VARIABLE EFFECTS OF BIOLOGICAL AND ENVIRONMENTAL PROCESSES ON COHO SALMON MARINE SURVIVAL IN SOUTHEAST ALASKA

By

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A

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Abstract

I examined the relationships between coho salmon *Oncorhynchus kisutch* marine survival and seven biological and physical covariates across 14 Southeast Alaska (SEAK) stocks. A primary focus of the study was to investigate the influence of pink *O. gorbuscha* and chum *O. keta* salmon fry abundances on marine survival. The coho salmon stocks exhibited strong covariation, suggesting common regional processes are influencing marine survival in SEAK. However, only two of the covariates, the North Pacific index and SEAK pink salmon harvest, had consistent relationships across all 14 stocks with both of the covariates relating positively with marine survival. The other covariates all had inconsistent relationships with marine survival. An index representing hatchery pink and chum salmon fry abundance had a stronger estimated effect on marine survival than an index of wild pink salmon fry abundance and SEAK pink salmon harvest numbers. The magnitude and sign of the hatchery pink and chum salmon effect varied greatly among different localities. This study 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.

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Acknowledgments

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Introduction

Variation in Pacific salmon *Oncorhynchus* spp. marine survival is associated with a broad range of physical 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. Ocean basin scale climate indices, such as the Pacific decadal oscillation (PDO) and Aleutian low pressure index (ALPI) have been shown to be linked with production trends of salmon along the west coast of North America (Beamish et al. 1997b; Mantua et al. 1997; Hare et al. 1999). However, salmon marine survival has been found to be more correlated with regional and local scale variables than ocean basin scale processes (Adkison et al. 1996; Mueter et al. 2002a; Mueter et al. 2002b; Pyper et al. 2005).

The majority of salmon marine mortality occurs during the early marine life phase (Parker 1968; Bax 1983; Briscoe et al. 2005; Wertheimer and Thrower 2007), with evidence for significant winter mortality if energy storage is not sufficient (Beamish et al. 1997a; 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; Henderson and Cass 1991; Willette et al. 2001; Moss et al. 2005; Quinn et al. 2005). However, other ecological factors such as sub-optimal prey abundance, predator abundance, and abundance of alternative prey resources for the predators of salmon have been found to be important in explaining variation in marine survival (Fisher and Pearcy 1988; Mortensen et al. 2000; Willette et al. 2001; Briscoe et al. 2005).

This study investigates biological and environmental variables thought to influence coho salmon *O. kisutch* marine survival in Southeast Alaska (SEAK). The 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 biological and environmental processes in the marine environment.

An important aspect of the SEAK region is the large hatchery releases of pink *O. gorbuscha* and chum *O. keta* salmon fry each spring. Since the late 1970's the hatchery releases were dominated by steadily increasing numbers of chum salmon (Figure 2). Hatchery releases in northern SEAK have been shown to strongly relate to marine survival rates for Auke Creek coho salmon, through a hypothesized predation buffering mechanism (Briscoe et al. 2005). It is thought that the abundant hatchery released pink 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 physical and biological covariates on coho salmon marine survival. In particular, the objective was to determine if hatchery pink and chum salmon are influencing marine survival of other coho salmon stocks throughout SEAK. Correlation analyses, linear regression models, and mixed effects models were used to address the primary goal of the research. In the process, I hoped to provide insight into the mechanisms controlling coho salmon marine survival in SEAK.

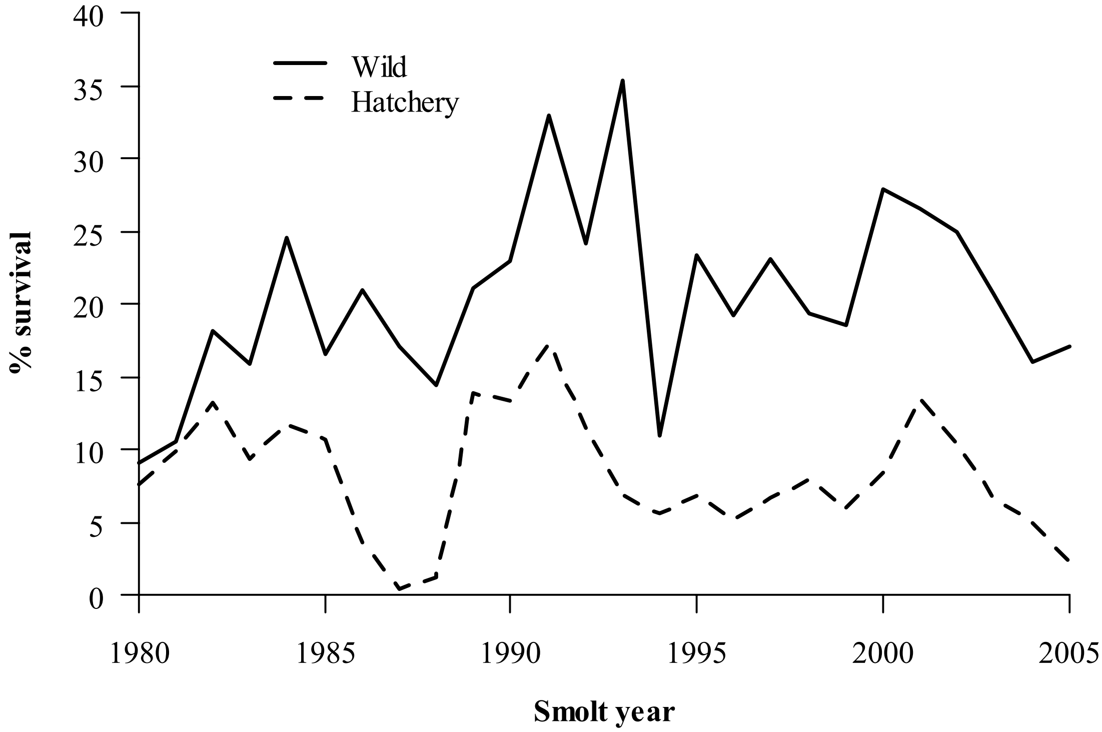

Figure 1.—Times series of marine survival rates for a single wild stock (Auke Creek, northern Southeast Alaska) and a single hatchery stock (Neets Bay, southern Southeast Alaska) located in Southeast Alaska (Gary Freitag, Southern Southeast Regional Aquaculture Association, personal communication; Shaul et al. 2005).

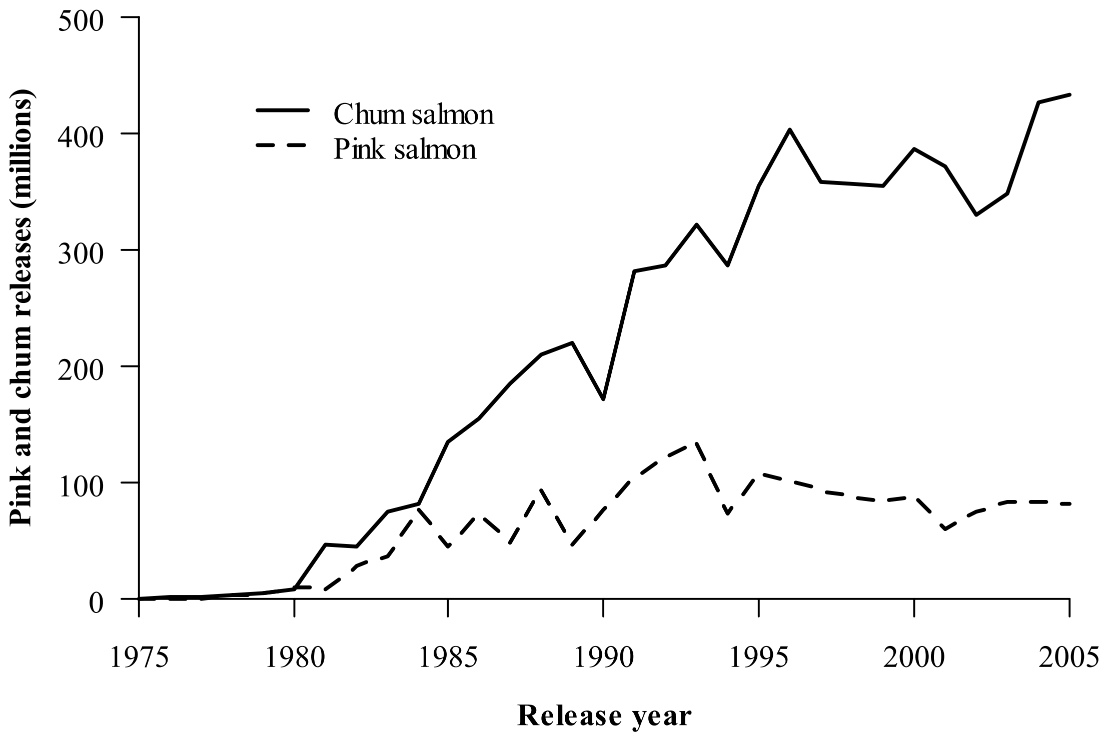

Figure 2.—Total hatchery pink and chum salmon fry releases in Southeast Alaska (ADFG 2008b).

Data and Methods

Study Area

The study area in SEAK encompasses both the Alexander Archipelago and the Alaska mainland south of 60N (Figure 3). The Alexander Archipelago is comprised of over 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.

Maintaining healthy coho salmon populations in SEAK is important to the local economy. The SEAK region has accounted for 54% of the total Alaskan commercial coho salmon harvest from 2003 to 2007, which represents approximately US$83 million dollars (ADFG 2008a). Coho salmon are also a popular sport fish, which results in substantial economic activity from both resident and non-resident anglers (Haley et al. 1999), thus increasing the value of the resource to the region beyond the ex-vessel commercial harvest value.

Marine Survival Data

Time series of coho salmon marine survival rates for 14 stocks were compiled from various agencies (Figure 3). The 14 stocks were composed of 9 hatchery and 5 wild stocks (Table 1). The hatchery stocks were produced by three hatchery organizations, including the Northern Southeast Regional Aquaculture Association (NSRAA), the Southern Southeast Regional Aquaculture Association (SSRAA), and Douglas Island Pink and Chum, Inc. (DIPAC). The time series data for the five wild 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.

The calculations of the marine survival rates were 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 and 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. There is uncertainty associated with the marine survival estimates, although the uncertainty is greater for the wild stocks than 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 (see Appendix).

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

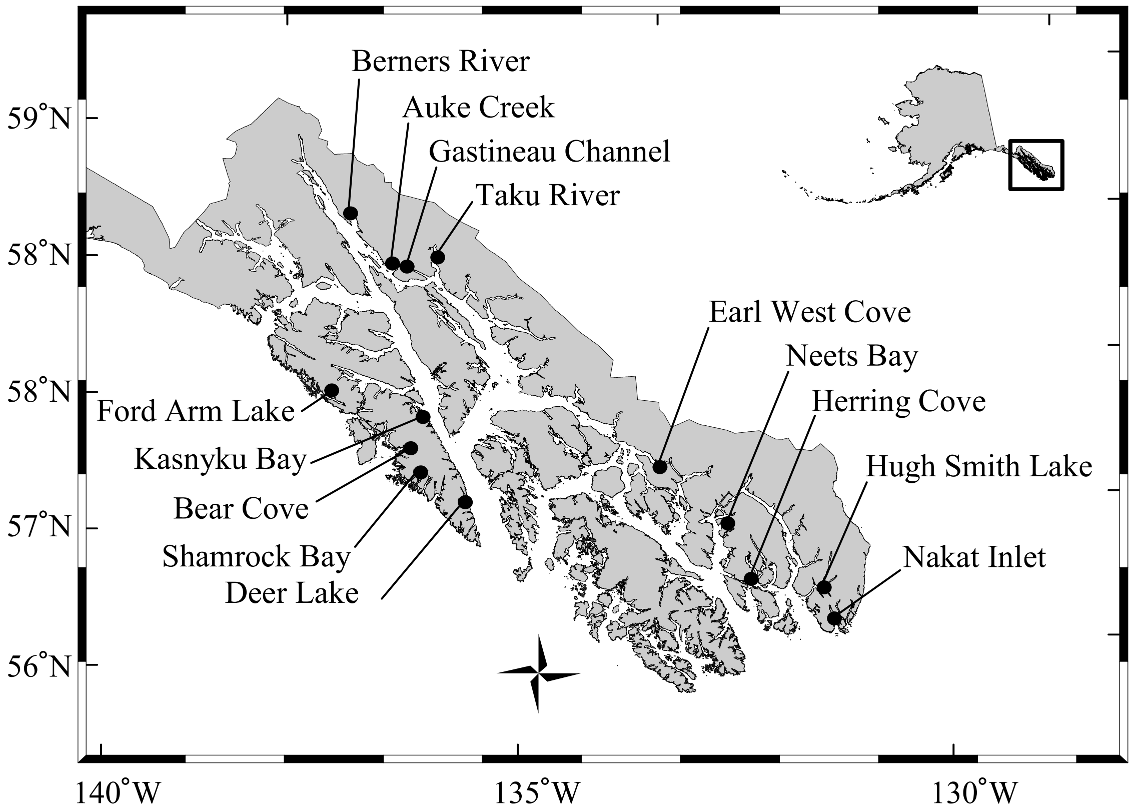

Figure 3.—Map of study area in Southeast Alaska with ocean entry points for the 14 coho salmon stocks used in this analysis.

Table 1.—Summary of 14 Southeast Alaska coho salmon marine survival data sets used in the analysis; Abb. is the abbreviation of the coho salmon stock, stock group is the name of the pink salmon stock group where the particular coho salmon stock is located, and N is the number of smolt years available for this analysis.

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

Biological Data

Pink and Chum Salmon Fry Abundance

Two independent indices were used to quantify the local abundance of pink 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). The second was an index representing hatchery pink and chum salmon fry abundance (HPC). In order 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 2 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). I used these adult aerial counts as an index for the relative abundance of pink salmon fry the following year. To compute the 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 to coho salmon marine survival rates from the next year (i.e., the year of marine entrance for the pink salmon fry). Following the predation buffer hypothesis the WP index was expected to relate positively with coho salmon marine survival.

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 8 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.

Pink Salmon Harvest

Southeast Alaska regional commercial harvest numbers for pink salmon were obtained for the years 1979 to 2005 (S. Heinl, ADFG, personal communication). Pink salmon harvest (PH) was used as another proxy for the SEAK region wide abundance of pink salmon fry of the previous year. Due to similar life history patterns between pink and coho salmon, and because pink salmon may act as an alternative prey resource for the predators of coho salmon, pink salmon harvest numbers were expected to relate positively with marine survival.

Environmental Data

Freshwater Discharge

In the coastal Gulf of Alaska region, salinity is thought to be a driving factor that controls spring stratification, with stronger stratification indicative of lower winter and spring sea surface salinity (Weingartner et al. 2002). Freshwater discharge (DIS) is used in this study as a surrogate for region wide sea surface salinity with higher discharge corresponding to lower sea surface salinity. Monthly freshwater discharge data for the SEAK region were available for the period of 1979 to 2005 (T.C. Royer, Old Dominion

University, personal communication). The late winter and 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 discharge 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

Temperature is a particularly important environmental factor for ectothermic animals such as fishes, since it affects 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; Mueter et al. 2005; Quinn et al. 2005). I used sea surface temperature (SST) as a proxy for water temperatures experienced by coho salmon smolts, since these fish are found in the surface waters when they first enter the ocean and during the 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 (ICOADS). All the monthly observations within a box located at 58N to 56N and 141W to 137W were averaged. Since fish grow faster in warmer temperatures as long as the temperature is below their stress threshold and food is not limited, a positive relationship was expected between SST and marine survival (Soderberg 1995).

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 known to be important in determining salmon marine survival rates (Parker 1971; Fukuwaka and Suzuki 2002; Mueter et al. 2005; Wertheimer and Thrower 2007), therefore, it seems the winter phase of the PDO prior to out migration of the smolts would be most appropriate for use in a coastal Gulf of Alaska marine survival model. The PDO was averaged over the months of November through March and compared to marine survival of the next year's coho salmon emigrants. The thought was that a higher PDO would increase salmon survival by providing better growing conditions during the early marine life phase (Mantua et al. 1997).

North Pacific Index

The North Pacific (NP) index is a measure of the Aleutian low and is defined as the area-weighted sea level pressure over the region of 30N, 65N and 160E,140W (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 (Hurrell 2008) were averaged over the months of December to March, corresponding to the peak of the

Aleutian low. This average was then compared to the survival of the next year's emigrants. Since 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 Analysis

Exploratory Analysis

Exploratory data analysis was conducted to verify that the data sets met the assumption of a normal distribution and to identify any unusual data points. This was implemented through the use of scatter plots, boxplots, histograms, and normal quantile plots. Due to the disparate units, the covariates were standardized for the linear regression analysis by subtracting the mean and dividing by the standard deviation to facilitate model fitting and interpretation. Similarly, for the mixed effects models the HPC index was rescaled by dividing the raw data by 1,000,000.

Correlation Analysis

Three correlation analyses were performed using Pearson correlation coefficients: (1) pairwise comparisons among 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 correlation was computed between the correlations among coho salmon stocks and the great circle distance separating each of the coho salmon stocks. 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 physical 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. Ten of the coho salmon stocks had data for all seven of the covariates, giving the full model,

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

were S is the marine survival for a particular stock, α is the intercept, β_i are interaction parameters, WP is the wild pink salmon fry abundance index, HPC is the hatchery pink and chum salmon abundance index, PH is the SEAK pink salmon harvest, PDO is the Pacific decadal oscillation, NP is the North Pacific index, 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 and chum salmon fry released in their vicinity, giving the full model for these four stocks as,

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

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 the Akaike Information Criterion (AIC_C), with a correction factor for small sample sizes (Burnham and Anderson 2002). The AIC_C was calculated as,

$$AIC_C = -2 * \log(L) + \frac{2kn}{n-k-1},$$

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 was rescaled relative to that of the most parsimonious model as follows:

$$\Delta AIC_{C_i} = AIC_{C_i} - \min AIC_C .$$

Model Averaging

For the set of R candidate models obtained from the stepwise model selection procedure, Akaike weights were calculated as,

$$w_i = \frac{\exp\left(-\Delta AIC_{C_i}/2\right)}{\sum_{r=1}^{R} \exp\left(-\Delta AIC_{C_r}/2\right)}.$$

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 Akaike weights of all models constructed for a coho salmon stock with $\Delta AIC_C < 10$ that included a particular variable.

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 squared 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 standard deviation of the error of prediction was then obtained by taking the square root of the MSE.

Mixed Effects Models

Linear multi-stock mixed effects models were used to further explore the relationship between the HPC index and marine survival across all ten stocks with HPC index data, giving the full model,

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

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

where the subscripts *i* and *t* represent the i^{th} stock at time *t*, *HPC* represents the HPC index, α and γ are fixed effects representing average survival and average HPC effects respectively, a_i and g_i are random effects representing average stock specific survival without the HPC effect, and stock specific HPC effects respectively, both of which were assumed to follow a normal distribution, 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 model selection procedure was comprised 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 the fixed and random HPC effect. The AIC_C was used as the model selection criterion.

Results

Exploratory Analysis

All time series of marine survival rates and the covariates appeared to approximately follow a normal distribution, although outliers, defined here as observations larger than 1.5 times the inter-quartile range of the data set, were found in four of the marine survival time series (AC, HC, NI, and TR). Two outliers existed for the HPC index in the Anan stock group. The WP index had at least one outlier for seven stock groups. Since the marine survival data sets approximately followed a normal distribution the data were not transformed and no transformations were applied to the HPC or WP indices so as to preserve the effect of large recruit and release years. The HPC index also showed significant serial correlation among the observations. This was corrected for in the correlation analysis by reducing the degrees of freedom in the significance test (Pyper and Peterman 1998). Although the average marine survival rates varied between stocks, the amount of variation around the mean for each stock was similar (Figure 4). Highest average survival was observed for Auke Creek (20.1%), while the Shamrock Bay coho salmon stock showed the lowest average survival (5.7%).

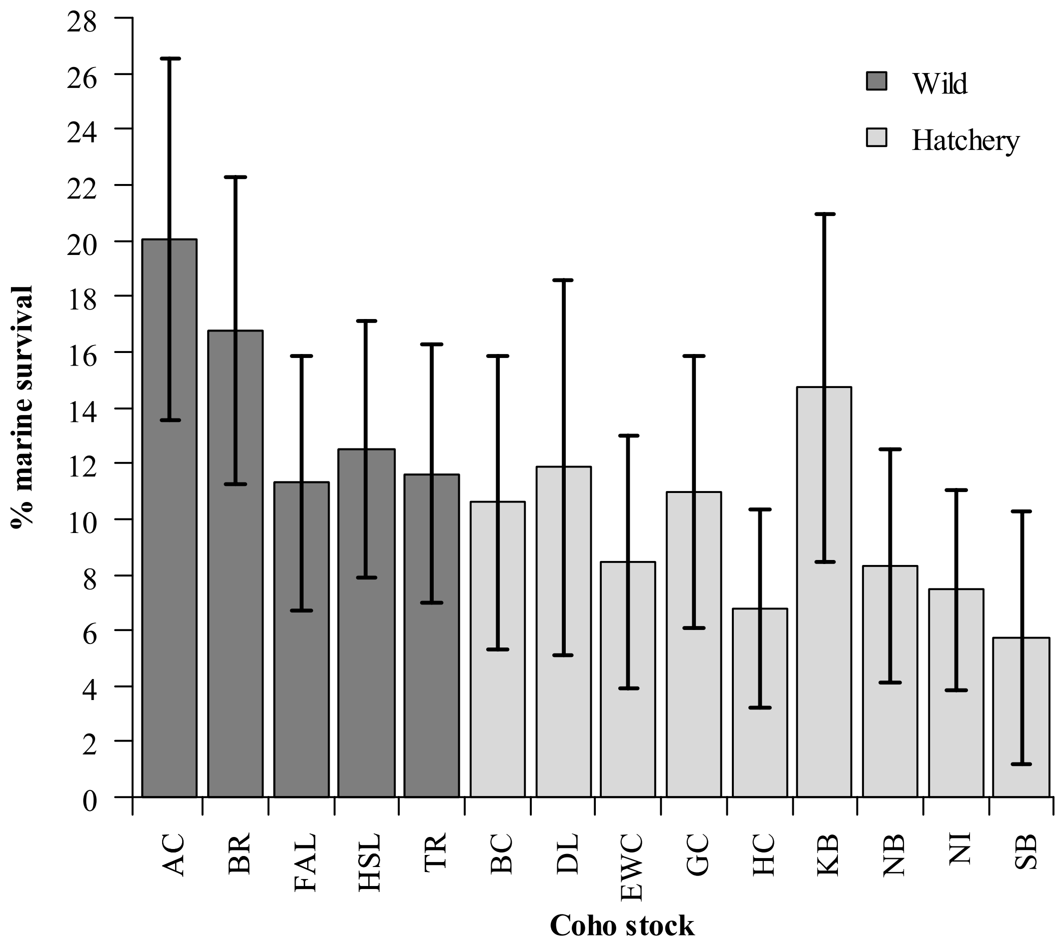

Figure 4.—Average marine survival rates of the 14 coho salmon stocks. The black bars represent plus and minus one standard deviation. AC: Auke Creek, BC: Bear Cove, BR: Berners River, DL: Deer Lake, EWC: Earl West Cove, FAL: Ford Arm Lake, GC: Gastineau Channel, HC: Herring Cove, HSL: Hugh Smith Lake, KB: Kasnyku Bay, NB: Neets Bay, NI: Nakat Inlet, SB: Shamrock Bay, TR: Taku River.

Correlation Analysis

Marine Survival

A total of 91 correlation coefficients were computed among the 14 time series of coho salmon marine survival. There were 88 positive correlations, of which 54 were significant ($P < 0.05$; Table 2); this represents many more significant correlations than the five that would be expected using $\alpha = 0.05$ 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. This provides strong evidence for region wide concordance of marine survival but also shows some variability which may be caused by local stock specific effects. The distance between stocks did not appear to affect the correlation between their marine survival rates ($r = -0.10$, $P = 0.36$; Figure 5).

Table 2.—Summary of pairwise correlations among the 14 coho salmon stocks marine survival rates. AC: Auke Creek, BC: Bear Cove, BR: Berners River, DL: Deer Lake, EWC: Earl West Cove, FAL: Ford Arm Lake, GC: Gastineau Channel, HC: Herring Cove, HSL: Hugh Smith Lake, KB: Kasnyku Bay, NB: Neets Bay, NI: Nakat Inlet, SB: Shamrock Bay, TR: Taku River.

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

$P < 0.05$

$0.05 < P < 0.10$

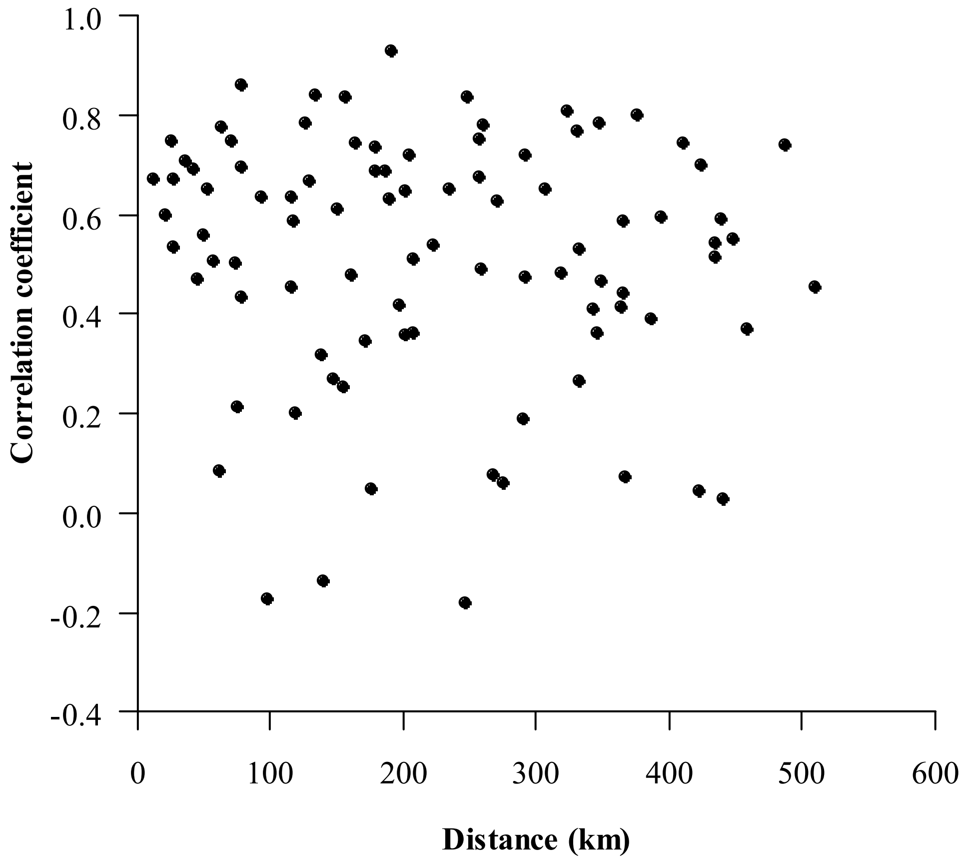

Figure 5.—Correlation coefficients among the coho salmon stocks' marine survival rates versus the distance between the stocks.

Marine Survival & Dependent Variables

Marine survival rates of all coho salmon stocks were positively correlated with both SEAK pink salmon harvest and the NP index. The SEAK pink salmon harvest showed 2 significant correlations ($P < 0.05$), while the NP index showed 3 significant correlations (Figure 6). The coho salmon stocks had mixed relationships with SST, discharge, the PDO, the HPC index (Figure 7), and the WP index (Table 3). Among all the covariates the PDO had the largest number of significant correlations with 4, followed by the NP index with 3.

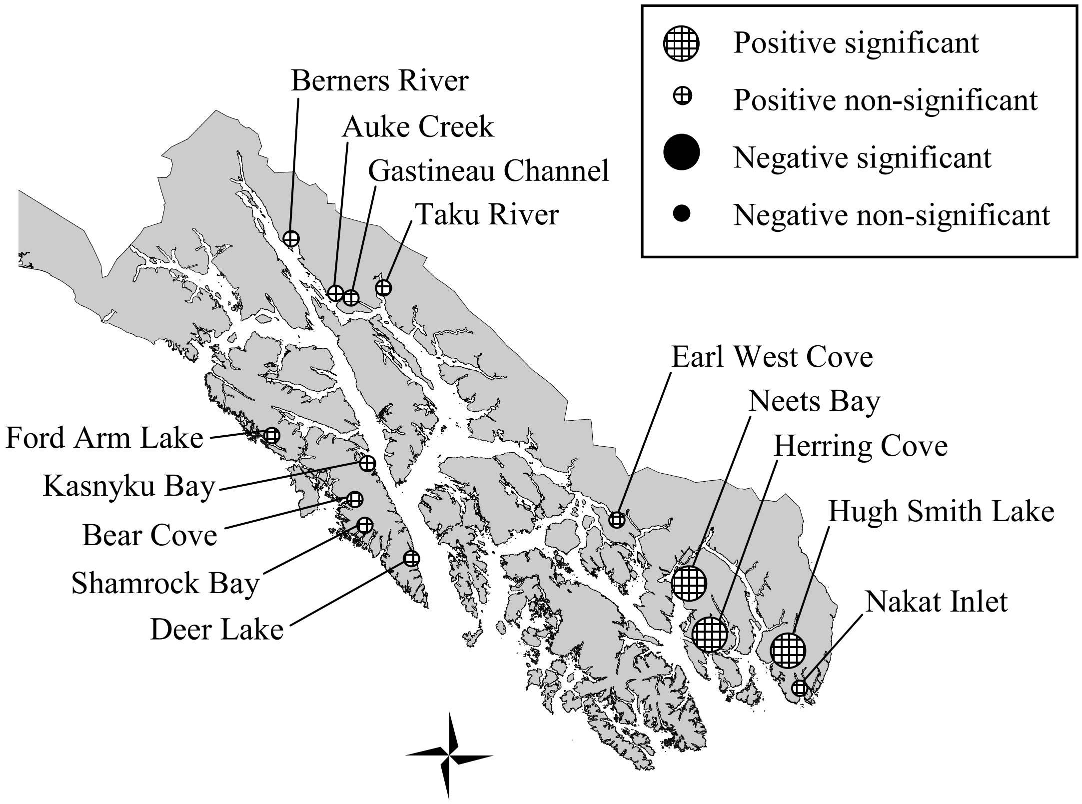

Figure 6.—Summary of correlations between the North Pacific index and coho salmon marine survival rates in SEAK (significance level = 0.05).

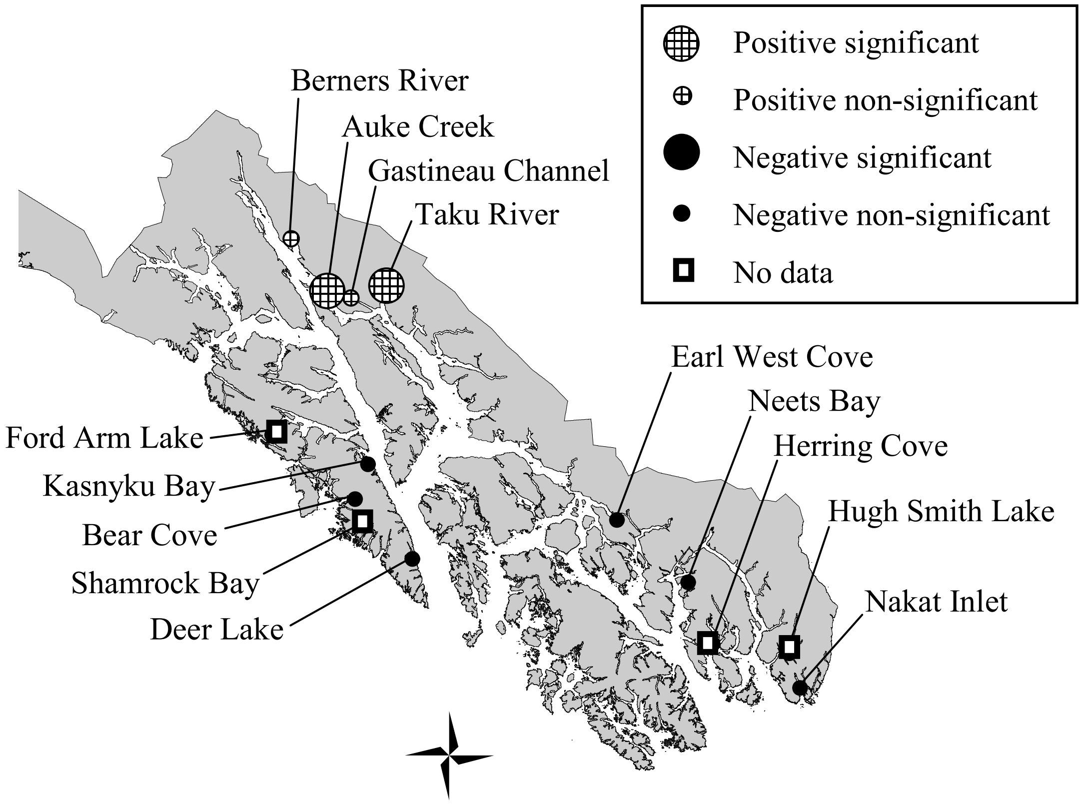

Figure 7.— Summary of correlations between the hatchery pink and chum salmon fry abundance index and coho salmon marine survival rates in SEAK (significance level = 0.05).

Table 3.—Summary of correlation coefficients among the marine survival time series and the covariates; DIS is April discharge, SST is summer sea surface temperature, NP is the North Pacific index, PDO is the Pacific decadal oscillation, PH is SEAK pink salmon harvest, WP is the wild pink salmon fry abundance index and HPC is the hatchery pink and chum salmon fry abundance index.

(dark shading)	*P* < 0.05
(light shading)	0.05 < *P* < 0.10

Stock	**DIS**	**SST**	**NP**	**PDO**	**PH**	**WP**	**HPC**
Auke Creek	-0.25	-0.04	0.13	-0.39	0.42	0.25	0.68
Bear Cove	0.16	-0.41	0.20	-0.07	0.29	-0.24	-0.56
Berners River	-0.46	-0.06	0.48	-0.18	0.04	-0.06	0.00
Deer Lake	-0.46	0.26	0.24	-0.08	0.33	-0.61	-0.31
Earl West Cove	-0.60	0.08	0.21	-0.35	0.12	0.10	-0.05
Ford Arm Lake	-0.21	0.08	0.21	-0.21	0.16	-0.02	na
Gastineau Channel	-0.15	-0.41	0.32	-0.35	0.23	-0.16	0.09
Herring Cove	-0.23	-0.33	0.48	-0.14	0.37	0.05	na
Hugh Smith Lake	-0.31	-0.15	0.53	-0.52	0.49	-0.29	na
Kasnyku Bay	-0.08	-0.32	0.12	-0.26	0.18	-0.34	-0.47
Neets Bay	-0.32	-0.29	0.39	-0.51	0.22	-0.30	-0.25
Nakat Inlet	-0.11	-0.06	0.34	-0.52	0.21	-0.36	-0.24
Shamrock Bay	0.15	0.25	0.27	0.38	0.27	-0.38	na
Taku River	-0.05	0.00	0.29	-0.18	0.07	-0.11	0.62

Linear Regression Models and Model Selection

The models that best predicted coho salmon marine survival rates differed greatly among the coho salmon stocks (Table 4). Five of the coho salmon stocks were best predicted by a single covariate while the best models for seven stocks contained multiple predictors. The Ford Arm Lake and Gastineau Channel stocks had no variables included in the best model. The number of similarly supported models ($\Delta AIC_C < 2$) varied among the stocks, with none of the stocks having only a single plausible model (Table 5). R-squared values ranged from as high as 0.54 to a low of 0.

The HPC index was included in 5 of the 10 models where HPC data was 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, indicating that the influence of the index is not consistent throughout SEAK. The PDO had the next highest percentage, being included in 4 of the 14 models, followed by the NP index and April discharge, both included in 3 models. Summer SST, SEAK pink salmon harvest, and the WP index were included in 2 of the 14 best models.

Table 4.—Summary of parameter values for the best predictive models for each coho salmon stocks marine survival; int is the intercept, DIS is April discharge, SST is summer sea surface temperature, NP is the North Pacific index, PDO is the Pacific decadal oscillation, PH is SEAK pink salmon harvest, WP is the wild pink salmon fry abundance index and HPC is the hatchery pink and chum salmon fry abundance index.

Stock	**int**	**DIS**	**SST**	**NP**	**PDO**	**PH**	**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	11.29	.	.	.	.	.	.	na	0.00
Gastineau Channel	10.98	.	.	.	.	.	.	.	0.00
Herring Cove	6.83	.	-1.04	1.31	.	1.17	.	na	0.39
Hugh Smith Lake	13.01	.	.	.	-2.33	2.01	.	na	0.45
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 5.—Summary of the number of models for each coho salmon stock with a ΔAIC_C less than two. Single asterisk indicates that the null model has a ΔAIC_C less than 2. Double asterisk indicates that the null model was selected as the best predictive model.

Stock	**# Models**	**Stock**	**# Models**
Auke Creek	7	Herring Cove	6
Bear Cove	2	Hugh Smith Lake	4
Berners River	3	Kasnyku Bay	2*
Deer Lake	2	Neets Bay	4
Earl West Cove	2	Nakat Inlet	4
Ford Arm Lake	5**	Shamrock Bay	5*
Gastineau Channel	4**	Taku River	3

Model Averaging

None of the explanatory variables had a consistently high relative importance across stocks (Figure 8). On average the HPC index had the highest relative importance followed by the PDO, April discharge, NP index, SST, SEAK pink salmon harvest, and the WP index (Figure 9). Additionally, these model averages don't 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 2 of the best models and negative relationships in 3 of the best models. The other 6 variables all had either consistent positive or negative signs, except for SST which was negative in one model and positive in another.

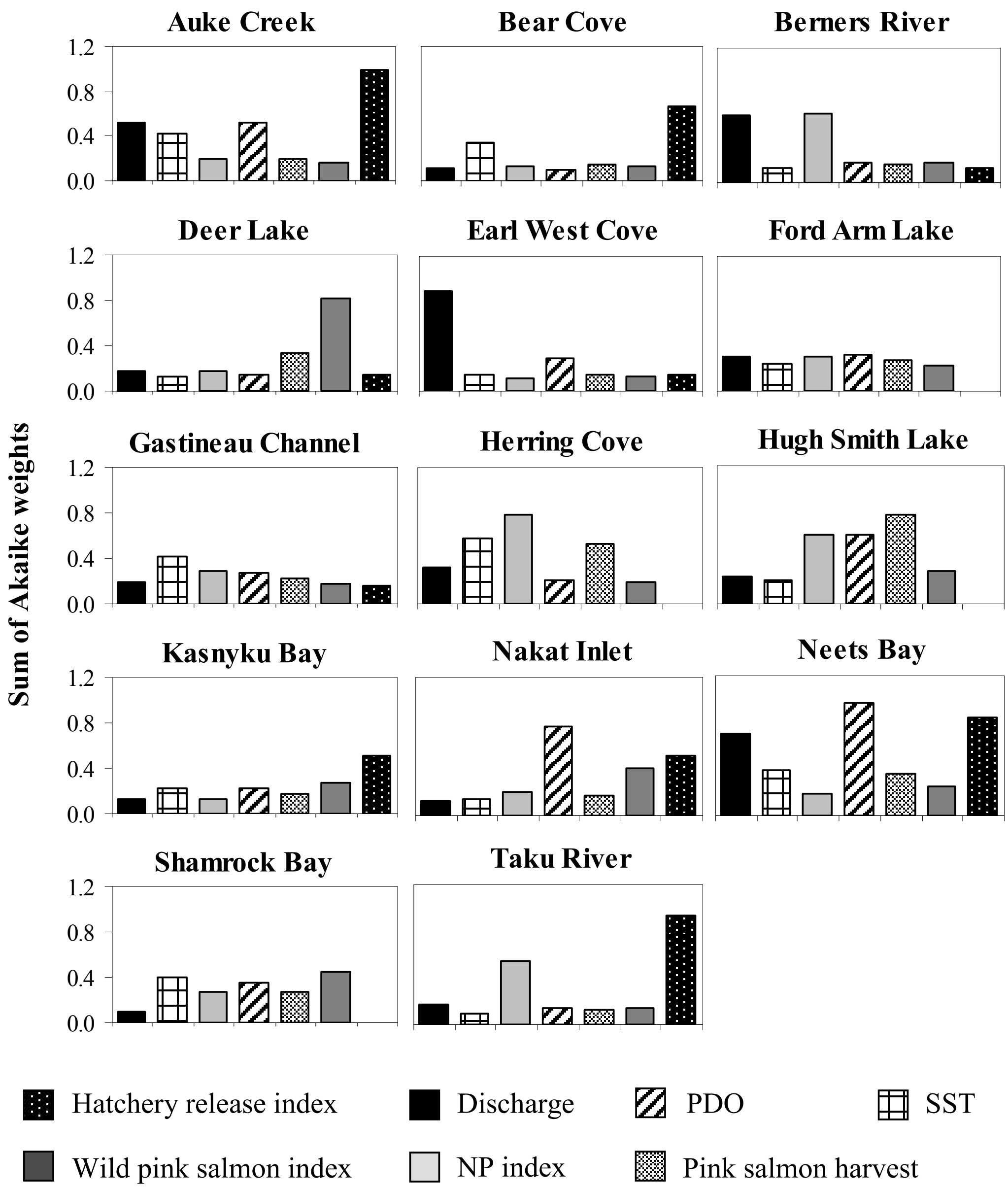

Figure 8.—The sum of Akaike weights for each covariate (x-axis) for all models with a ΔAIC_C less than 10 for each coho salmon stock.

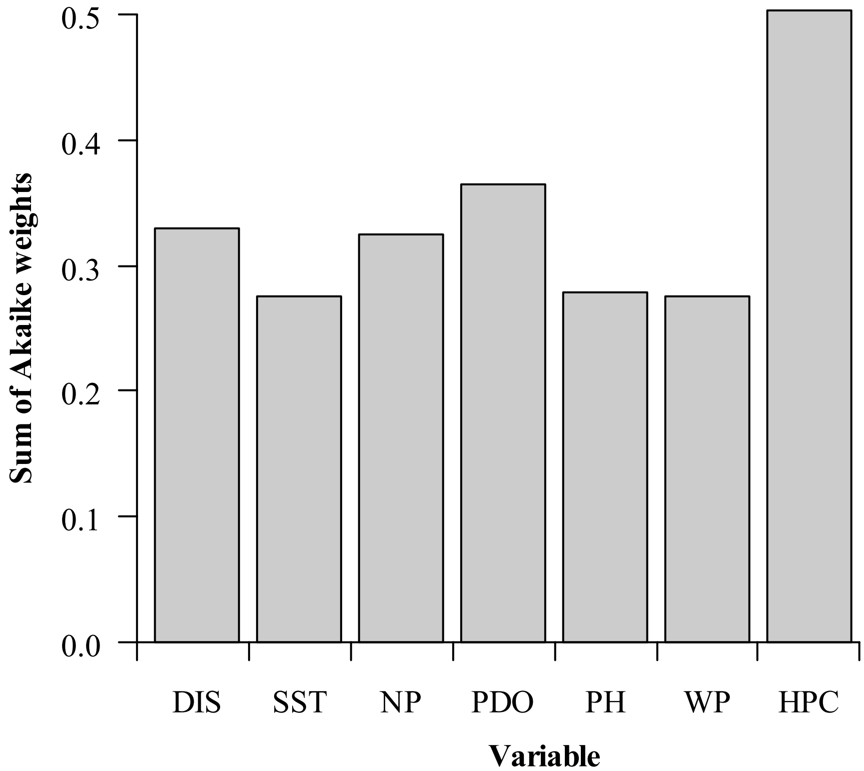

Figure 9.—Averages of the sum of Akaike weights for each covariate across all stocks for all models with a ΔAIC_C less than 10. DIS is April discharge, SST is summer sea surface temperature, NP is the North Pacific index, PDO is the Pacific decadal oscillation, PH is SEAK pink salmon harvest, WP is the wild pink salmon fry abundance index and HPC is the hatchery pink and chum salmon fry abundance index.

Cross Validation

Based upon cross validation, predictions using the best models appeared to have fairly large standard deviations (Table 6). The lowest standard deviation, in units of percent survival, was for the Herring Cove stock at 3.12 and the largest was 5.97 for the Kasnyku Bay stock.

Table 6.—Summary of the standard deviations of the marine survival time series, the standard deviations of the residuals from the best fit regression models, and the prediction standard deviations for the best models of each coho salmon stock calculated from cross validation.

Stock	**Data Mean**	**Data SD**	**Residual SD**	**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	2.96	3.12
Hugh Smith Lake	12.50	4.62	3.60	4.42
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

Mixed Effects Models

The results of the model selection for the mixed effects models suggest that hatchery pink and chum salmon releases have a moderate effect on coho salmon marine survival throughout SEAK (Figure 10). The most parsimonious model included both survival terms but only the random HPC effect besting the model with only a fixed HPC effect and the model where both the fixed and random HPC effects were removed. The model with only the random HPC effect had about the same AIC_C score as the full model, showing the lack of support for the fixed HPC effect (Table 7). 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.

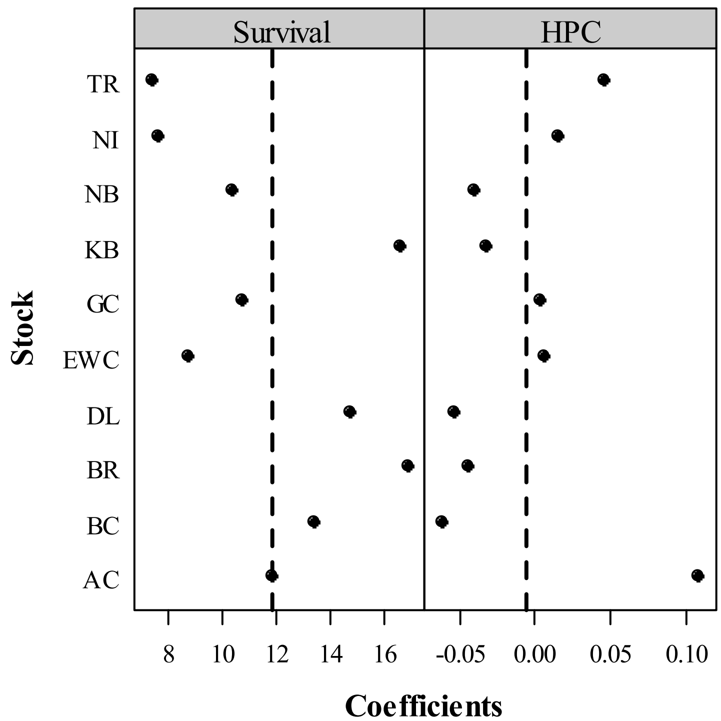

Figure 10.— Variation of random effects coefficients around the mean survival effect and the mean hatchery pink and chum (HPC) index effect. AC: Auke Creek, BC: Bear Cove, BR: Berners River, DL: Deer Lake, EWC: Earl West Cove, GC: Gastineau Channel, KB: Kasnyku Bay, NB: Neets Bay, NI: Nakat Inlet, TR: Taku River.

Table 7.— Summary of mixed effects model selection results for 4 candidate models. AC included represents the models that included all 10 coho salmon stocks while the AC excluded represents the models that included 9 of the coho salmon stocks.

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

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 quantify the apparent influence of the HPC index on Auke Creek marine survival, predictions were made with the most parsimonious model for average high and average low HPC index abundances for the stock group containing Auke Creek. The average low and high values were calculated by sorting the HPC index corresponding to Auke Creek by size and averaging the lower and upper halves of the data set. The average low and high values for the HPC index were 39 million fry and 104 million fry, corresponding to estimated marine survival rates of 16% and 23% respectively.

To further test the significance of Auke Creek on the analysis this stock was removed from the model and the analysis was repeated. Deleting the Auke Creek stock only moderately influenced the results; like the 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 while the estimated HPC effect is stronger for Auke Creek than the other stocks, it is not large enough to significantly influence the results of the analysis.

Discussion

The overall goal of my 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 and chum salmon have a larger estimated effect on marine survival than wild pink salmon abundances, and the magnitude and sign of the effect varies 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 the marine life phase. One notable exception to the overall covariation pattern is the Ford Arm Lake stock. Unlike other stocks, the juvenile coho salmon for this stock are enumerated in freshwater as pre-smolts; variability in the freshwater phase may lead to the lack of covariation of this stock with others in SEAK.

Regional concordance of survival rates parallels other research that has shown broad scale similarities in coho salmon marine survival rates. These analyses have shown that SEAK marine survival rates often cluster with a broader region that extends as far south as Vancouver Island but is distinct from more southern stocks in Washington, Oregon, and California (Coronado and Hilborn 1998; Hobday and Boehlert 2001). Other research has also identified important regional covariation patterns in salmon marine survival at scales on the order of 100 to 1000 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. Stock specific factors that might influence marine survival in SEAK include initial marine conditions, early marine growth, and predator distributions. Due to the complex geography of the SEAK inside waters, these conditions may not be homogenous throughout the region.

Hatchery releases of pink and chum salmon appeared more important in explaining marine survival than did the abundance of wild pink salmon fry. There doesn’t appear to be a consistent regional effect of the hatchery releases of pink and chum salmon; for some stocks, however, the local effect seems of major importance. For example, the HPC index is significantly related to the Taku River stock, but not to the Gastineau Channel stock (Table 2; Figure 8), both of which are in geographic proximity with the Auke Creek stock, which had the strongest relationship with the HPC index.

Mortality during the early marine life phase is thought to primarily occur from size selective predation (Foerster 1954; Holtby et al. 1990; Henderson and Cass 1991; Willette et al. 2001; Moss et al. 2005; Quinn et al. 2005) and coho salmon are known predators of pink and chum salmon (Hargreaves and LeBrasseur 1985; Hargreaves and LeBrasseur 1986). Juvenile coho salmon have also been found to prey on juvenile salmon as large as 46% of their own length (Pearsons and Fritts 1999). Therefore, hatchery pink and chum salmon could serve as an abundant food source for juvenile coho salmon, allowing for faster growth and reduced size selective predation. However, juvenile coho salmon have been found to selectively take pink salmon over chum salmon (Hargreaves and LeBrasseur 1985). Since the hatchery releases in SEAK have been dominated by chum salmon since 1980 (Figure 2) it weakens the idea that the hatchery releases are acting as a prey resource for juvenile coho salmon in SEAK. Additionally, there is not a strong relationship between early marine growth of Auke Creek coho salmon and marine survival (Briscoe 2004; Robins 2006), again weakening the idea that hatchery releases increase the growth rates of coho salmon in SEAK.

As an alternative explanation for the positive relationships between marine survival and hatchery releases, it has been proposed that the abundant pink 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 Pearcy 1988), and pink salmon in Prince William Sound (Willette et al. 2001). Predation buffering seems to be the best explanation for the strong positive effects that the HPC index had on marine survival rates of a few of the stocks in this study.

The explanation for the lack of regional concordance in response to the hatchery releases may again be the complexity of the SEAK inside waters. Coho salmon located on the inside of SEAK are required to migrate through corridors that are comprised of narrow strait habitat in order to reach the Gulf of Alaska (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). These narrow migration corridors may, however, 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 two biological indices of early marine pink salmon abundance differed in their estimated effects. The weak positive correlations between SEAK pink salmon harvest and marine survival corresponds with previous findings that SEAK coho salmon harvests are positively related to regional pink salmon harvests (Shaul et al. 2007; LaCroix et al. in press), but are not an important factor in explaining the variability in marine survival (Briscoe et al. 2005). The strong relationships between coho and pink salmon harvest supports the idea that region wide processes are influencing salmon in the marine phase and the influences may be similar across species. A possible explanation for the apparent strong relationship between coho and pink salmon harvest but the weak relationship between coho salmon marine survival and pink salmon harvest may be linked with the scales of the response variable. Coho salmon commercial harvest is an aggregate measure of coho salmon production throughout all of SEAK, which fails to include local stock specific variation into the relationship. The individual stock data used in this study does incorporate local variability in the marine phase which may be the reason that only weak relationships were found between marine survival and the aggregate commercial harvest of pink salmon throughout SEAK.

The negative relationships between marine survival and the WP index, a surrogate for the local abundance of pink salmon fry, is in contradiction to the positive relationship between pink salmon harvest and marine survival, and seems to contradict the hypothesis that pink and chum salmon may reduce predation on coho salmon by serving as alternative prey for coho salmon predators. 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.

Out of the two ocean basin scale indices the PDO showed a stronger estimated effect on marine survival than the NP index. Both of these indices showed consistent relationships with marine survival; the NP index was consistent over all 14 stocks while the PDO was consistent over 13 stocks (Table 3). This is not surprising because of the large geographic scale that these covariates encompass. However, the direction of the relationships between marine survival and both of these indices contradicted my initial thinking and previous research (Mantua et al. 1997; Hare et al. 1999; Mueter et al. 2002a; LaCroix et al. in press). A large component of the previous research focused on pink, chum, and sockeye salmon, all of which exhibit much different marine distributions in SEAK than coho salmon, which might explain the apparent reversal of the relationship between these indices and survival (Jaenicke and Celewycz 1994). The greater apparent effect of the PDO over the NP index (from the regression analysis) should be viewed with caution. Both of these variables were correlated with each other, which may make it difficult to distinguish the effects of one variable from the other.

Two regional scale physical variables (SST and discharge) had similar relative importances to those 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; Mueter et al. 2002b; Pyper et al. 2005). However, the other research investigated survival over much larger geographic ranges than this study and since there was strong covariation among the stocks in this study, it may explain why there is not a clear distinction between the regional scale variables and the ocean basin scale variables. Additionally, the other research focused on pink, chum, and sockeye salmon all of which have different life history patterns than coho salmon (Quinn 2005).

Both of the regional scale physical variables related negatively, on average, to marine survival. This was surprising because my initial thinking was that warmer SST would lead to faster growth while increased discharge would lead to higher food availability, both allowing for increased survival. The negative relationships also contradict previous studies that have demonstrated positive correlations of SST (Mortensen et al. 2000; Mueter et al. 2002a) and discharge with marine survival (Mueter et al. 2005).

These discrepancies may arise due to a number of factors. Both of these variables might act as proxies for other indirect effects on survival, which may act differently on coho salmon in SEAK than they do on stocks previously investigated. Also, the assumption that SST, averaged from a box off the outer coast of SEAK, is a good representation of SST throughout SEAK may not be valid. The unexpected effect of discharge might 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, misrepresenting the actual conditions experienced by coho salmon smolts.

In sum, these results suggest that marine survival in SEAK is influenced by a host of biological and environmental variables that are acting on 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 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 small number of coho salmon stocks analyzed.

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 and chum salmon releases. Similarly, ocean basin scale variables, like the NP index and the PDO, appear to have about the same importance as regional scale physical variables such as SST and freshwater discharge. Research investigating 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.

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Appendix: Marine Survival Calculations

The marine survival rates for all of the coho salmon stocks were calculated using the formula,

$$S = \frac{N_R}{N_S},$$

where S is the estimated survival rate, N_R is the number of returning salmon, and N_S is the number of emigrants. The N_R component of the estimate was calculated using,

$$N_R = H + E,$$

where H is the number of salmon in the harvest and E is the number of salmon in the escapement. The H component of the estimator is typically calculated from a sample taken from the fishery catch and examined for coded wire tags. The formulas given by Bernard and Clark (1996) are then used to estimate the commercial and recreational harvests and the associated variances for both wild and hatchery stocks. The estimation of the commercial harvest is the largest contributor to the uncertainty in the marine survival estimates for the hatchery stocks, while it is only one of many sources of uncertainty associated with the wild stock survival estimates.

The escapement component of the N_R term is typically assumed known for the hatcheries. For the wild stocks, a mark-recapture experiment is usually performed in order to estimate E. The estimation of E contributes a large component to the overall uncertainty in the marine survival estimates and is not equal for all the wild stocks. For example, the Taku River is a large river that also has in river subsistence harvest, which makes the estimation procedure more difficult than for the Auke Creek stock, which has a permanent weir in the lower reach of the creek and no in river harvest.

The N_S component of the survival calculation differs between the hatchery and wild stocks. Southeast Alaska hatcheries have a count of smolts released while smolt abundance has to be estimated for the wild stocks. The wild stock juvenile emigration is usually determined from performing a mark-recapture experiment and is calculated using the Chapman modification to the Petersen estimator,

$$\hat{N}_S = \frac{(M+1)(C+1)}{R+1} - 1,$$

where M is the number of marked fish, C is the number of fish caught in the second sampling period and R is the number of marks recovered in the second sampling period (Seber 2002). The variance associated with this estimate is,

$$\text{var} = \frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}.$$

Some of the wild stocks require a slight modification of these equations depending on the sampling protocol to ensure that assumptions are not violated (Tydingco 2005). For a detailed example of the marine survival calculations and associated variances see Jones et al. (2006).