

Variable Effects of Biological and Environmental Processes on Coho Salmon Marine Survival in Southeast Alaska

MICHAEL J. MALICK*

School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau Center,
17101 Point Lena Loop Road, Juneau, Alaska 99801, USA

MILO D. ADKISON

School of Fisheries and Ocean Sciences, University of Alaska Fairbanks,
235 O'Neill, Post Office Box 757220, Fairbanks, Alaska 99775, USA

ALEX C. WERTHEIMER

National Marine Fisheries Service, Auke Bay Laboratories, Ted Stevens Marine Research Institute,
17109 Point Lena Loop Road, Juneau, Alaska 99801, USA

Abstract.—Correlation analyses, linear regression models, and multistock mixed effects models were used to examine the relationships between coho salmon *Oncorhynchus kisutch* marine survival and six biological and environmental covariates across 14 southeast Alaska (SEAK) stocks. A primary focus of the study was to investigate the influence of pink salmon *O. gorbuscha* and chum salmon *O. keta* fry abundances on coho salmon marine survival. The coho salmon stocks exhibited strong covariation; 88 of the 91 pairwise comparisons among the coho salmon stocks covaried positively and 54 of them were significant ($P < 0.05$). Only one of the covariates, the North Pacific index, which is a measure of the Aleutian low pressure zone, had consistent relationships (positive) across all 14 stocks. The other covariates, including freshwater discharge, the Pacific decadal oscillation, sea-surface temperature, and two indices of pink salmon and chum salmon fry abundances, all had inconsistent relationships with marine survival. The best-fit linear regression models varied greatly among the 14 stocks, as did the R^2 values, which ranged from 0.00 to 0.54. An index representing local hatchery pink salmon and chum salmon fry abundance was the most important variable in explaining the variation in marine survival, having a stronger estimated effect on survival than an index of local wild pink salmon fry abundance. The magnitude and sign of the hatchery pink salmon and chum salmon effect varied greatly among different localities. Our results suggest that (1) SEAK coho salmon stocks are not equally influenced by the same factors and (2) there are factors that appear to affect marine survival of SEAK coho salmon stocks at varying spatial scales. This study also provides evidence that coho salmon stocks throughout SEAK experience some degree of regional concordance in the marine environment but also that local stock-specific conditions are important in fully understanding variation in marine survival.

Variation in Pacific salmon *Oncorhynchus* spp. marine survival is associated with a broad range of environmental and biological processes that fluctuate on interannual and interdecadal time scales (Nickelson 1986; Hare et al. 1999). These processes can be evaluated on a variety of spatial scales, ranging from the ocean-basin scale to the local scale. This study investigates environmental and biological variables—on a variety of spatial scales—that are thought to influence coho salmon *O. kisutch* marine survival in southeast Alaska (SEAK).

The majority of salmon marine mortality occurs during the early marine life phase (Parker 1968; Bax 1983; Wertheimer and Thrower 2007), with evidence

for significant winter mortality if energy storage is not sufficient (Beamish and Mahnken 2001; Farley et al. 2007). The primary mechanism for mortality during the early marine period is thought to be size-selective predation (Foerster 1954; Holtby et al. 1990; Moss et al. 2005). However, other ecological factors, such as suboptimal prey abundance, predator abundance, and abundance of alternative prey resources for the predators of salmon, are important in explaining variation in marine survival (Fisher and Pearcy 1988; Willette et al. 2001; Briscoe et al. 2005).

Ocean-basin-scale climate indices, such as the Pacific decadal oscillation (PDO) and Aleutian low pressure index, are linked with production trends of Pacific salmon along the west coast of North America with opposite relationships in northern and southern domains (Beamish et al. 1997; Mantua et al. 1997; Hare et al. 1999). However, salmon marine survival is more correlated with regional- and local-scale variables

* Corresponding author: mjmalick@alaska.edu

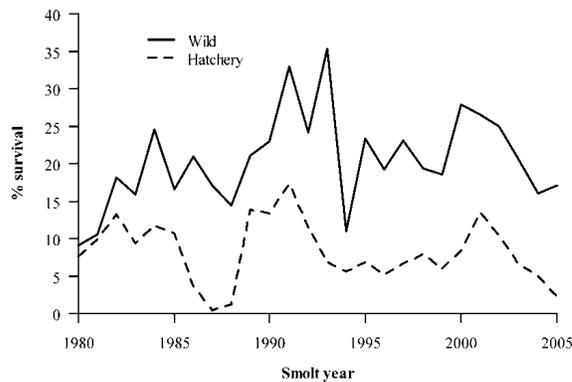


FIGURE 1.—Time series of coho salmon marine survival rates for a single wild stock (Auke Creek, northern southeast Alaska [SEAK]) and a single hatchery stock (Neets Bay, southern SEAK; Shaul et al. 2005; Gary Freitag, Southern Southeast Regional Aquaculture Association, personal communication).

than ocean-basin-scale processes (Adkison et al. 1996; Mueter et al. 2002a, 2002b; Pyper et al. 2005).

Regional-scale variables thought to influence salmon marine survival in the Gulf of Alaska region include ocean temperature and sea-surface salinity. Temperature is a particularly important environmental factor for ectothermic animals such as fishes, affecting all metabolic processes, including growth. Increased temperature may lead to increased growth rates, thus reducing the period of intense size-selective predation for coho salmon smolts during their early marine residence (Nickelson 1986; Koslow et al. 2002; Mueter et al. 2002a, 2005; Quinn et al. 2005).

Salinity is thought to be a driving factor that controls spring stratification in the coastal Gulf of Alaska region, with stronger stratification indicative of lower winter and spring sea-surface salinity (Weingartner et al. 2002). Spring stratification is a primary factor in determining food availability for out-migrating salmon, which is closely coupled with early marine growth rates (Bilton et al. 1982). Research investigating the links between sea-surface salinity and marine survival has found that pink salmon *O. gorbuscha* marine survival tends to positively covary with sea-surface salinity (Mueter et al. 2005).

The SEAK region has approximately 2,500 coho salmon-producing streams (Clark et al. 2006) as well as 14 hatcheries that release coho salmon at a variety of sites (Brase and Stopha 2000). Significant interannual variation in marine survival rates is evident in both the wild and hatchery stocks (Figure 1) and is presumably a function of both environmental and biological processes in the marine environment.

An important aspect of the SEAK region is the large

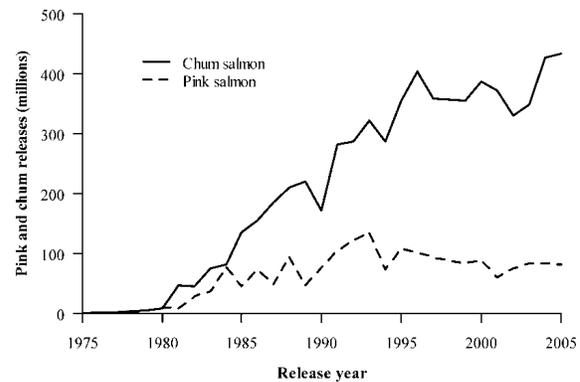


FIGURE 2.—Total hatchery pink salmon and chum salmon fry releases in southeast Alaska (ADFG 2008).

hatchery releases of pink salmon and chum salmon *O. keta* fry each spring. Since the late 1970s, the hatchery releases have steadily increased, predominately due to the numbers of chum salmon released (Figure 2). Hatchery releases in northern SEAK relate positively to marine survival rates for Auke Creek coho salmon through a hypothesized predation-buffering mechanism (Briscoe et al. 2005), which postulates that the abundant hatchery-released pink salmon and chum salmon act as an alternative prey resource for the predators of coho salmon, thus decreasing predation rates on coho salmon during the early marine life phase.

The primary goal of this research was to quantify the relative importance of specific biological and environmental covariates for coho salmon marine survival at both local and regional scales. In particular, the objective was to determine whether hatchery pink salmon and chum salmon are influencing marine survival of coho salmon stocks, other than the Auke Creek stock, throughout SEAK. The covariates used in this study span three distinct spatial scales: local, regional, and ocean basin. Correlation analyses, linear regression models, and mixed-effects models were used to address the primary goal of the research. In the process, we hoped to provide insight into the mechanisms controlling coho salmon marine survival in SEAK.

Methods

Study Area

The study area in SEAK encompasses both the Alexander Archipelago and the Alaska mainland south of 60°N latitude (Figure 3). The Alexander Archipelago consists of more than 1,000 islands. This leads to complexities in both oceanography and biological interactions in the marine environment throughout the region and allows for a diversity of marine habitats.

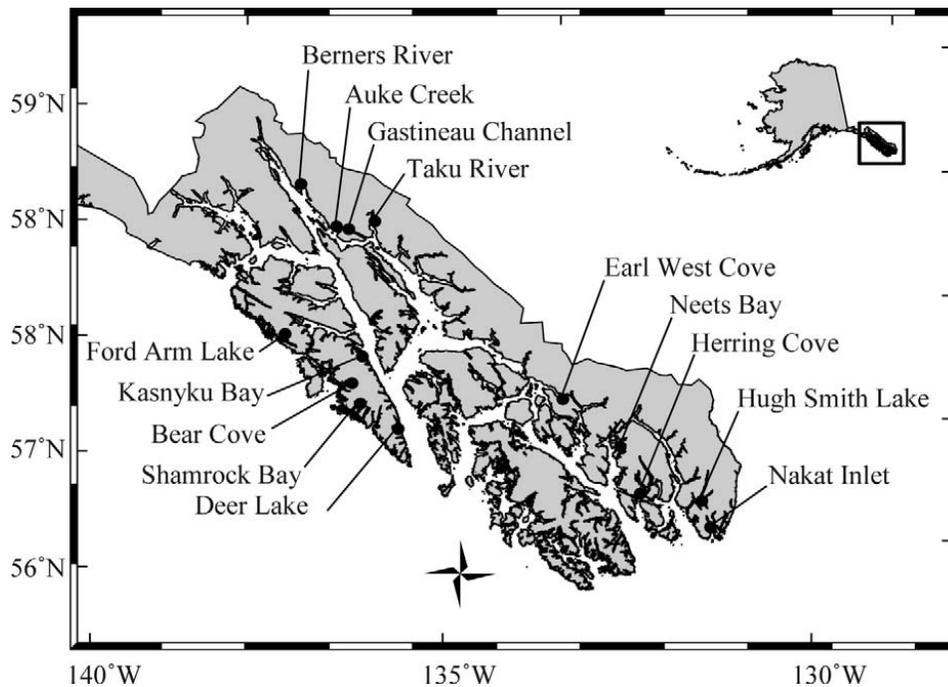


FIGURE 3.—The study area in southeast Alaska and ocean entry points for the 14 coho salmon stocks used in this analysis. Inset shows the location of the study area in Alaska.

Marine Survival Data

Time series of coho salmon marine survival rates for 14 stocks were compiled from various agencies. The 14 stocks were composed of nine hatchery and five wild stocks (Table 1). The hatchery stocks were produced by three hatchery organizations: the Northern Southeast Regional Aquaculture Association, the Southern Southeast Regional Aquaculture Association

(SSRAA), and Douglas Island Pink and Chum, Inc. The time series data for the five wild coho salmon stocks were available through the Alaska Department of Fish and Game (ADFG; Shaul et al. 2005). All the time series used in this study have at least 12 years of data and were aligned by smolt year (i.e., year in which fish underwent smoltification and out-migration).

The calculations of the marine survival rates were

TABLE 1.—Summary of 14 southeast Alaska coho salmon marine survival data sets used in the analysis (Abb. = stock abbreviation; stock group = name of the pink salmon stock group where the particular coho salmon stock is located; n = number of smolt years available for this analysis). Information was provided by (1) Leon Shaul (Alaska Department of Fish and Game, personal communication); (2) Chip Blair (Northern Southeast Regional Aquaculture Association, personal communication); (3) Gary Freitag (Southern Southeast Regional Aquaculture Association, personal communication); and (4) Rick Focht (Douglas Island Pink and Chum, Inc., personal communication).

Stock	Abb.	Origin	Stock group	Smolt years	n	Source
Auke Creek	AC	Wild	Stephens	1979–2005	27	1
Berners River	BR	Wild	Lynn Canal	1989–2005	17	1
Ford Arm Lake	FAL	Wild	Slocum Arm	1981–2005	24	1
Hugh Smith Lake	HSL	Wild	E. Behm	1983–2005	23	1
Taku River	TR	Wild	Stephens	1991–2005	15	1
Bear Cove	BC	Hatchery	Sitka Sound	1992–2005	14	2
Deer Lake	DL	Hatchery	SE Baranof	1986–2005	17	2
Kasnyku Bay	KB	Hatchery	Kelp Bay	1990–2005	16	2
Shamrock Bay	SB	Hatchery	W. Crawfish	1993–2005	12	2
Earl West Cove	EWC	Hatchery	Anan	1983–2000	16	3
Herring Cove	HC	Hatchery	E. Behm	1980–2005	26	3
Neet Bay	NB	Hatchery	W. Behm	1980–2005	26	3
Nakat Inlet	NI	Hatchery	Portland	1986–2005	20	3
Gastineau Channel	GC	Hatchery	Stephens	1990–2005	16	4

not homogenous among the 14 stocks. All of the wild stocks' survival rates were calculated using the same method, while each hatchery organization calculated their own marine survival rates. The major difference between the calculations is that a mark-recapture estimation procedure is used to estimate the number of wild smolts and adult returns, while the hatcheries rely on counts of their smolt releases and adult returns (L. Shaul, ADFG, personal communication). There is uncertainty associated with the marine survival estimates, although the uncertainty is greater for the wild stocks than for the hatchery stocks. Uncertainty is incorporated into the survival estimates of both the wild and hatchery stocks through estimating the commercial and recreational harvest of coho salmon. Additional uncertainty in the wild stock estimates comes from the estimation of the coho salmon emigrants and adult escapement (Tydingco 2005).

Another difference is that SSRAA includes precious coho salmon (jacks) in their estimates of adult returns, while the estimates for the other hatchery and wild stocks do not include jacks. However, this discrepancy should not significantly influence the calculations due to the low number of jacks returning to that facility (<1% of the total number of coho salmon returning; G. Freitag, SSRAA, personal communication).

Auxiliary Biological Data

Two independent indices were used to quantify the local abundance of pink salmon and chum salmon fry around the mouth of the natal stream of each coho salmon stock. The first was an index representing wild pink salmon fry abundance (WP index). The second was an index representing hatchery pink salmon and chum salmon fry abundance (HPC index). To localize these indices, SEAK was divided into 52 areas corresponding to ADFG pink salmon stock groups (Zadina et al. 2004). The 14 coho salmon stocks were located in 11 such areas, with two of the areas containing multiple coho salmon stocks.

The WP index was computed from ADFG aerial survey counts of SEAK wild adult pink salmon (X. Zhang, ADFG, personal communication). The aerial surveys are performed yearly on 718 SEAK pink salmon spawning streams (Zadina et al. 2004). We used these adult aerial counts as an index for the relative abundance of pink salmon fry the following year. The use of the WP index as an index of pink salmon fry abundance makes the assumption that this abundance is linearly related to pink salmon escapement of the previous year. The validity of this assumption may be compromised by nonlinearity in the relationship between pink salmon escapement and

pink salmon fry abundance due to compensatory and depensatory mortality processes in freshwater (Heard 1991). Similarly, the significance of the WP index may be obscured by high variability in freshwater survival observed for pink salmon (Heard 1991).

To compute the WP index, the peak counts in aerial pink salmon survey data were summed over all streams in a given pink salmon area. Subsequently, these counts were compared with coho salmon marine survival rates from the next sea-entry year. Following the predation-buffer hypothesis, the WP index was expected to relate positively with coho salmon marine survival (Briscoe et al. 2005).

The HPC index data were obtained from the ADFG coded wire tag database. The data were filtered to only include a release site if it had at least one release of 500,000 fish. All remaining releases within an area that comprised a pink salmon stock group were summed for each year from 1979 to 2005. The index was only used as a predictor of local coho salmon survival if an area had more than 10 years of hatchery release data. This left eight areas with HPC index data corresponding to 10 coho salmon stocks. Like the WP index, the HPC index was expected to covary positively with marine survival.

Auxiliary Environmental Data

Four auxiliary environmental variables were chosen for the analysis: freshwater discharge (DIS), sea-surface temperature (SST), the PDO, and the North Pacific (NP) index. These four covariates represent two different spatial scales. Discharge and SST are incorporated as regional oceanographic variables, while the PDO and NP index are incorporated as ocean basin-scale variables.

Freshwater discharge.—Freshwater discharge was used in this study as a surrogate for regionwide sea-surface salinity, with higher discharge corresponding to lower sea-surface salinity. Monthly DIS data for the SEAK region were available for the period from 1979 to 2005 (T. C. Royer, Old Dominion University, personal communication). The late-winter–spring period is the time that sea-surface salinity would be most influential on stratification, resulting in either increased or decreased food for coho salmon smolts when they enter the ocean. The month of April was chosen as the time frame for the DIS covariate, since a higher discharge in April may lead to a stronger stratification (Royer et al. 2001) and, thus, to higher productivity and increased marine survival of juvenile coho salmon.

Sea-surface temperature.—Sea-surface temperature was used as a proxy for water temperatures experienced by coho salmon smolts because these fish are

found in the surface waters when they first enter the ocean and during their first summer at sea (Orsi and Wertheimer 1995). A temporal average of SST was computed for the months of May through August. Monthly SST data were obtained from the International Comprehensive Ocean Atmosphere Data Set (Worley et al. 2005). All the monthly observations within a box located at 58°N to 56°N latitude and 141°W to 137°W longitude were averaged. Because fish grow faster in warmer temperatures as long as (1) the temperature is below their stress threshold and (2) food is not limited (Soderberg 1995), a positive relationship was expected between SST and marine survival.

Pacific decadal oscillation.—Climate regimes control long-term productivity of the Pacific Ocean and are thought to be important in explaining trends in marine survival of salmon (Mantua et al. 1997; Hare et al. 1999; Beamish et al. 2000). Due to the large geographic scale of the PDO index, the time frame used when comparing it to marine survival can represent different life phases of the salmon. The early marine life phase is important in determining salmon marine survival rates (Parker 1971; Fukuwaka and Suzuki 2002; Mueter et al. 2005; Wertheimer and Thrower 2007); therefore, the winter phase of the PDO before out-migration of the smolts was selected as a variable in the coastal Gulf of Alaska marine survival model. Monthly PDO values (jisao.washington.edu/pdo/PDO.latest) were averaged over the months of November through March and compared with marine survival of the next year's coho salmon emigrants. A higher PDO may result in better growing conditions during the early marine life phase, thereby increasing salmon survival (Mantua et al. 1997).

North Pacific index.—The NP index is a measure of the Aleutian low and is defined as the area-weighted sea-level pressure over the region from 30°N to 65°N and from 160°E to 140°W (Trenberth and Hurrell 1994). The Aleutian low pressure zone controls the intensity of storms in the coastal Gulf of Alaska region during the winter. Therefore, the strength of the Aleutian low affects the amount of precipitation and runoff into the coastal Gulf of Alaska region (Weingartner et al. 2002). Monthly NP index values (www.cgd.ucar.edu/cas/jhurrell/npindex.html) were averaged over the months of December through March, corresponding to the peak of the Aleutian low. This average was then compared with the survival of the next year's emigrants. Because lower NP index values are indicative of a deepened Aleutian low, which may provide for better productivity in the early marine environment, a negative relationship was expected between the NP index and marine survival.

Statistical Analyses

Correlation analyses.—Three correlation analyses were performed using Pearson's product-moment correlation coefficients: (1) pairwise comparisons of the coho salmon stocks' marine survival rates, (2) pairwise comparisons between coho salmon marine survival rates and each of the physical and biological covariates, and (3) a Pearson's product-moment correlation coefficient was computed between the pairwise correlation coefficients of coho salmon stocks' survival rates and the great circle distance separating the stocks belonging to each pair. The first correlation analysis was done to determine if all of the coho salmon stocks were subject to similar influences. The second analysis was done to identify relationships between SEAK coho salmon marine survival and various biological and environmental variables. The last comparison was done to investigate the spatial scales of covariation in coho salmon marine survival. The great circle distance was calculated using the Haversine formula (Sinnott 1984). None of the significance levels in the correlation analyses were corrected for multiple comparisons.

Linear regression models and model selection.—Linear regression models were also used to investigate the relationships between marine survival and the covariates for each of the 14 coho salmon stocks. Due to the disparate units, the covariates were standardized for the linear regression analysis by subtracting the mean and dividing by the standard deviation (SD) to facilitate model fitting and interpretation. Ten of the coho salmon stocks had data for all six of the covariates, giving the full model as follows:

$$S = \alpha + \beta_W WP + \beta_H HPC + \beta_O PDO + \beta_N NP \\ + \beta_T SST + \beta_D DIS + \varepsilon,$$

where S is the marine survival for a particular stock, α is the intercept, β_i are interaction parameters, SST is the May through August average SST, DIS is the average April discharge, and ε is the error term.

Four of the coho salmon stocks did not have hatchery pink salmon and chum salmon fry released in their vicinity, giving the full model for these four stocks as:

$$S = \alpha + \beta_W WP + \beta_O PDO + \beta_N NP + \beta_T SST \\ + \beta_D DIS + \varepsilon,$$

Backwards stepwise model selection was performed to determine the most parsimonious model for each coho salmon stock. Model selection during the stepwise procedure was based on Akaike's information criterion with a correction factor for small sample sizes

(AIC_c; Burnham and Anderson 2002). The AIC_c was calculated as,

$$AIC_c = -2 \log L + [2kn / (n - k - 1)],$$

where *L* is the likelihood of the model, *n* is the sample size, and *k* is the number of parameters in the model. The most parsimonious model is defined as the one with the lowest AIC_c value. Accordingly, the AIC_c score for each model *i* was rescaled relative to that of the most parsimonious model by calculating the AIC_c difference (ΔAIC_c):

$$\Delta AIC_{c,i} = AIC_{c,i} - \text{minimum}(AIC_c).$$

If a ΔAIC_c value is greater than 10, it shows strong evidence that the model is not competitive as the best model, while models that have ΔAIC_c values less than 2 are considered to be as equally plausible as the model with the lowest AIC_c value (Burnham and Anderson 2002).

Model averaging.—For the set of *R* candidate models obtained from the stepwise model selection procedure, Akaike weights (*w_i*) were calculated as:

$$w_i = \frac{\exp(-AIC_{c,i}/2)}{\sum_{r=1}^R \exp(-AIC_{c,r}/2)}.$$

These weights represent a normalized set of model likelihoods, meaning that the *w_i* for a model shows the relative support for model *i*.

In addition to calculating the support for each constructed model, the support for each variable was also calculated. This was accomplished by summing the *w_i* values of all models constructed for a coho salmon stock with ΔAIC_c less than 10 that included a particular variable (Burnham and Anderson 2002).

Cross validation.—Standard errors of prediction for the model with the minimum AIC_c for each coho salmon stock were estimated using leave-one-out cross validation techniques (Efron and Tibshirani 1993). The cross validation mean square error (MSE) was computed as,

$$MSE = \sum_{i=1}^n (y_i - \hat{y}_i^{-i})^2 / n,$$

where *y_i* is the observed percent survival for the *i*th year, \hat{y}_i^{-i} is the predicted survival rate of the *i*th-removed observation, and *n* is the sample size. An estimate of the SD of the error of prediction was then obtained by taking the square root of the MSE.

Mixed-effects models.—Linear multistock mixed-effects models were used to further explore the relationship between the HPC index and marine

TABLE 2.—Summary of the standard deviations (SDs) of the marine survival time series for 14 coho salmon stocks in southeast Alaska; the SDs of the residuals from the best-fit regression models; and the prediction SDs for the best models of each stock, calculated from cross validation.

Stock	Data Mean	Data SD	Residual ISD	Prediction SD
Auke Creek	20.06	6.49	4.58	5.09
Bear Cove	10.59	5.25	4.52	4.99
Berners River	16.76	5.53	4.58	5.00
Deer Lake	11.85	6.73	5.51	5.73
Earl West Cove	8.49	4.54	3.75	3.80
Ford Arm Lake	11.29	4.60	4.60	4.70
Gastineau Channel	10.98	4.91	4.91	5.07
Herring Cove	6.81	3.56	3.19	3.31
Hugh Smith Lake	12.50	4.62	4.02	4.14
Kasnyku Bay	14.73	6.25	5.70	5.97
Neets Bay	8.30	4.19	3.05	3.94
Nakat Inlet	7.47	3.61	3.16	3.85
Shamrock Bay	5.73	4.52	3.52	3.99
Taku River	11.63	4.62	3.41	3.80

survival. Unlike the single-stock regression models that work on the local level, the mixed-effects models work at the regional level, incorporating data from all the coho salmon stocks. Ten of the coho salmon stocks had data for the HPC index, giving the full model:

$$S_{i,t} = \alpha + a_i + \gamma HPC_{i,t} + g_i HPC_{i,t} + \varepsilon_{i,t},$$

$$a_i \sim N(0, \sigma_a^2) \quad g_i \sim N(0, \sigma_g^2) \quad \varepsilon_{i,t} \sim N(0, \sigma^2),$$

where the subscripts *i* and *t* represent the *i*th stock at time *t*; α and γ are fixed effects representing average survival and average HPC effects, respectively; *a_i* and *g_i* are random effects assumed to follow a normal distribution representing average stock-specific survival without the HPC effect and stock-specific HPC effects, respectively; and ε is the error term. The model was fit using restricted maximum likelihood to obtain parameter estimates and fit by maximum likelihood for model selection purposes (Pinheiro and Bates 2000). The HPC index was rescaled by dividing the raw data by 1,000,000 to facilitate model fitting and interpretation.

The model selection procedure consisted of sequentially removing three parts of the full model and testing the significance of the removed portion against the full model. The components tested included the random HPC effect, the fixed HPC effect, and both the fixed and random HPC effects. The AIC_c was used as the model selection criterion.

Results

Marine Survival Rates

The average marine survival rates varied between stocks, but the amount of variation around the mean for each stock was similar (Table 2). The highest average

TABLE 3.—Summary of pairwise correlations among the 14 coho salmon stocks' marine survival rates. Stock codes are defined in Table 1.

	AC												
BC	0.25	BC											
BR	0.65	0.36	BR										
DL	0.36	0.08	0.68	DL									
EWC	0.63	0.42	0.81	0.84	EWC								
FAL	0.45	0.43	0.27	-0.14	0.08	FAL							
GC	0.67	0.61	0.78	0.65	0.78	0.20	GC						
HC	0.39	0.19	0.59	0.65	0.59	0.07	0.80	HC					
HSL	0.54	0.36	0.74	0.72	0.74	0.04	0.70	0.51	HSL				
KB	0.67	0.53	0.69	0.69	0.93	0.21	0.78	0.47	0.78	KB			
NB	0.41	0.49	0.60	0.51	0.75	0.26	0.77	0.56	0.63	0.75	NB		
NI	0.37	0.42	0.45	0.65	0.69	0.03	0.55	0.50	0.67	0.59	0.63	NI	
SB	0.05	0.60	0.54	0.69	0.63	-0.17	0.34	0.06	0.53	0.47	-0.18	0.47	SB
TR	0.71	0.48	0.86	0.72	0.84	0.32	0.75	0.44	0.74	0.84	0.48	0.51	0.74

■ $P < 0.05$.
 □ $P < 0.10$.

survival was observed for Auke Creek (20.1%), while the Shamrock Bay coho salmon stock showed the lowest average survival (5.7%).

Correlation Analyses

A total of 91 correlation coefficients were computed among the 14 time series for coho salmon marine survival. There were 88 positive correlations, of which 54 were significant ($P < 0.05$; Table 3); this represents many more significant correlations than the five that would be expected using an α value of 0.05 if there were no correlation. There were no significant negative correlations. The marine survival of most stocks appeared to covary, with the exception of one stock, Ford Arm Lake. The average correlation coefficient for each stock, with the exception of Ford Arm Lake, ranged from 0.37 to 0.67. The distance between stocks did not appear to affect the correlation between their marine survival rates ($r = -0.10$, $P = 0.36$; Figure 4).

Marine survival rates of all coho salmon stocks were positively correlated with the NP index and had three significant correlations ($P < 0.05$; Table 4). The stocks that had significant correlations with the NP index were all located in the southern portion of SEAK. The coho salmon stocks had mixed relationships with SST, DIS, the PDO, the HPC index, and the WP index (Table 4). The PDO, which was negatively correlated with all but one stock, had the largest number of significant correlations with four. The HPC index had two significant positive correlations and no significant negative correlations, although 6 of the 10 HPC correlations were negative. Both of the significant

positive correlations for the HPC index were located in northern SEAK (Figure 5).

Linear Regression Models and Model Selection

The models that best predicted coho salmon marine survival rates differed greatly among the coho salmon stocks (Table 5). Seven of the coho salmon stocks were best predicted by a single covariate, while the best models for five stocks contained multiple predictors. The Ford Arm Lake and Gastineau Channel stocks had no variables included in the best model. The R^2 values

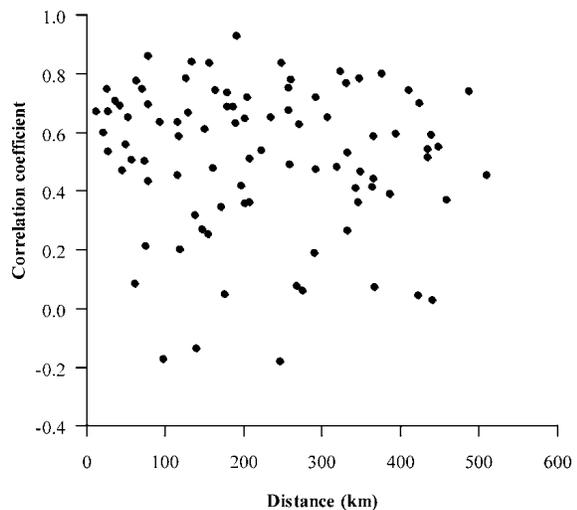


FIGURE 4.—Correlation coefficients among southeast Alaska coho salmon stocks' marine survival rates versus the distance between the stocks.

TABLE 4.—Summary of correlation coefficients among the coho salmon marine survival time series and the covariates (DIS = April discharge; SST = summer sea-surface temperature; NP = North Pacific index; PDO = Pacific decadal oscillation; WP = wild pink salmon fry abundance index; HPC = hatchery pink salmon and chum salmon fry abundance index; na = no data available).

Stock	DIS	SST	NP	PDO	WP	HPC
Auke Creek	-0.25	-0.04	0.13	-0.39	0.25	0.68
Bear Cove	0.16	-0.41	0.20	-0.07	-0.24	-0.56
Berners River	-0.46	-0.06	0.48	-0.18	-0.06	0.00
Deer Lake	-0.46	0.26	0.24	-0.08	-0.61	-0.31
Earl West Cove	-0.60	0.08	0.21	-0.35	0.10	-0.05
Ford Arm Lake	-0.21	0.08	0.21	-0.21	-0.02	na
Gastineau Channel	-0.15	-0.41	0.32	-0.35	-0.16	0.09
Herring Cove	-0.23	-0.33	0.48	-0.14	0.05	na
Hugh Smith Lake	-0.31	-0.15	0.53	-0.52	-0.29	na
Kasnyku Bay	-0.08	-0.32	0.12	-0.26	-0.34	-0.47
Neets Bay	-0.32	-0.29	0.39	-0.51	-0.30	-0.25
Nakat Inlet	-0.11	-0.06	0.34	-0.52	-0.36	-0.24
Shamrock Bay	0.15	0.25	0.27	0.38	-0.38	na
Taku River	-0.05	0.00	0.29	-0.18	-0.11	0.62

■ $P < 0.05$.

▒ $P < 0.10$.

for the best models ranged from 0.00 to 0.54. The number of similarly supported models ($\Delta AIC_c < 2$) varied among the stocks, with only the Deer Lake stock having a single plausible model (Table 6).

The HPC index was included in 5 of the 10 models where HPC data were available, which was the highest percentage among all the variables. However, the direction of the estimated effect varied. The HPC index was positive in two of the models and negative in three of the models. The NP index had the next highest percentage, being included in 4 of the 14 models, and was consistently positive. The PDO and April DIS were both included in three models and were consistently negative. The WP index was included in two of the best models, while summer SST was included in one model. In these models, the estimated effect of the WP index was negative and the effect of summer SST was positive.

Model Averaging

None of the explanatory variables had a consistently high relative importance across stocks (Figure 6). On

average, the HPC index had the highest relative importance, followed by the PDO, April DIS, NP index, SST, and the WP index (Figure 6). Additionally, these model averages do not account for differences in the sign of the relationship among different coho salmon stocks. Even though the HPC index had the highest relative importance among all the stocks, its effect was inconsistent; it had positive relationships in two of the best models and negative relationships in three of the best models. The other six variables all had either consistent positive or negative signs.

Cross Validation

Based upon cross validation, predictions using the best models appeared to have fairly large SD values (Table 2). The lowest SD, in units of percent survival, was for the Herring Cove stock at 3.31, and the largest SD was 5.97 for the Kasnyku Bay stock.

Mixed-Effects Models

All the models tested included both survival terms, α (average survival) and a_i (average stock-specific

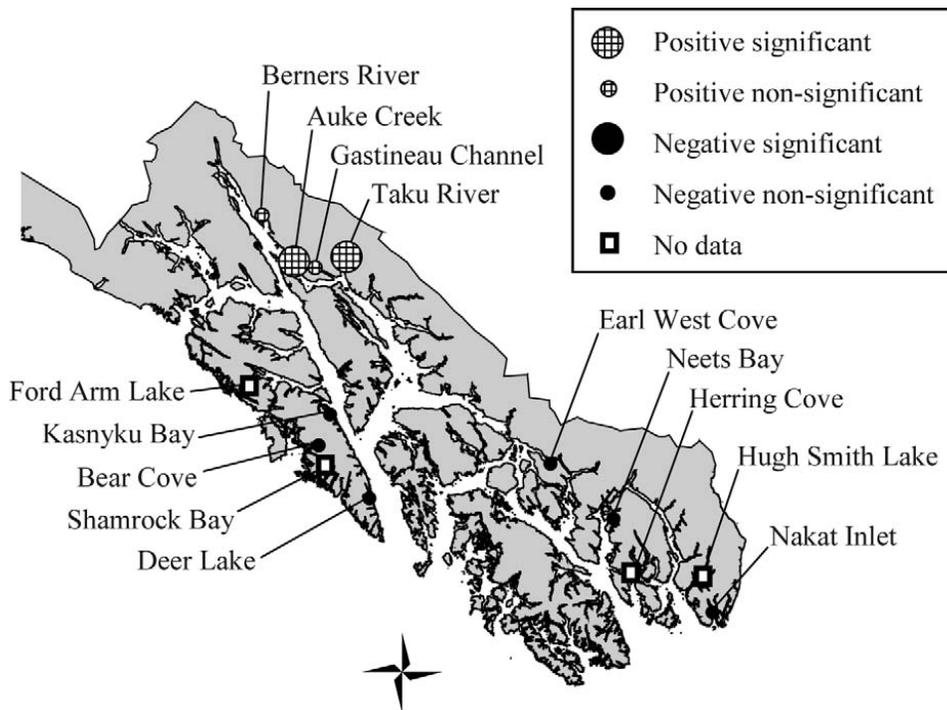


FIGURE 5.—Summary of correlations between the hatchery pink salmon and chum salmon fry abundance index and coho salmon marine survival rates in southeast Alaska (significance level = 0.05).

survival without the HPC effect). The most parsimonious model also included g_r , the random HPC effect (Table 7). This model had about the same AIC_c score as the full model, therefore indicating that the fixed HPC effect did not explain much of the variation in survival among the stocks. The overall fixed effect for the HPC index was only slightly negative for the full model, suggesting a lack of a consistent relationship

(positive or negative) between local hatchery releases and coho salmon marine survival (Figure 7).

For all models, the estimated effect of the HPC index on the Auke Creek stock was consistently larger than for any of the other stocks. To test the significance of Auke Creek on the analysis, this stock was removed from the data, the models were refit, and the model selection process was repeated. Deleting the Auke Creek stock moderately influenced the results; like the

TABLE 5.—Summary of parameter values for the best predictive models for each southeast Alaska coho salmon stock’s marine survival (Int = intercept; DIS = April discharge; SST = summer sea-surface temperature; NP = North Pacific index; PDO = Pacific decadal oscillation; WP = wild pink salmon fry abundance index; HPC = hatchery pink salmon and chum salmon fry abundance index; na = no data available).

Stock	Int	DIS	SST	NP	PDO	WP	HPC	R ²
Auke Creek	20.76				-2.06		4.12	0.54
Bear Cove	14.80						-6.38	0.32
Berners River	15.80	-2.33		3.07				0.40
Deer Lake	12.25					-3.46		0.37
Earl West Cove	9.05	-3.05						0.36
Ford Arm Lake	11.23						na	0.00
Gastineau Channel	11.49							0.00
Herring Cove	6.89			1.72			na	0.23
Hugh Smith Lake	12.58			2.54			na	0.28
Kasnyku Bay	20.06						-7.88	0.23
Neets Bay	9.62	-1.58			-2.88		-2.01	0.53
Nakat Inlet	7.97				-2.00			0.27
Shamrock Bay	5.38		3.31			-3.39	na	0.50
Taku River	7.66			2.79			5.72	0.53

TABLE 6.—Summary of the number of models for each southeast Alaska coho salmon stock with a difference in Akaike's information criterion (ΔAIC_c ; corrected for small-sample bias) less than 2. A single asterisk indicates that the null model has a ΔAIC_c less than 2. Double asterisks indicate that the null model was selected as the best predictive model.

Stock	No. of models	Stock	No. of models
Auke Creek	7	Herring Cove	4
Bear Cove	2	Hugh Smith Lake	8
Bemers River	3	Kasnyku Bay	2*
Deer Lake	1	Neets Bay	2
Earl West Cove	2	Nakat Inlet	4
Ford Arm Lake	4**	Shamrock Bay	4*
Gastineau Channel	4**	Taku River	3

previous analysis, the most parsimonious model included only the random HPC effect. However, the other three models were equally plausible according to the AIC_c scores (Table 7). This indicates that the data are uninformative about the SEAK regional HPC effect and that Auke Creek appears to be influencing the importance of the local HPC effect in the most parsimonious model.

Discussion

The overall goal of this study was to evaluate the effects of various biological and physical variables on coho salmon marine survival in SEAK. The results suggest that (1) SEAK coho salmon stocks are not equally influenced by the same factors; (2) hatchery releases of pink salmon and chum salmon have a larger effect on marine survival than an index we used as a surrogate for wild pink salmon fry abundances, but the magnitude and sign of the effect vary greatly among different localities and stocks; and (3) there are factors that appear to affect marine survival of SEAK coho salmon stocks at each of the three spatial scales analyzed (i.e., ocean basin, regional, and local).

Coho salmon marine survival rates in SEAK showed strong covariation, but there was no evidence that the distance between the stocks influenced the strength of the correlations. This regional concordance of marine survival rates suggests that coho salmon throughout SEAK are subjected to similar environmental conditions during some phases of their marine life. One notable exception to the overall covariation pattern is the Ford Arm Lake stock. Unlike other stocks, the juveniles of this stock are enumerated in freshwater as presmolts (Shaul 1994); variability in the freshwater phase may lead to the lack of covariation of this stock with others in SEAK.

Regional concordance of survival rates supports other research that has shown broad-scale similarities

in Pacific salmon marine survival rates. These analyses showed that SEAK coho salmon marine survival rates often cluster with a broader region that extends as far south as Vancouver Island, British Columbia, but is distinct from the more southerly stocks of coho salmon in Washington, Oregon, and California (Coronado and Hilborn 1998; Hobday and Boehlert 2001). Other research has also identified important regional covariation patterns in marine survival of pink salmon, chum salmon, and sockeye salmon *O. nerka* at scales on the order of 100–1,000 km (Mueter et al. 2002b), with correlations between survival rates being greater at distances less than 500 km (Pyper et al. 2005).

Even with the strong covariation among stocks, there is still considerable variation not explained by regional concordance, suggesting that local stock-specific factors are also important. Local factors that influence other coho salmon stocks include initial marine conditions (Holtby et al. 1990; Koslow et al. 2002), early marine growth (Holtby et al. 1990), and predation intensity (Fisher and Pearcy 1988). Similarly, hatchery practices influence coho salmon marine survival rates, which might predispose some hatchery stocks to having lower marine survival rates (Labelle et al. 1997). These hatchery practices include size at release (Bilton et al. 1982), date of release (Bilton et al. 1982; Mathews and Ishida 1989), and broodstock genetics (Labelle et al. 1997).

Hatchery releases of pink salmon and chum salmon (i.e., HPC index) appeared to be more important in explaining marine survival than did the WP index. There does not appear to be a consistent regional effect of the hatchery releases of pink salmon and chum salmon; for some stocks, however, the local effect seems to be of major importance. For example, the HPC index is significantly related to marine survival of the Taku River stock but not to that of the Gastineau Channel stock (Table 4; Figure 6), both of which are in geographic proximity with the Auke Creek stock, which had the strongest relationship with the HPC index.

Both positive and negative relationships were evident between the HPC index and marine survival. This indicates that local factors may influence a particular stock's relationship with hatchery releases of pink salmon and chum salmon. The negative relationships could result from density dependence wherein the coho salmon compete with the pink salmon and chum salmon for food in some local areas. Similarly, a possible explanation for the positive relationships is that coho salmon are preying upon the pink salmon and chum salmon. Local early marine conditions may be pressuring different stocks in opposite ways, resulting in different mechanisms.

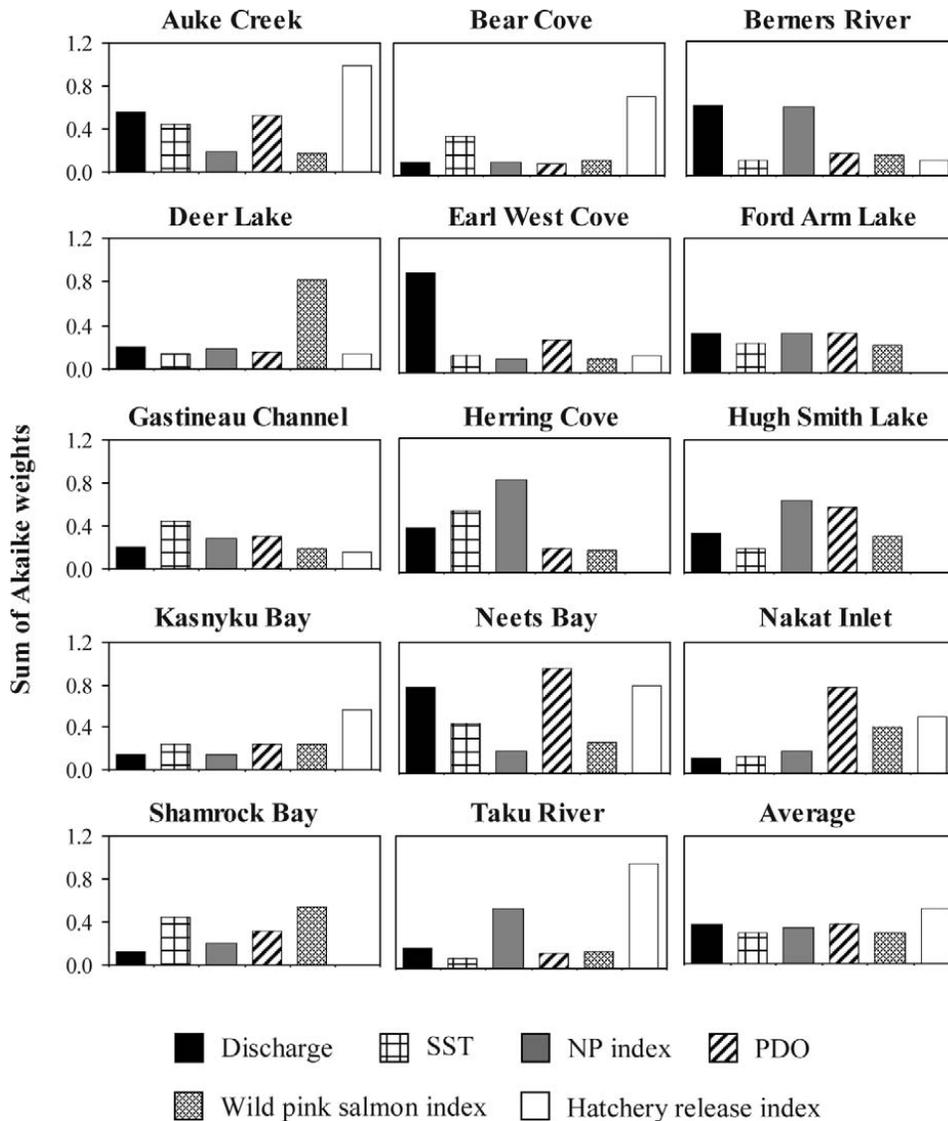


FIGURE 6.—Sum of Akaike weights for each covariate (x-axis; SST = sea-surface temperature; NP index = North Pacific index; PDO = Pacific decadal oscillation) for all marine survival models with a difference in the corrected Akaike's information criterion (ΔAIC_c) less than 10 for each coho salmon stock. The sum of Akaike weights represents the relative support for each covariate. The lower right panel shows the averages of the sum of Akaike weights for each covariate across all stocks for all models with a ΔAIC_c less than 10.

An alternative explanation for the positive relationships between marine survival and hatchery releases is that the abundant pink salmon and chum salmon may act as a predation buffer for the juvenile coho salmon (Briscoe et al. 2005; LaCroix et al., in press). Similar mechanisms have been proposed for coho salmon in Oregon (Fisher and Percy 1988) and for pink salmon in Prince William Sound (Willette et al. 2001). However, this could also result in a negative relationship for coho salmon marine survival if the predators selectively choose the larger coho salmon.

The explanation for the lack of regional concordance in response to the hatchery releases may be related to the complexity of the SEAK inside waters. To reach the Gulf of Alaska, coho salmon located on the inside of SEAK are required to migrate through corridors that comprise narrow strait habitat (Jaenicke and Celewycz 1994; Courtney et al. 2000). Research conducted in northern SEAK on coho salmon distributions throughout various marine habitats found that coho salmon prefer strait habitats during early marine residency (Orsi et al. 2000). However, these narrow migration

TABLE 7.—Summary of mixed-effects model selection results for four candidate models of southeast Alaska coho salmon marine survival; “AC included” represents the models that included all 10 stocks, while “AC excluded” represents the models that included nine of the stocks (ΔAIC_c = difference in the corrected Akaike’s information criterion; α = average survival term; a_i and g_i = random effects further defined in Methods; γ = fixed effect of the hatchery pink salmon and chum salmon fry index [HPC]; ε = error term; $S_{i,t}$ = survival of the i th stock at time t).

Model	ΔAIC_c (AC included)	ΔAIC_c (AC excluded)
$S_{i,t} = \alpha + a_i + \varepsilon_{i,t}$	12.90	0.02
$S_{i,t} = \alpha + a_i + \gamma HPC_{i,t} + \varepsilon_{i,t}$	9.78	1.72
$S_{i,t} = \alpha + a_i + g_i HPC_{i,t} + \varepsilon_{i,t}$	0.00	0.00
$S_{i,t} = \alpha + a_i + \gamma HPC_{i,t} + g_i HPC_{i,t} + \varepsilon_{i,t}$	2.14	2.05

corridors may act as bottlenecks that make coho salmon especially vulnerable to predation. Consequently, predation buffering could be more important for those stocks that use these corridors, such as the Auke Creek stock. This hypothesis is supported by research conducted in Icy Strait (northern SEAK) that showed that juvenile pink salmon abundance in the strait was the best predictor of coho salmon year-class strength (LaCroix et al., in press).

The negative relationships between marine survival and the WP index, a surrogate for the local abundance of pink salmon fry, seem to contradict the hypothesis that pink salmon and chum salmon may reduce predation on coho salmon by serving as alternative prey for the predators of coho salmon. However, the WP index, which is based on parental abundance, could be a poor index of pink salmon fry abundance; it is undoubtedly confounded by factors that influence embryo survival, including water temperature (Murray and McPhail 1988), dissolved oxygen (Sowden and Power 1985), fine-sediment accumulation (Chapman 1988), and streambed scour (Lisle and Lewis 1992; Montgomery et al. 1996). The variability in embryo survival, combined with variability in aerial survey counts (Jones et al. 1998), may lead to significant biases in the WP index. Similarly, density-dependent mortality factors, such as redd superimposition (McNeil 1964; Fukushima et al. 1998), may cause nonlinearity in the relationship between pink salmon escapement and fry abundance in the following year. This could cause misleading conclusions as to the direction of the effect on coho salmon marine survival as well as obscuring the significance.

Both the PDO and NP index showed consistent relationships with marine survival; the NP index was consistent over all 14 stocks, while the PDO was

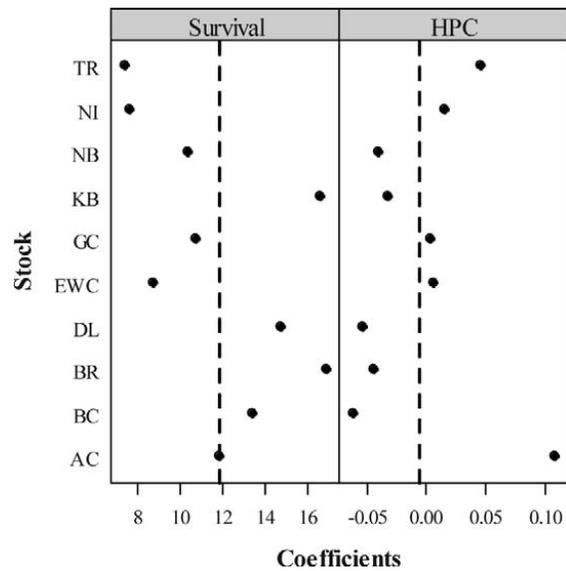


FIGURE 7.—Variation of random effects coefficients around the mean survival effect and the mean hatchery pink salmon and chum salmon (HPC) index effect for coho salmon in southeast Alaska (stock codes are defined in Table 1).

consistent over 13 stocks (Table 4). However, the direction of the relationships between marine survival and both of these indices contradicted expectations based on previous research (Mantua et al. 1997; Hare et al. 1999; Mueter et al. 2002a; LaCroix et al., in press). Previous research focused on pink salmon, chum salmon, and sockeye salmon, which have much different life history strategies than coho salmon (Quinn 2005); this might explain the apparent reversal of the relationship between these indices and survival. The greater apparent effect of the PDO compared with the NP index (from the regression analysis) should be viewed with caution. These variables are correlated with each other, which may make it difficult to distinguish the effects of one variable from those of the other variable.

Two regional-scale physical variables, SST and DIS, had similar relative importance to that of the ocean-basin-scale variables. This conflicts with recent work showing that regional-scale environmental processes are more important than ocean-basin-scale processes in explaining variations in salmon survival (Peterman et al. 1998; Mueter et al. 2002a, 2002b; Pyper et al. 2005). However, the other research investigated survival over much larger geographic ranges than this study. The strong covariation among the stocks in this study may explain why there is not a clear distinction in importance between the regional-scale variables and the ocean-basin-scale variables.

Sea-surface temperature had mixed relationships

with marine survival. Previous research on pink salmon, chum salmon, and sockeye salmon has shown that northern British Columbia and SEAK compose a transitional area between opposing effects of SST on marine survival (Mueter et al. 2002a). Our mixed results may be a result of our study area falling in a transitional area or may reflect the lack of an inverse relationship between northern and southern domains for coho salmon. Curvilinear relationships have been identified between coho salmon marine survival and SST in the northwestern United States (Ryding and Skalski 1999). Similar relationships may exist in SEAK and, with the complex geography of the region, may result in inconsistent relationships between marine survival and SST. Also, the assumption that SST averaged from the outer coast of SEAK is a good representation of SST throughout SEAK may not be valid.

Freshwater discharge related negatively with marine survival, which differs from both our initial thinking and previous research that showed a positive relationship between survival of pink salmon and DIS (Mueter et al. 2005). This discrepancy may arise from a number of factors. Discharge may act as a proxy for other indirect effects on survival, which may act differently on coho salmon in SEAK than they do on stocks previously investigated. The unexpected effect of DIS might also be associated with the time frame used in the study. April was thought to correspond to the period that would set the conditions in the marine environment for out-migrating coho salmon, but this might be too narrow and might misrepresent the actual conditions experienced by coho salmon smolts.

There was much uncertainty regarding the most parsimonious models in the linear regression analysis (Table 6; Figure 6). This reflects ambiguity in the data, as well as the relationships between the covariates and marine survival. This uncertainty leads to the conclusion that one particular variable is not necessarily more important than another but that marine survival in SEAK is influenced by a host of biological and environmental variables acting at a variety of spatial scales. There does not seem to be one particular spatial scale that best relates to marine survival, but instead it seems to be a balance between the ocean basin, regional, and local scales. The increase in localized releases of hatchery-reared pink salmon and chum salmon over the past 25 years does not seem to have had a strong influence on coho salmon marine survival throughout SEAK. It may, however, have had a more localized influence on a few individual stocks in the region. It should be noted, though, that these interpretations are limited by the relatively small

number of coho salmon stocks for which marine survival data are available.

Increased research into the localized marine habitat use of the Auke Creek stock may help to elucidate the mechanism underlying the unique relationship between this coho salmon stock and hatchery pink salmon and chum salmon releases. Similarly, research into the causal links between large-scale and local-scale biophysical factors in SEAK may help to more clearly identify the links between these processes and early marine survival of coho salmon in SEAK.

Acknowledgments

Funding for this research was provided by the U.S. Global Ocean Ecosystem Dynamics research program through the National Science Foundation. We thank L. Shaul, C. Blair, G. Freitag, R. Focht, X. Zhang, M. Plotnick, S. Heintl, and T. Royer for graciously providing auxiliary data. We also thank N. Hillgruber, B. Smoker, and two anonymous reviewers for comments on early manuscripts.

References

- ADFG (Alaska Department of Fish and Game). 2008. Online reports. ADFG Coded Wire Tag Laboratory. Available: <http://tagotoweb.adfg.state.ak.us>. (April 2008).
- 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. *Fisheries Oceanography* 5:137–152.
- Bax, N. J. 1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. *Canadian Journal of Fisheries and Aquatic Sciences* 40:426–435.
- 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. *Progress in Oceanography* 49:423–437.
- Beamish, R. J., C. E. M. Neville, and A. J. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in climate and the ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 54:543–554.
- Beamish, R. J., D. J. Noakes, G. A. McFarlane, W. Pinnix, R. Sweeting, and J. King. 2000. Trends in coho marine survival in relation to the regime concept. *Fisheries Oceanography* 9:114–119.
- Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. *Canadian Journal of Fisheries and Aquatic Sciences* 39:426–447.
- Brase, A., and M. Stopha. 2000. Hatchery coho salmon *Oncorhynchus kisutch* production, contribution to the commercial fisheries, and catch timing in the commercial fisheries, with comparisons to wild coho salmon stocks in southeast Alaska, 1999. Alaska Department of Fish and

- Game, Regional Information Report Number 1J00-26, Douglas.
- Briscoe, R. J., M. D. Adkison, A. Wertheimer, and S. G. Taylor. 2005. Biophysical factors associated with the marine survival of Auke Creek, Alaska, coho salmon. *Transactions of the American Fisheries Society* 134:817–828.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretical approach, 2nd edition. Springer-Verlag, New York.
- Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117:1–21.
- Clark, J. H., A. McGregor, R. D. Mecum, P. Krasnowski, and A. M. Carroll. 2006. The commercial salmon fishery in Alaska. *Alaska Fishery Research Bulletin* 12:1–146.
- Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2067–2077.
- Courtney, D. L., D. G. Mortensen, J. A. Orsi, and K. M. Munk. 2000. Origin of juvenile Pacific salmon recovered from coastal southeastern Alaska identified by otolith thermal marks and coded wire tags. *Fisheries Research* 46:267–278.
- Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. *Monographs on Statistics and Applied Probability* 57.
- Farley, E. V., J. M. Murphy, M. D. Adkison, L. B. Eisner, J. H. Helle, J. H. Moss, and J. Nielsen. 2007. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). U.S. National Marine Fisheries Service Fishery Bulletin 105:121–130.
- 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. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1036–1044.
- Foerster, R. E. 1954. On the relation of adult sockeye salmon (*Oncorhynchus nerka*) returns to known smolt seaward migrations. *Journal of the Fisheries Research Board of Canada* 11:339–350.
- Fukushima, M., T. J. Quinn, and W. W. Smoker. 1998. Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. *Canadian Journal of Fisheries and Aquatic Sciences* 55:618–625.
- Fukuwaka, M., and T. Suzuki. 2002. Early sea mortality of mark-recaptured juvenile chum salmon in open coastal waters. *Journal of Fish Biology* 60:3–12.
- Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. *Fisheries* 24(1):6–14.
- Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). Pages 212–230 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver.
- Hobday, A. J., and G. W. Boehlert. 2001. The role of coastal ocean variation in spatial and temporal patterns in survival and size of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:2021–2036.
- 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*). *Canadian Journal of Fisheries and Aquatic Sciences* 47:2181–2194.
- Jaenicke, H. W., and A. G. Celewycz. 1994. Marine distribution and size of juvenile Pacific salmon in southeast Alaska and northern British Columbia. U.S. National Marine Fisheries Service Fishery Bulletin 92:79–90.
- Jones, E. L., T. J. Quinn, and B. W. Van Alen. 1998. Observer accuracy and precision in aerial and foot survey counts of pink salmon in a southeast Alaska stream. *North American Journal of Fisheries Management* 18:832–846.
- Koslow, J. A., A. J. Hobday, and G. W. Boehlert. 2002. Climate variability and marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. *Fisheries Oceanography* 11:65–77.
- Labelle, M., C. J. Walters, and B. Riddell. 1997. Ocean survival and exploitation of coho salmon (*Oncorhynchus kisutch*) stocks from the east coast of Vancouver Island, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1433–1449.
- LaCroix, J. J., A. C. Wertheimer, J. A. Orsi, M. V. Sturdevant, E. A. Fergusson, and N. A. Bond. 2009. A top-down survival mechanism during early marine residency explains coho salmon year-class strength in southeast Alaska. *Deep Sea Research II*. DOI: 10.1016/j.dsr2.2009.03.006.
- Lisle, T. E., and J. Lewis. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream: a simulation approach. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2337–2344.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069–1079.
- Mathews, S. B., and Y. Ishida. 1989. Survival, ocean growth, and ocean distribution of differentially timed releases of hatchery coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 46:1216–1226.
- McNeil, W. J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. *Journal of the Fisheries Research Board of Canada* 21:1385–1396.
- Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Scheutt-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1061–1070.
- Moss, J. H., D. A. Beauchamp, A. D. Cross, K. W. Myers, E. V. Farley, J. M. Murphy, and J. H. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. *Transactions of the American Fisheries Society* 134:1313–1322.
- Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002a. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Canadian Journal of Fisheries and Aquatic Sciences* 59:456–463.

- Mueter, F. J., B. J. Pyper, and R. M. Peterman. 2005. Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. *Transactions of the American Fisheries Society* 134:105–119.
- Mueter, F. J., D. M. Ware, and R. M. Peterman. 2002b. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the northeast Pacific Ocean. *Fisheries Oceanography* 11:205–218.
- Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. *Canadian Journal of Zoology* 66:266–273.
- Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. *Canadian Journal of Fisheries and Aquatic Sciences* 43:527–535.
- 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 southeast Alaska. *North Pacific Anadromous Fish Commission Bulletin* 2:111–122.
- Orsi, J. A., and A. C. Wertheimer. 1995. Marine vertical distribution of juvenile Chinook and coho salmon in southeastern Alaska. *Transactions of the American Fisheries Society* 124:159–169.
- Parker, R. R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. *Journal of the Fisheries Research Board of Canada* 25:757–794.
- Parker, R. R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *Journal of the Fisheries Research Board of Canada* 28:1503–1510.
- Peterman, R. M., B. J. Pyper, M. F. Lapointe, M. D. Adkison, and C. J. Walters. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2503–2517.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effects Models in S and S-Plus: Statistics and Computing*. Springer-Verlag, New York.
- Pyper, B. J., F. J. Mueter, and R. M. Peterman. 2005. Across-species comparisons of spatial scales of environmental effects on survival rates of Northeast Pacific salmon. *Transactions of the American Fisheries Society* 134:86–104.
- Quinn, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. American Fisheries Society, Bethesda, Maryland and University of Washington Press, Seattle.
- Quinn, T. P., B. R. Dickerson, and L. A. Vollestad. 2005. Marine survival and distribution patterns of two Puget Sound hatchery populations of coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon. *Fisheries Research* 76:209–220.
- Royer, T. C., C. E. Grosch, and L. A. Mysak. 2001. Interdecadal variability of Northeast Pacific coastal freshwater and its implications on biological productivity. *Progress in Oceanography* 49:95–111.
- Ryding, K. E., and J. R. Skalski. 1999. Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:2374–2384.
- Shaul, L. 1994. A summary of 1982–1991 harvests, escapements, migratory and marine survival rates of coho salmon stocks in southeast Alaska. *Alaska Fishery Research Bulletin* 1:10–34.
- Shaul, L., S. E. Jones, and K. Crabtree. 2005. Coho salmon stock status and escapement goals in southeast Alaska. Pages 105–152 in J. A. Hovanisian and H. J. Geiger, editors. *Stock status and escapement goals for salmon stocks in southeast Alaska 2005*. Alaska Department of Fish and Game, Special Publication 05-22, Anchorage.
- Sinnott, R. W. 1984. *Virtues of the Haversine*. Sky and Telescope 68:159.
- Soderberg, R. W. 1995. *Flowing water fish culture*. CRC Press, Boca Raton, Florida.
- Sowden, T. K., and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. *Transactions of the American Fisheries Society* 114:804–812.
- Trenberth, K. E., and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics* 9:303–319.
- Tydingco, T. 2005. Smolt production, adult harvest, and spawning escapement of coho salmon from the Nakwasina River in southeast Alaska, 2001–2002. Alaska Department of Fish and Game, Fishery Data Series Number 05-04, Anchorage.
- Weingartner, T. J., K. Coyle, B. Finney, R. Hopcroft, T. Whitley, R. Brodeur, M. Dagg, E. Farley, D. Haidvogel, L. Haldorson, A. Hermann, S. Hinckley, J. Napp, P. Stabeno, T. Kline, L. C. Lastname, E. Lessard, T. Royer, and S. Strom. 2002. The Northeast Pacific GLOBEC program: coastal Gulf of Alaska. *Oceanography* 2:48–63.
- Wertheimer, A. C., and F. P. Thrower. 2007. Mortality rates of chum salmon during their early marine residency. Pages 233–247 in C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, editors. *Ecology of juvenile salmon in the Northeast Pacific Ocean: regional comparisons*. American Fisheries Society, Symposium 57, Bethesda, Maryland.
- Willette, T. M., R. T. Cooney, V. Patrick, D. M. Mason, G. L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. *Fisheries Oceanography* 10(Supplement 1):14–41.
- Worley, S. J., S. D. Woodruff, R. W. Reynolds, S. J. Lubkar, and N. Lott. 2005. ICOADS release 2.1 data and products. *International Journal of Climatology* 25:823–842.
- Zadina, T. P., S. C. Heintz, A. J. McGregor, and H. J. Geiger. 2004. Pink salmon stock status and escapement goals in southeast Alaska and Yakutat. Pages 263–316 in H. J. Geiger and S. McPherson, editors. *Stock status and escapement goals for salmon stocks in southeast Alaska*. Alaska Department of Fish and Game, Special Publication 04-02, Anchorage.