawner for each freshwater age group were between 70% and 135%.

The MSW1 growth index was not significantly related to survival in any of the LTF models except for Egegik freshwater age group 1 (Table 2). Parsimonious univariate models were reasonable explanations of survival for both river systems and age groups, having values of SBC nearly as low as the "best" models. The sample autocorrelation and partial autocorrelation functions indicated that a lag-1 autoregressive parameter was appropriate for the all of the univariate survival rate time series models. The estimates of the lag-1 autoregressive parameter were positive for all of the univariate models.

Analyses of data from juveniles collected by trawling

The distribution of juvenile sockeye salmon along the eastern Bering Sea varied among years (Fig. 3). During 2000 and 2001, 75% of the total catch of juvenile sockeye salmon occurred south of 56°N, within the middle domain and south within the stratified waters near the

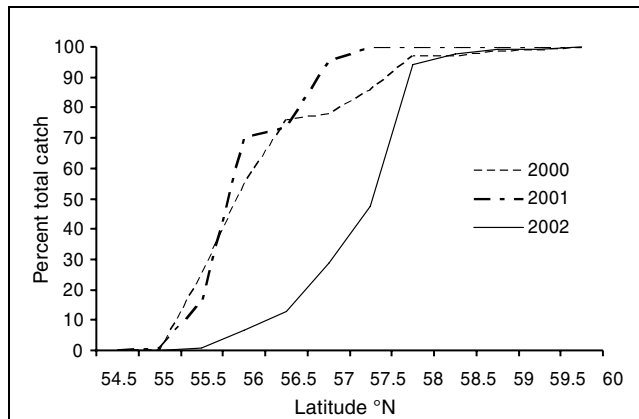


Figure 3

The percentage of total catch of juvenile sockeye salmon (*Oncorhynchus nerka*) in relation to latitude ($^{\circ}$ N) along the eastern Bering Sea shelf during August–September 2000, 2001, and 2002.

coastal domain along the Alaska Peninsula. During 2002, 75% of the total catch of juvenile sockeye salmon occurred north of 57° N, with 50% of the total catch occurring north of 58° N within the shallow stratified waters near the northern coastal domain.

Average fork length of juvenile sockeye salmon was significantly smaller during 2001 than during 2000 and 2002 for growth rates greater than 0.3 mm/day (t -test; $P < 0.01$) and not significantly different from 2000 (t -test; $P = 0.05$) for growth rates equal to 0 mm/day (Table 3). The rank order of juvenile sockeye salmon fork lengths was the same for all growth rates, and the largest fish taken in 2002 and the smallest, in 2001. For all three growth rates, average fork length was significantly larger during 2002 than during 2000 and 2001 (t -test; $P < 0.01$).

The marine-stage survival rate and abundance in the indices mirrored the observed variation in fish fork length; they were highest during 2002 and at or near their lowest during 2001 (Table 4). In addition, the nearshore distribution of juvenile sockeye salmon (2001; Fig. 3) appeared to coincide with lower indices of abundance and marine-stage survival rate, whereas fish distributed in the northern area of our survey (2002; Fig. 3) exhibited higher marine-stage survival rate and abundance.

Discussion

Our study indicates that the size of Bristol Bay sockeye salmon after their first year at sea is not directly related to their survival, when size is measured from growth rings on the scales of adults returning to the Egegik and Kvichak rivers. Analyses of the MSW1 growth index indicated that most of the time series had a constant mean and variance. Similar studies where adult scales

Table 3

Average fork length of juvenile sockeye salmon (*Oncorhynchus nerka*) collected along the eastern Bering Sea during 2000, 2001, and 2002. Daily growth rate (mm) was assumed to be 0, 0.30, and 1.7. Statistics include sample size (n), average fork lengths, and standard deviation (SD) of the original length data.

Year	m	Average fork length (mm)			
		0	0.3	1.7	SD
2000	834	174.77	176.53	184.76	19.99
2001	802	171.91	170.61	164.53	35.55
2002	1936	197.96	197.94	197.83	34.74

Table 4

Indices of abundance (IA), marine-stage survival rate (IMS), and relative marine-stage survival rate (RS) for juvenile sockeye salmon (*Oncorhynchus nerka*) collected along the eastern Bering Sea during 2000, 2001, and 2002.

Year	IA	IMS	RS
2000	130	21%	3.8
2001	137	15%	1.9
2002	180	34%	6.0

from Atlantic (*Salmo salar* L.; Crozier and Kennedy, 1999), coho (*O. kisutch*; Briscoe, 2004), and chum (*O. keta*; Helle, 1979) salmon were used to measure growth (size) of salmon during their first year at sea revealed that the survival rate of a cohort was statistically unrelated to variation in growth (size) of the salmon. The relative uniformity in the size of salmon after their first year at sea and the lack of a relationship between size and survival rate is contrary to the prevailing paradigm that the size achieved by fish after their first summer at sea is important to survival (Beamish and Mahnken, 2001). However, these results do not necessarily invalidate this paradigm; the adult scale samples available for analysis may reflect only those juvenile salmon that had attained sufficient size in order to survive to adulthood, and not those that died at sea (Crozier and Kennedy, 1999).

In support of this possibility, when we directly measured the fork length of juvenile sockeye salmon (Tables 3 and 4) during late summer and early fall surveys along the eastern Bering Sea shelf (2000–02), smaller fish had lower indices of marine-stage survival rate. This result is consistent with that from other studies of teleost fish, where larger individuals gained a survival advantage over smaller conspecifics during the juvenile life-history stage (Parker, 1968; Healey, 1982; Holtby et

al., 1990; Pearcy, 1992; Sogard, 1997; Mortensen et al., 2000; Beamish and Mahnken, 2001; Moss et al., 2005). This result is also in accord with the critical-size and critical-period hypothesis in which brood-year survival is determined by the number of juvenile salmon that have reached a critical size by the end of their first marine summer (Beamish and Mahnken, 2001; Beamish et al., 2004). The assumption with this hypothesis is that fish that do not reach a critical size after their first summer at sea will die because they are unable to meet minimum metabolic requirements during late fall and winter (Beamish and Mahnken, 2001). Although our results indicate that larger juvenile sockeye salmon have higher relative marine-stage survival rate after their first year at sea, it is difficult to directly address when the mortality would occur because sockeye salmon can spend an average of 2 to 3 years at sea. However, the overwhelming evidence from field and laboratory studies of juvenile stages of teleost fishes seems to indicate that size-selective mortality occurs during winter because larger members of a cohort are better than smaller members at tolerating physical extremes and enduring longer periods without food (Sogard, 1997).

One other test of the critical-size and critical-period hypothesis is that mortality rates after this period should be large in relation to other sources of early marine mortality (Beamish et al., 2004). To interpret our indices of marine-stage survival rate as the actual post-survey marine survival rate requires making a variety of questionable assumptions (e.g., that the vulnerability of juvenile salmon to our gear is known). However, if our estimates are close to correct, they would indicate that marine-stage mortality rates of juvenile sockeye salmon may be greater than 70% (Table 4) after our late-summer-early-fall surveys. These marine-stage mortality rates are substantial and approach late fall and winter mortality rates of greater than 90% found for other Pacific salmon (Beamish et al., 2004).

Lengths of juvenile sockeye salmon differed significantly among years if we assumed daily growth rates of 0.3 mm and greater. Differences in fork length of juvenile sockeye salmon could reflect annual differences in early marine growth rates or may also reflect annual differences in the size of smolt leaving Bristol Bay lake systems. However, limited surveys of sockeye salmon smolt from the Kvichak and Ugashik Rivers during 2000 through 2002 (Egegik River sampling was not undertaken in 2002) by ADF&G indicate that differences in smolt length among years and within age classes and river systems were less than 9%. In addition, the smallest average smolt size among these three years was seen during 2002, the year with the largest juvenile sockeye salmon size. Thus, it is likely that annual differences in length observed during our survey were due to differences in marine growth rates between years.

The annual variability in juvenile sockeye salmon size and in indices of marine-stage survival rates may be linked to the early marine migration of these salmon along the eastern Bering Sea shelf. Although we had

only three years of data, size and survival indices of Bristol Bay sockeye salmon were lowest when juvenile sockeye salmon were distributed nearshore along the Alaska Peninsula (i.e., the coastal migration pathway) and highest when they were distributed farther north and offshore. In support of this theory, the coastal migration pathway of juvenile Bristol Bay sockeye salmon observed by Straty (1981) during the late 1960s and early 1970s coincided with a significantly lower production of Bristol Bay sockeye salmon that occurred before the mid 1970s (Adkison et al., 1996).

The annual variability in seaward migration pathways is likely related to ocean conditions on the shelf during spring and summer. Recent studies indicate that sea surface temperatures along the eastern Bering Sea in summer, the period when juvenile sockeye salmon are present on the shelf, is positively correlated with Bristol Bay sockeye salmon survival rates (Mueter et al., 2002). It is possible that the effect of sea surface temperatures on survival rates of juvenile Bristol Bay sockeye salmon is a result of its influence on early marine distribution of juvenile sockeye salmon. For example, during the late 1960s and early 1970s, the nearshore migration of juvenile Bristol Bay sockeye salmon was thought to be a result of sockeye salmon using the warmer nearshore waters rather than the colder sea surface temperatures offshore in order to maximize their growth (Straty, 1981). Depth-averaged sea temperatures from an oceanographic mooring along the eastern Bering Sea middle shelf domain from mid-July to mid-September were consistently warmer during 2001 through 2002 than during 1995 through 1997 (Overland and Stabeno, 2004). Presumably, the warmer sea temperatures during 2001 would have been conducive to offshore migration of juvenile sockeye salmon during that year. Although sea temperatures were warmer during 2001 through 2002, sea temperatures along the shelf were 1° to 2°C cooler from late June to September during 2001 than during 2002 (Overland and Stabeno, 2004). Thus, it may be that warmer sea temperatures during the time juvenile sockeye salmon first are present over the eastern Bering Sea shelf (beginning in June) provide a conduit for rapid offshore migration (and possibly higher survival) and that cooler sea temperatures delay offshore migration.

Our results indicate that after the first summer in the Bering Sea, larger juvenile sockeye salmon may gain a survival advantage over smaller individuals. This result, coupled with previous findings of reduced juvenile-to-adult survival for pink (Moss et al., 2005) and coho (Beamish et al., 2004) salmon that spend their first summer in the coastal waters of the Gulf of Alaska and Strait of Georgia, indicates that reduced growth of Pacific salmon during their first year at sea may lead to substantial salmon mortality, presumably during their first winter at sea. This phenomenon may not be seen if size of the salmon after their first year at sea is inferred from the scale growth increments of returning adults, because these individuals could be a biased sample from the faster-growing portion of the

population (Crozier and Kennedy, 1999). We suggest that annual variability in the size of sockeye salmon may be related to summer sea surface temperatures along the eastern Bering Sea shelf temperatures that appear to influence the spatial distribution and early marine migration pathways of this species.

Acknowledgments

P. Hagen, formally with the Alaska Department of Fish and Game in Juneau, Alaska, was instrumental in aging and creating digital pictures of juvenile sockeye salmon scales. We gratefully appreciate the help of the captains (M. Cavanaugh and S. Brandstitter) and the crew of the FV *Sea Storm* and captain C. Bronson and the crew of the FV *Great Pacific* for their fine efforts and technical assistance in all aspects of the field surveys. We thank A. Wertheimer, G. Kruse, and three anonymous reviewers for suggestions during this study and comments on the manuscript.

Literature cited

- Adkison, M. D., R. M. Peterman, M. F. Lapointe, D. M. Gillis, and J. Korman.
1996. Alternative models of climatic effects on sockeye salmon, *Oncorhynchus nerka*, productivity in Bristol Bay, Alaska, and the Fraser River, British Columbia. *Fish. Oceanogr.* 5:137–152.
- Beamish, R. J., 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.
- Beamish, R. J., C. Mahnken, and C. M. Neville.
2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Trans. Am. Fish. Soc.* 133:26–33.
- Burgner, R. L.
1991. Life history of sockeye salmon (*Oncorhynchus nerka*). In *Pacific salmon life histories* (C. Groot and L. Margolis, eds.), p. 3–117. Univ. British Columbia Press, Vancouver, Canada.
- Briscoe, R. J.
2004. Factors affecting marine growth and survival of Auke Creek, Alaska coho salmon (*Oncorhynchus kisutch*). M.S. thesis, 57 p. Univ. Alaska Fairbanks, Fairbanks, AK.
- Crozier, W. W., and J. A. Kennedy.
1999. Relationships between marine growth and marine survival of one sea winter Atlantic salmon, *Salmo salar* L., from the River Bush, Northern Ireland. *Fish. Manage. Ecol.* 6:89–96.
- Farley, E. V., Jr., J. M. Murphy, B. W. Wing, J. H. Moss, and A. Middleton.
2005. Distribution, migration pathways, and size of western Alaska juvenile salmon along the eastern Bering Sea shelf. *Alaska Fish. Res. Bull.* 11(1):15–26.
- Fisher, J. P., and W. G. Pearcy.
1988. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of differing coastal upwelling. *Can. J. Fish. Aquat. Sci.* 45:1036–1044.
1990. Spacing of scale circuli versus growth rate in young coho salmon. *Fish. Bull.* 88:637–643.
- Francis, R. I.
1990. Back-calculation of fish length: a critical review. *J. Fish Biol.* 36:883–902.
- Fukuwaka, M., and M. Kaeriyama.
1994. A back-calculation method for estimating individual growth of juvenile chum salmon by scale analysis. *Scientific Reports of the Hokkaido Salmon Hatchery* 48:1–9.
1997. Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. *Can. J. Fish. Aquat. Sci.* 54:631–636.
- Hartt, A. C.
1980. Juvenile salmonids in the oceanic ecosystem: the critical first summer. In *Salmonid ecosystems of the North Pacific* (W. J. McNeil and D. C. Himsworth, eds.), p. 25–57. Oregon State Univ. Press, Corvallis, OR.
- Healey, M. C.
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. H.
1979. Influence of marine environment on age and size at maturity, growth, and abundance of chum salmon, (*Oncorhynchus keta*) from Olsen Creek, Prince William Sound, Alaska. Ph.D. diss., 118 p. Oregon State Univ., Corvallis, OR.
- Holtby, L. B., B. C. Andersen, and R. K. Kadowaki.
1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 47:2181–2194.
- Kinder, T. H., and J. D. Schumacher.
1981. Hydrographic structure over the continental shelf of the southeastern Bering Sea. In *The eastern Bering Sea shelf: oceanography and resources*, vol. 1 (D. W. Hood and J. A. Calder, eds.), p. 31–52. Univ. Washington Press, Seattle, WA.
- Koo, T. S. Y.
1962a. Age designation in salmon. In *Studies of Alaska red salmon* (T. S. Y. Koo, ed.), p. 41–48. Publications in Fisheries, New Series 1, Univ. Washington, Seattle, WA.
- 1962b. Age and growth studies of red salmon scales by graphical means. In *Studies of Alaska red salmon* (T. S. Y. Koo, ed.), p. 49–121. Publications in Fisheries, New Series 1, Univ. Washington, Seattle, WA.
- Liu, L., and G. B. Hudak.
1992. Forecasting and time series analysis using the SCA statistical system, 435 p. Scientific Computing Associates Corporation, Oak Brook, IL.
- Mortensen, D., A. Wertheimer, S. Taylor, and J. Landingham.
2000. The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. *Fish. Bull.* 98:319–335.
- Moss, J. H., D. A. Beauchamp, A. D. Cross, K. Myers, E. V. Farley Jr., J. M. Murphy, and J. H. Helle.
2005. Higher marine survival associated with faster growth for pink salmon (*Oncorhynchus gorbuscha*). *Trans. Am. Fish. Soc.* 134:1313–1322.

- Mueter, F. J., D. M. Ware, and R. M. Peterman.
2002. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific Ocean. *Fish. Oceanogr.* 11(4):205–218.
- Orsi, J. A., M. V. Sturdevant, J. M. Murphy, D. G. Mortensen, and B. L. Wing.
2000. Seasonal habitat use and early marine ecology of juvenile Pacific salmon in southeastern Alaska. *N. Pac. Anad. Fish Comm. Bull.* 2:111–122.
- Overland, J. E., and P. J. Stabeno.
2004. Is the climate of the Bering Sea warming and affecting the ecosystem? *EOS, Trans. Am. Geophys. Union.* 85(33):309–312.
- Parker, R. R.
1968. Marine mortality schedules of pink salmon of the Bella Coola River, Central British Columbia. *J. Fish. Res. Board Can.* 25:757–794.
- Pearcy, W. G.
1992. Ocean ecology of the North Pacific salmonids, p. 179. Univ. Washington Press, Seattle, WA.
- Peterman, R. M., B. J. Pyper, M. F. Lapointe, and M. D. Adkison.
1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Can. J. Fish. Aquat. Sci.* 55:2503–2517.
- Quinn, T. J., II, and R. B. Deriso.
1999. Quantitative fish dynamics, 542 p. Oxford Univ. Press, New York, NY.
- Ricker, W. E.
1992. Back-calculation of fish lengths based on proportionality between scale and length increments. *Can. J. Fish. Aquat. Sci.* 49:1018–1026.
- Ruggerone, G. T., E. V. Farley Jr., 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.
- Shuntov, V. P., V. I. Radchenko, V. V. Lapko, and Y. N. Poltev.
1993. The distribution of the Pacific salmon in the Sakhalin-Kuril region at a period of anadromous migration (in Russian). *J. Ichthy. Moscow* 33:348–358.
- Sogard, S. M.
1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* 60(3):1129–1157.
- Straty, R. R.
1981. Ecology and behavior of juvenile sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay and the eastern Bering Sea. *In* The eastern Bering Sea shelf: oceanography and resources, vol. 2 (D. W. Hood and J. A. Calder, eds.), p. 285–320. Univ. Washington Press, Seattle, WA.
- Wei, W. W. S.
1990. Time series analysis: univariate and multivariate methods, 478 p. Addison-Wesley Publ. Company, Redwood City, CA.
- Willette, T. M., R. T. Cooney, and K. Hyer.
1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Can. J. Fish. Aquat. Sci.* 56:364–376.