

Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*)

Kristen E. Ryding and John R. Skalski

Abstract: Washington State hatcheries have released coded wire tagged coho salmon (*Oncorhynchus kisutch*) since the early 1970s and have recorded data on the number and ages of adult returns. From these data, we isolated marine survival from release to age 2 using a multinomial model incorporating the multivariate structure of the age-at-return data. Only hatcheries on or near the coast were used in the analysis in order to isolate marine effects. Using models to explore linear and curvilinear relationships, early marine survival was regressed against environmental covariates of sea surface temperature (SST), coastal upwelling, and the date of spring transitions. With hatcheries serving as replicates, curvilinear relationships were found between survival and both June SST and the date of spring transition. Maximum survival occurred for a June SST of 13.45°C and for a spring transition date around April 2. The regression results support the idea of optimal environmental conditions for coho salmon survival and may help fisheries managers better understand the dynamics of early marine survival of salmonids.

Résumé : Les piscicultures de l'État du Washington libèrent des saumons cohos (*Oncorhynchus kisutch*) marqués par fils codés depuis le début des années 1970 et elles ont recueilli des données sur le nombre et l'âge des adultes qui sont revenus aux installations. Nous avons déterminé, à partir de ces données, le taux de survie en mer, entre le moment de la mise à l'eau et l'âge 2, en utilisant un modèle multinomial tenant compte de la structure multivariée des données sur l'âge au moment du retour. L'analyse n'a porté que sur les piscicultures situées sur la côte ou à proximité de celle-ci afin d'isoler les effets liés à la mer. Des modèles permettant d'examiner les relations linéaires et non linéaires ont été utilisés pour effectuer une régression de la survie en mer peu de temps après l'arrivée des poissons en fonction des covariables environnementales que sont la température de la surface de la mer (TSM), les remontées côtières et la date des transitions de printemps. En utilisant les piscicultures comme témoins, des relations non linéaires ont été trouvées entre la survie et la TSM de juin et la date de transition de printemps. La survie maximale a été notée pour une TSM de juin de 13,45°C et pour une date de transition de printemps se situant aux environs du 2 avril. Les résultats de la régression appuient l'hypothèse de conditions environnementales optimales pour la survie du saumon coho et pourraient aider les gestionnaires des pêches à mieux comprendre la dynamique de la survie des salmonidés peu de temps après leur arrivée en mer.

[Traduit par la Rédaction]

Introduction

The success of salmon management practices is measured by the numbers of adult returns, and when adult returns are low, freshwater influences rather than marine influences often take much of the blame as the source for high mortality (Snake River Salmon Recovery Team 1993). But what if mortality in the marine environment is the major source for the variation in adult returns? For example, if survival in the ocean is on the order of 5%, a 1–2% change in survival will be reflected in a 20–40% change in adult returns. However, when in-river survival during smolt outmigration to the

ocean is of the order of 50%, a 1–2% change in freshwater survival will produce only a 2–4% change in adult returns. This is why small changes in ocean survival can be important to the fisheries resources and industries that rely on adult returns. It is becoming increasingly clear that understanding the relationship between the marine environment and salmon survival is central to better management of our salmonid resources.

The purpose of this paper is to introduce a multivariate approach to analyzing coded wire tagged (CWT) age-at-return data in order to regress first-year ocean survival probabilities against coastal ocean conditions and climate covariates. Survival probabilities, regression coefficients, and associated variances of the parameter estimates will be derived using maximum likelihood theory (Casella and Berger 1990). The methods will be illustrated using regional data from 15 coho salmon (*Oncorhynchus kisutch*) hatchery stocks in Washington State from 1970 to 1991. Meta-analysis (Eddy et al. 1992) will be subsequently used to make broad regional inferences regarding the effect of climate conditions on the interannual variability of marine survival of coastal coho stocks. The analysis of coho hatchery

Received October 15, 1998. Accepted July 10, 1999.
J14831

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data will illustrate the importance of basing inferences concerning ocean effects on regional tag return data and the need to examine nonlinear survival relationships when exploring climate conditions.

Numerous studies have found correlations between marine survival of Pacific Northwest salmon and other commercial fish and ocean conditions off the coast of Oregon, Washington, and the North Pacific. Positive correlations have been found between cumulative upwelling and salmon survival (Gunsolus 1978; Scarnecchia 1981; Nickelson and Lichatowich 1984; Nickelson 1986) and cumulative upwelling and salmon growth rates (Fisher and Percy 1988; Holtby et al. 1990). Fewer studies have pointed to a relationship between sea surface temperature (SST) and smolt survival. Negative correlations between coastal SST and smolt survival in the year of migration for both coho and chinook salmon (*Oncorhynchus tshawytscha*) have been reported (Nickelson 1986; Holtby and Scrivner 1989; Hyun 1996). Holtby and Scrivener (1989) also noted lower smolt survival during years of higher temperatures and low salinity and suggested that variability in smolt survival was associated with variations in SST during the first few months of ocean residence. Nickelson (1986) reported that in years of strong upwelling conditions, smolt survival was negatively correlated with June SST in the year of smolt outmigration. Additionally, McFarlane and Beamish (1992) found an increase in year-class abundance of sablefish (*Anoplopoma fimbria*) after extended periods of below-average SST off the coast of Vancouver Island.

Many studies of the past decade have also focused on the concepts of decadal-scale fluctuations in climate conditions in the North Pacific Ocean and the subsequent effect on marine ecosystems. Of particular relevance to the time period of this study is the abrupt shift in oceanic conditions that occurred in the winter of 1976–1977 (Beamish 1993; Beamish and Bouillon 1993; Francis and Hare 1994; Trenberth and Hurrell 1994). The “shift” was marked by a rise in SST along the North American coast and a deepening and eastward movement in the center of the Aleutian Low pressure system, affecting wind-driven currents. Ocean conditions occurring after 1977 are thought to be unfavorable for the survival of Pacific Northwest salmon (Francis et al. 1998). Nevertheless, considerable variability in the return rates of salmonids appears to exist within these regimes. The purpose of this paper is to describe those factors that may be responsible for these short-term interannual changes in early coho survival.

The analysis in this paper differs from previous studies in two ways. First, the historical approaches to regression used in analyzing CWT data (Gunsolus 1978; Scarnecchia 1981; McCarl and Rettig 1983; Nickelson and Lichatowich 1984; Nickelson 1986) have been to collapse the multidimensional return data into one-dimensional estimates of total returns or recovery proportions. However, return data of adult salmonids are multivariate in nature, with one cohort having adult returns over several age-classes. Ignoring the multivariate nature of the data risks losing information. Second, the relationships between survival and ocean conditions have been generally assumed to be linear (Gunsolus 1978; Scarnecchia 1981; Nickelson and Lichatowich 1984; Nickelson 1986; Fisher and Percy 1988; Holtby et al. 1990; Hyun 1996). In contrast, this paper will examine the

multivariate structure of the age-at-return data using multivariate and quadratic regression techniques to more accurately describe the survival relationships.

Materials and methods

Study area

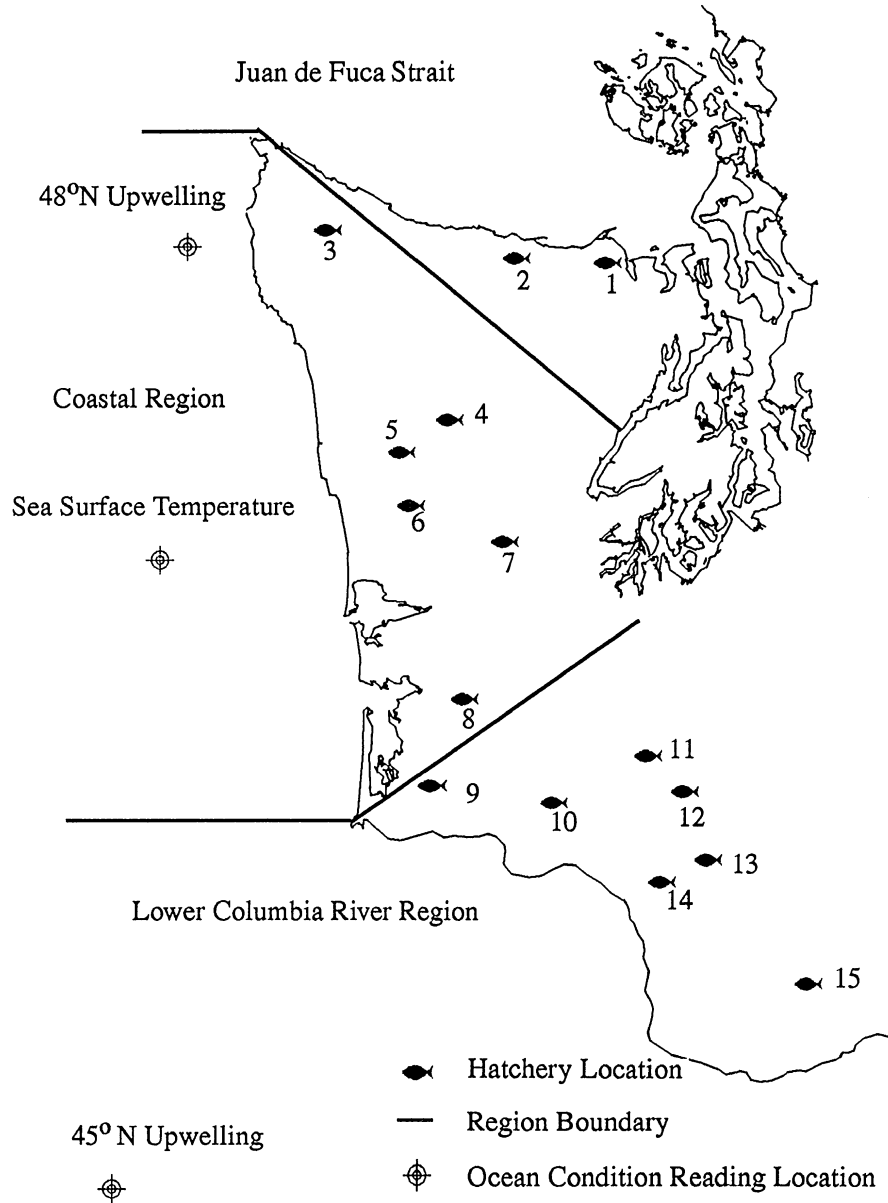
The study area (Fig. 1) incorporated 15 Washington State hatcheries located in the Juan de Fuca Strait, coastal Washington, and on the Columbia River below Bonneville Dam (river kilometre 234). Hatchery fish with outmigration routes free of dams were chosen for the analysis in order to minimize the confounding effects of hydroelectric production. Puget Sound hatcheries were left out of the analysis because fish from these hatcheries appear to have different migration patterns (Percy and Fisher 1988). The hatcheries were divided into three geographic regions determined by location of ocean entry. The Juan de Fuca Strait region included two hatcheries with outmigrants passing through the Strait. The coastal region included hatcheries located on rivers with outmigration routes leading directly to the ocean. Hatcheries located in the Lower Columbia River region had outmigration routes passing through the mouth of the Columbia River (Fig. 1; Table 1). Each hatchery served as a replicate in the analysis, and inferences were made both by region and across all hatcheries. The specific brood years from each hatchery used in the analysis are summarized in Table 1.

Data

Data used to calculate survival estimates were CWT release numbers and adult recovery numbers of coho salmon obtained from the Regional Mark Processing Center (1993), managed by the Pacific States Marine Fisheries Commission. The CWT data for hatchery fish were chosen for the analysis because more accurate recovery information was available from hatchery sources than from wild stocks. The specific CWT release data used in the analysis included the tag (batch) numbers, release numbers per batch, the hatchery where the releases occurred, date of release, and brood year of the fish. CWT recovery data include the year of recovery, the batch number, and the total number of expanded recoveries for a particular batch from the commercial fishery and hatcheries. The analysis encompassed the brood years from 1970 to 1991, although no one hatchery included all years (Table 1). The CWT release and return data for each hatchery are given in Ryding (1998) and are available upon request.

The ocean conditions that were used as covariates in the analysis included (i) SST, (ii) coastal upwelling conditions, and (iii) the date of spring transition (Table 2). The two measures of SST used in the analysis were the (a) average June SST and (b) the summer SST. Ryding (1998) also looked at the North Pacific index (NPI) (Trenberth and Hurrell 1994) and the Pacific Northwest index (Ebbesmeyer and Strickland 1995), but found no convincing relationships with early ocean survival of coho. The summer SST was calculated as the average of the monthly averages of SST from May to September. Measurements of SST were taken from observations made off the coast of Washington State. Upwelling conditions used in the analysis were monthly averages measured on the Bakun index, taken at 45°N latitude and 48°N latitude (both at 125°W longitude). The units in the Bakun index are in metric tons·s⁻¹·100 mi of coastline⁻¹ (Bakun 1973). The upwelling covariate was calculated as the total of the monthly averages from March through September. The spring transition was defined as the approximate calendar date when coastal upwelling replaces the downwelling conditions of winter. The specific date was calculated for the coastal waters near the mouth of the Columbia River from data on changes in wind patterns off the coast of Washington and Oregon (Ingraham and Miyihara 1988).

Fig. 1. Locations of hatcheries used in the CWT analysis and the regions in which they occur. The locations of upwelling and SST measurements are also shown. Numbers correspond to the hatchery names listed in Table 1.



Statistical methods

A multinomial survival model incorporating marine survival probabilities to age-at-return was developed to take advantage of the multivariate age-at-return data of the CWT returns. The expected number of fish at any age recovered in the fishery or at the hatchery can be expressed as

$$(1) \quad E(O_{ij}) = R_i P_{ij} \left(\prod_{n=2}^j S_{in} \right) M_{ij}$$

for fishery recoveries and

$$(2) \quad E(H_{ij}) = R_i (1 - P_{ij}) \left(\prod_{n=2}^j S_{in} \right) M_{ij}$$

for hatchery returns, where R_i is the total number of CWT marked smolts released from a hatchery for the i th brood year ($i = 1, 2, \dots, n$), O_{ij} is the number of CWT-marked fish recovered in the fishery of the i th brood year ($i = 1, 2, \dots, n$) of the j th age-class ($j = 2, 3, 4$), H_{ij} is the number of CWT-marked fish recovered at the hatchery of the i th brood year ($i = 1, 2, \dots, n$) of the j th age-class ($j = 2, 3, 4$), S_{ij} is the probability of a fish from the i th brood year ($i = 1, 2, \dots, n$) surviving to the j th age-class given survival to age-class $j - 1$ ($j = 2, 3, 4$), P_{ij} is the probability of being caught in the fishery for the i th brood year ($i = 1, 2, \dots, n$) at the j th age-class ($j = 2, 3, 4$), M_{ij} is the probability of maturing at the j th age-class ($j = 2, 3, 4$) for the i th brood year ($i = 1, 2, \dots, n$), and $t_{ij} = H_{ij} + O_{ij}$ is the number of expanded recoveries of CWT-tagged fish from both the fishery and hatchery of the i th brood year ($i = 1, 2, \dots, n$) in the j th age-class ($j = 2, 3, 4$).

The expected number of j -year fish recovered from the fishery and hatchery (total recoveries) is then

Table 1. Location and available brood years of data for the 15 Washington State hatcheries used in the CWT analysis.

Region	Hatchery*	Brood years	Years of data
Juan de Fuca Strait	Dungeness Hatchery (1)	1970–1972, 1975–1980, 1983, 1986, 1989, 1991	13
	Lower Elwha Hatchery (2)	1978–1982, 1985–1989, 1991	11
Coastal	Soleduck Hatchery (3)	1971, 1972, 1974–1976, 1980–1988, 1990, 1991	16
	Quinalt Lake Hatchery (4)	1977–1986, 1988–1991	14
	Quinalt National Fish Hatchery (5)	1973–1991	19
	Humtulpis Hatchery (6)	1980, 1982–1991	11
	Bingham Creek (Simpson) Hatchery (7)	1971–1975, 1980–1991	17
	Willapa Hatchery (8)	1971, 1974, 1980–1986	9
Lower Columbia	Grays River Hatchery (9)	1974–1985, 1988–1991	16
	Elochomin Hatchery (10)	1972, 1974, 1983–1985, 1988–1990	8
	Cowlitz Hatchery (11)	1972, 1980–1991	13
	Toutle Hatchery (12)	1972, 1977, 1978, 1986–1991	9
	Kalama Creek Hatchery (13)	1977, 1985–1989, 1991	7
	Kalama Falls Hatchery (14)	1983–1985, 1988–1991	7
	Washougal Hatchery (15)	1974, 1977–1982, 1988–1991	11

*Number corresponds to locations in Fig. 1.

$$(3) \quad E(H_{ij} + O_{ij}) = E(t_{ij}) = R_i P_{ij} \left(\prod_{n=2}^j S_{in} \right) M_{ij} + R_i (1 - P_{ij}) \left(\prod_{n=2}^j S_{in} \right) M_{ij}$$

$$E(t_{ij}) = R_i P_{ij} \left(\prod_{n=2}^j S_{in} \right) M_{ij} - R_i P_{ij} \left(\prod_{n=2}^j S_{in} \right) M_{ij} + R_i \left(\prod_{n=2}^j S_{in} \right) M_{ij}$$

$$E(t_{ij}) = R_i \left(\prod_{n=2}^j S_{in} \right) M_{ij}$$

The parameter M_{ij} may also be thought of as the probability that the fish will be of a certain size or type (i.e., jack or adult) so as to be seen in either the fishery or the hatchery. The important aspect of eq. 3 is that by combining recoveries from both the fishery and hatchery, calculations of fishing effort become unnecessary.

The multinomial model uses the probabilities of recovery at 2, 3, and 4 years of age as the cell probabilities. The observations were the number of adults of each age-class estimated to have returned using tag recoveries from both the fishery and hatchery (i.e., t_{i2} , t_{i3} , and t_{i4}). The regression of survival from release to age 2 (i.e., about 1.5 years of age) for a cohort against covariate values of ocean conditions in the year of outmigration (early ocean residence) was based on a proportional hazards (PH) model (McCullagh and Nelder 1989), given by

$$(4) \quad S_2 = S_0 e^{x\beta}$$

where S_0 is the baseline survival, x is the vector of the covariates of interest, and β is the vector of regression coefficients.

The PH model was chosen because of its flexibility and the ease of parameter interpretation. Positive values of the regression coefficient β indicate a negative association of survival with the covariate, and negative coefficients indicate positive relationships

between survival and the covariate. Substituting the PH model for survival to age 2 (i.e., eq. 4), θ_1 for the probability of surviving to and maturing at age 3 given survival to age 2 (i.e., $\theta_1 = S_3 M_3$), and θ_2 for the probability of surviving and maturing to age 4 given survival to age 2 (i.e., $\theta_2 = S_3 S_4 M_4$) yields the following likelihood model:

$$(5) \quad L(S_0, \beta, M_2, \theta_1, \theta_2 | R_i, t_{i2}, t_{i3}, t_{i4}, x_i) = \prod_{i=1}^n \left(\frac{R_i}{\prod_{j=2}^4 t_{ij}} \right) (S_0 e^{x\beta} M_2)^{t_{i2}} (S_0 e^{x\beta} \theta_1)^{t_{i3}} \times (S_0 e^{x\beta} \theta_2)^{t_{i4}} (1 - S_0 e^{x\beta} (M_2 + \theta_1 + \theta_2))^{R_i - \sum_{j=2}^4 t_{ij}}$$

The model parameters S_0 , β , θ_1 , and θ_2 were estimated using maximum likelihood methods (Casella and Berger 1990, pp. 289–297). Numerical optimization, using FLETCH (Fletcher 1970), iteratively solved for the maximum likelihood estimates and provided asymptotic variance estimates.

The stochastic CWT model used several assumptions about the tag data that are standard to mark–recapture data analysis. The tag groups were assumed to be representative of the population of inference, and all tagged fish had an equal probability of surviving and migrating back to the hatchery in a particular year. In addition, release numbers of tagged smolts were assumed to be known without error, and recovered fish were correctly identified to batch, brood year, and age-at-recovery. Fish caught in the fishery were assumed to be a random sample of the fish migrating in that year (i.e., no bias toward tagged fish in the fishery). The fish inspected for tags in the fishery were also assumed to be representative of all fish in the fishery and the fraction of fish sampled was known without error. In addition, the model also assumed that the release groups were closed to emigration and immigration and the number of tagged hatchery fish straying to the spawning grounds, an area where tags are less likely to be detected, was negligible. Also, the parameter M_{ij} was assumed constant across all brood years (i.e., $M_{ij} = M_j \forall j$) for a stock from the same hatchery.

The four parameters (i.e., S_0 , M_2 , θ_1 , and θ_2) plus one regression coefficient (β) for each of the covariates in the PH model were estimated independently for each of the 15 hatcheries. Each estima-

Table 2. Covariate values used in the regression analysis.

Observation year	Brood year	June SST (°C)	Summer average SST (°C)	45°N June upwelling (Bakun units)	48°N upwelling (Bakun units)	Spring transition date (calendar day)
1972	1970	13.13	12.716	55	51	103.103
1973	1971	12.72	13.768	27	122	74.192
1974	1972	12.67	13.590	80	76	102.707
1975	1973	11.84	12.964	98	156	73.967
1976	1974	12.66	13.414	56	25	84.664
1977	1975	12.63	13.190	71	125	71.799
1978	1976	14.84	13.704	34	83	85.182
1979	1977	12.78	14.296	86	173	74.417
1980	1978	12.90	13.720	32	197	109.416
1981	1979	13.86	14.162	8	94	94.603
1982	1980	11.98	13.284	59	213	83.305
1983	1981	14.51	14.596	19	67	95.214
1984	1982	12.20	13.550	37	88	107.567
1985	1983	12.84	13.702	52	197	70.756
1986	1984	14.22	13.966	25	132	94.796
1987	1985	12.99	13.922	43	133	101.224
1988	1986	13.78	13.808	14	119	88.555
1989	1987	13.44	14.372	43	93	99.036
1990	1988	13.40	14.654	15	113	83.043
1991	1989	12.87	13.754	59	112	71.920
1992	1990	14.57	14.420	61	152	69.205
1993	1991	14.89	14.280	24	11	130.761

ble parameter required one brood year's worth of data, or degree of freedom. For purposes of estimation, it was necessary to have more degrees of freedom than estimable parameters. A minimum of seven brood years of data were deemed necessary from a hatchery in order to estimate the parameters in a likelihood model with one covariate and have at least two degrees of freedom remaining. There were only 15 Washington State hatcheries out of 29 hatcheries releasing coho salmon from the Juan de Fuca Strait, coastal, and Lower Columbia River regions with an adequate amount of brood year data for an analysis with one covariate. Eight of the 15 hatcheries had 11 or fewer years of data, and most of these hatcheries were located in the Lower Columbia River region (Table 1). Models with more than two regression covariates would have excluded most of the hatcheries from the Lower Columbia River region. For this reason, no more than two covariates were modeled at a time.

Interannual variability in the CWT returns was high, so there was reason to believe that the variances derived from the multinomial likelihood model were underestimated. The variances obtained directly from the likelihood (eq. 5) were based only on multinomial sampling error and do not take into account the extra-likelihood variation resulting from changes in parameter values over time. Therefore, the estimated variances were multiplied by a scale parameter calculated from differences between the observed and expected CWT return numbers to account for some of the year-to-year variability not explained by the covariates. The scale parameter (SP) was calculated according to the expressions

$$(6) \quad SP = \frac{\sum_{i=1}^n \left(\frac{\sum_{j=i}^4 (\text{Observed}_{ij} - \text{Expected}_{ij})^2}{\text{Expected}_{ij}} \right)}{df}$$

$$(7) \quad df = 3(n - p)$$

where j is a cell from the multinomial likelihood, n is the number of brood years, p is the number of parameters estimated in the model, and df is the degrees of freedom.

If a covariate has an effect on the marine survival of juvenile coho, then the effect should be seen across the replicate hatcheries within a region. Therefore, the weighted mean for a regression coefficient (i.e., $\hat{\beta}_i$) was estimated to test the hypothesis $H_0: \bar{\beta} = 0$ versus $H_a: \bar{\beta} \neq 0$ at a significance level of $\alpha = 0.10$. The weighted mean was calculated according to the formula (Neter et al. 1996)

$$(8) \quad \hat{\bar{\beta}} = (X'WX)^{-1}X'W\hat{\beta}$$

where X was a vector of ones of length equal to the number of regression coefficients, W was a diagonal matrix of weights equal to the inverse of the variances of the coefficients, and $\hat{\beta}$ was the vector of the estimated regression coefficients. The variance estimate of $\hat{\bar{\beta}}$ was calculated according to the formula

$$(9) \quad \hat{V}ar(\hat{\bar{\beta}}) = \frac{\sum_{i=1}^n W_i(\hat{\beta}_i - \hat{\bar{\beta}})^2}{n-1} \frac{1}{n \sum_{i=1}^n W_i}$$

where n was now the number of regression coefficients averaged over. A weighted t test

$$(10) \quad t_{df} = \frac{\hat{\bar{\beta}} - 0}{\sqrt{\hat{V}ar(\hat{\bar{\beta}})}}$$

was performed to test the null hypothesis (i.e., $H_0: \bar{\beta} = 0$), where $df = n - 1$ degrees of freedom. A significant t test result was interpreted to mean that the effect of a covariate was consistent across hatcheries and correlated with survival from release to age 2.

Table 3. Correlation matrix for ocean covariates used in the survival analysis.

Covariate	June SST	Summer SST	45°N June upwelling	48°N cumulative upwelling	Spring transition date
June SST	1.0				
Summer SST	0.6061*	1.0			
45°N June upwelling	-0.5761*	-0.4943*	1.0		
48°N cumulative upwelling	-0.4022*	-0.0640	0.2718	1.0	
Spring transition date	0.2819	0.1001	-0.4079*	-0.4982*	1.0

*Significant at the $\alpha = 0.10$ level.

Results

Our first step in examining survival relationships over time was to test whether coho survival differed before and after the 1976–1977 regime shift hypothesized (Beamish 1993; Francis and Hare 1994). Most of the cohorts used in the study were released after the 1976–1977 regime shift took place. However, for the four hatcheries with enough brood years of releases before 1977, we found no significant differences in coho marine survival for the releases before or after 1977 ($p = 0.238$). Subsequently, we explored whether oceanographic variables may account for the interannual variation in adult returns observed in the CWT data.

Four covariates associated with ocean conditions were found to have a significant linear relationship with coho survival to age 2, based on the results of the meta-analysis using the weighted t test. Summer average temperature had a significant positive relationship with survival ($p = 0.034$), while June upwelling strength at 45°N was negatively correlated with survival ($p = 0.088$). Cumulative upwelling had only a marginally positive correlation with survival ($p = 0.108$). The date of spring transition showed a negative association with survival to age 2 ($p = 0.001$). Cumulative upwelling at 45°N, summer upwelling at 48°N, and summer upwelling at 45°N had no significant association with survival ($p > 0.10$).

Correlation between the environmental covariates, however, makes it difficult to determine which factors are driving the survival processes and which are spurious relationships (Table 3). Although the correlation between June SST and the date of spring transition was small ($r = 0.282$), there is nevertheless a functional relationship between these variables. An early spring transition would lead to lower June SST because there would be a longer period in which cooler water was brought to the surface layer than in years of a late spring transition. However, upwelling strength may be a more important factor in influencing SST than duration alone, as indicated by a strong negative correlation between June SST and both cumulative upwelling ($r = -0.402$) and June upwelling at 45°N ($r = -0.576$). Cumulative upwelling, which incorporates both upwelling strength and duration, also had a strong negative correlation with spring transition ($r = -0.499$).

The covariates were also analyzed using quadratic models based on the suggestion of Cury and Roy (1989) and Gargett (1997) that optimal ocean conditions for salmonid survival might exist. The four significant linear covariates and June SST were analyzed using a quadratic model for survival to

age 2. The mean of the quadratic term for the June SST in the survival model was nonsignificant when all hatcheries were taken into account (Table 4). However, plots of the survival curves for each region strongly suggest a curvilinear relationship (Fig. 2). When the quadratic terms from each of the regions were analyzed separately, the quadratic regression coefficient for the Juan de Fuca Strait was significantly negative ($p = 0.006$), for the coast was significantly positive ($p = 0.059$), and for the Lower Columbia River was also positive but nonsignificant. The hatcheries in the Juan de Fuca Strait showed a different June SST – survival relationship than found in the other two regions and in part explains why the overall effect was nonsignificant. The hatcheries from the coastal and Lower Columbia River regions all showed similar convex relationships between survival and June SST and have maximum survival probabilities in a narrow band in the middle of the temperature range (Fig. 2). The average maximum from the survivorship curves for the coastal and Lower Columbia River hatcheries was 13.45°C, with a maximum survival occurring in a range from 13.07 to 13.71°C across hatcheries.

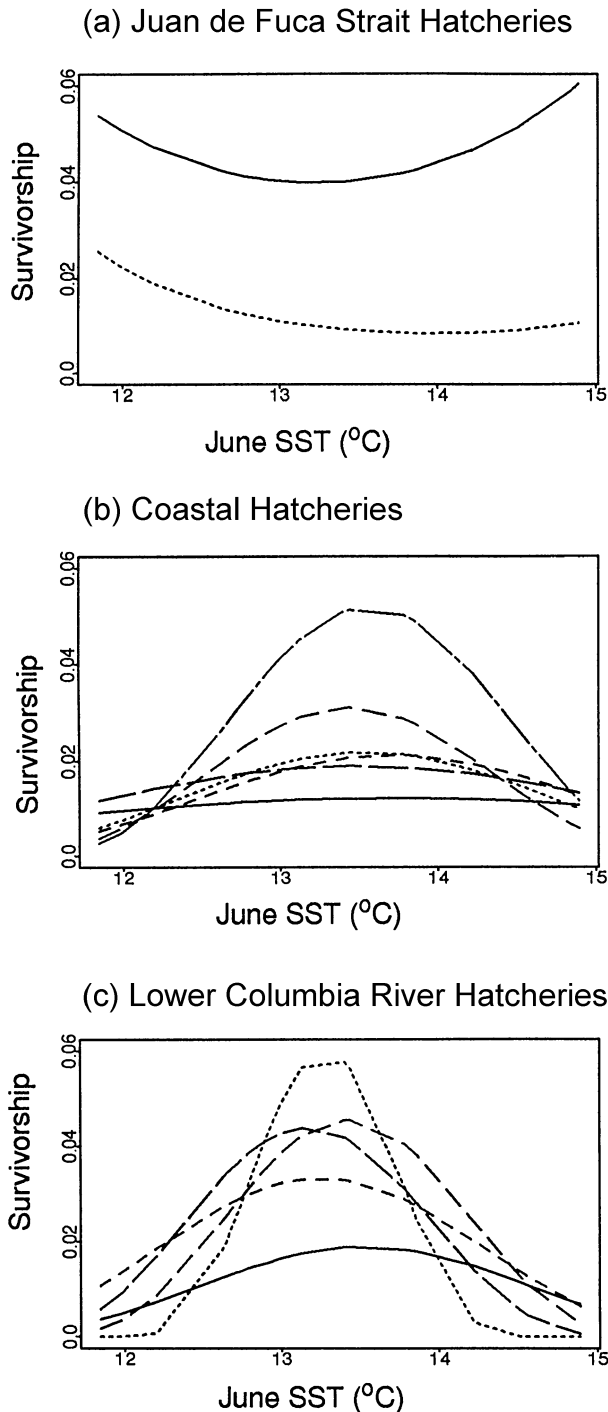
The quadratic relationship between spring transition and survivorship was highly significant ($p < 0.001$) (Table 5). This result is seen most clearly in the survivorship curves (Fig. 3). Only two hatcheries in the coastal region did not exhibit the same convex survivorship curves as the other hatcheries; however, they both did show a decrease in survivorship with an increase in spring transition date. The average maximum across all hatcheries was on day-of-the-year 91 (i.e., April 2). The coastal and Lower Columbia River hatcheries had the same average maximum on day-of-the-year 89 (i.e., March 31). Both June SST (Fig. 2) and spring transition (Fig. 3) had positive quadratic terms and as a result show similar convex survivorship curves.

The nonlinear relationship between cumulative upwelling at 48°N and survival to age 2 was also found to be significant ($p = 0.051$) (Table 6). Both the Juan de Fuca Strait and coastal regions had significant quadratic terms (Table 6), and the similarity between the regions is reflected in the survivorship curves (Fig. 4). However, the Lower Columbia River region shows less of a quadratic relationship overall (Fig. 4c) than the other two regions, and this is reflected in the nonsignificance of the quadratic term ($p = 0.295$).

Discussion

This analysis of ocean survival of coho salmon relies on three important aspects: a multivariate analysis of age-at-

Fig. 2. Fitted curves from the quadratic PH model for June SST versus survivorship for hatcheries in the (a) Juan de Fuca Strait, (b) coastal, and (c) Lower Columbia River regions. Each line represents a different hatchery used in the CWT analysis.



return data, examination of curvilinear relationships, and the use of replicate hatcheries in a meta-analysis of regional effects. The significance of each of these aspects is discussed below in detail, along with a discussion of the data and the assumptions of the statistical method.

Data quality and assumptions

As mentioned earlier, none of the hatcheries had CWT re-

Table 4. Average regression coefficients estimated from the CWT analysis of June SST for the linear and quadratic models for each region and overall.

Model	Linear model coefficient	Quadratic model	
		Linear term	Quadratic term
Juan de Fuca Strait hatcheries			
$\hat{\beta}$	-0.0191	0.0228	-0.0431
SE($\hat{\beta}$)	0.0900	0.0570	0.0004
<i>p</i> value	0.9560	0.7580	0.0060
Coastal hatcheries			
$\hat{\beta}$	-0.0180	-0.0488	0.0733
SE($\hat{\beta}$)	0.0062	0.0133	0.0300
<i>p</i> value	0.0770	0.0140	0.0590
Lower Columbia River hatcheries			
$\hat{\beta}$	0.1324	0.0189	0.1618
SE($\hat{\beta}$)	0.0599	0.0336	0.1178
<i>p</i> value	0.0690	0.6040	0.2420
Overall (across all hatcheries)			
$\hat{\beta}$	0.0982	-0.0003	0.1008*
SE($\hat{\beta}$)	0.0730	0.0226	0.0841
<i>p</i> value	0.2000	0.9910	0.2534*

*For June SST, the average of the quadratic terms across all hatcheries in the coastal and Lower Columbia River regions was significant.

lease and return data for all years between 1970 and 1991, leaving gaps in the time series. However, these data gaps should have had little effect on the analysis for two reasons. A time series analysis that is sensitive to missing observations was not performed. Instead, a regression analysis was performed between observations of first-year survival and predictor variables of ocean condition, where it is more important to cover the potential range of predictor values (Table 1) than it is to have consecutive observations. The focus was on the estimates of first-year survival that should be independent over time and not reliant upon consecutive years of cohort data.

Many of the assumptions in the analysis of mark-recapture data apply equally well to CWT data. Overestimation of tagged returns would over estimate survival estimates, and the underestimation of returns could underestimate survival estimates. Errors in sampling fractions, release numbers, and reporting rates could bias the survival estimates in either direction. Unfortunately, information to verify these numbers is generally unavailable. Tag loss rates for CWT data are not often estimated or are not estimated reliably. However, the numbers of observed recoveries are adjusted slightly upward to account for unreadable tags or tag loss during reading (Markey et al. 1991). The assumption that the population of CWT fish was closed to emigration seems reasonable because even if a fish did stray to another hatchery, it would be detected and recorded as a CWT return. The use of jacks as a metric of year-class success is consistent with the assumption that the parameter is constant across brood years.

Table 5. Average regression coefficients estimated from the CWT analysis of spring transition for the linear and quadratic models for each region and overall.

Model	Linear model coefficient	Quadratic model	
		Linear term	Quadratic term
Juan de Fuca Strait hatcheries			
$\hat{\beta}$	0.0008	-0.0243	0.0537
SE($\hat{\beta}$)	0.0018	0.0356	0.0010
<i>p</i> value	0.7540	0.6180	0.0120
Coastal hatcheries			
$\hat{\beta}$	0.0342	0.0053	0.0603
SE($\hat{\beta}$)	0.0091	0.0125	0.0122
<i>p</i> value	0.0130	0.6900	0.0040
Lower Columbia River hatcheries			
$\hat{\beta}$	0.0741	0.00228	0.0754
SE($\hat{\beta}$)	0.0133	0.0315	0.0054
<i>p</i> value	0.0010	0.7240	<0.001
Overall (across all hatcheries)			
$\hat{\beta}$	0.0464	0.0066	0.0653
SE($\hat{\beta}$)	0.0109	0.0120	0.0054
<i>p</i> value	<0.001	0.5920	<0.001

Multinomial survival model

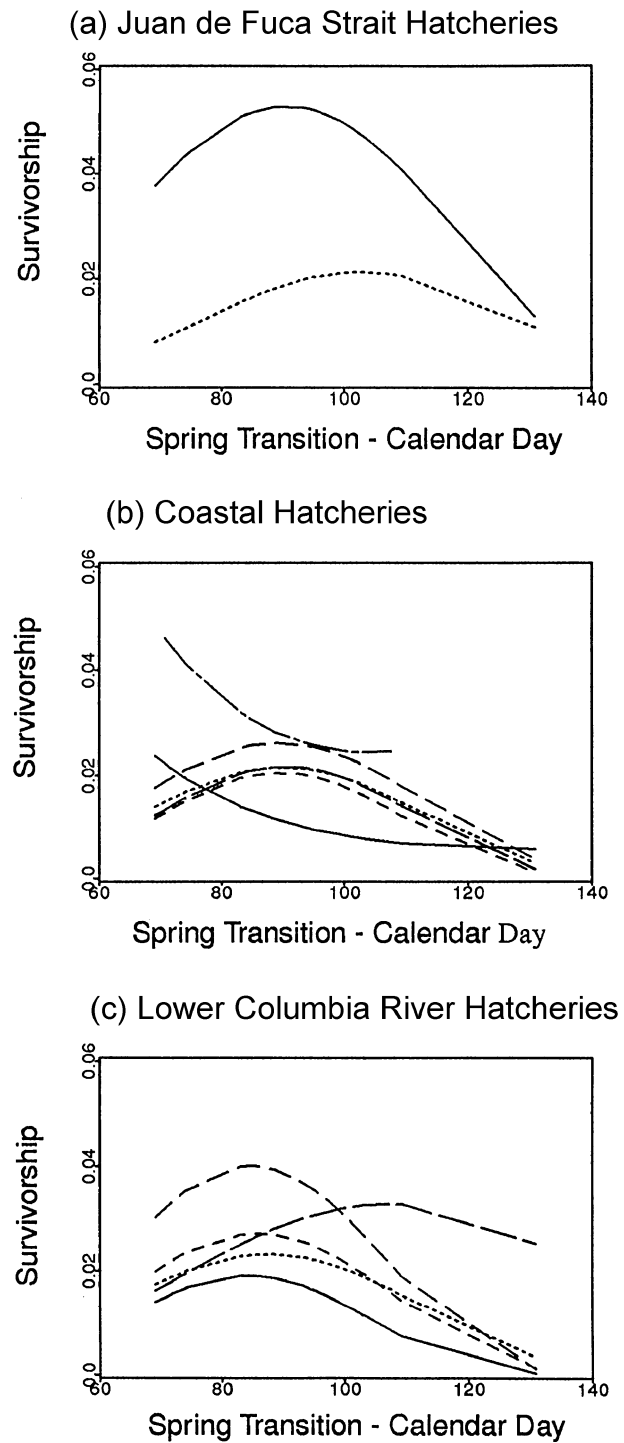
The multivariate data analysis provides a means to estimate first-year ocean survival concurrently with investigating survival relationships. All model parameters were estimated from the CWT data alone, using likelihood equations (eq. 5) and maximum likelihood methods. Estimates of model parameters based on auxiliary data were unnecessary. Furthermore, estimates of fishing effort were unnecessary in order to differentiate the effects of ocean survival from the effects of the salmonid fisheries. By using total returns from both the fisheries and hatchery escapement, the variability induced by fluctuations in fishing effort and success can be minimized. The age-structure information from the CWT returns also retains the underlying error structure of the original data. Analyses based on the proper error structure and response model should have greater power to identify survival relationships.

Curvilinear survival relationships

The quadratic relationships between the environmental covariates and age-2 survival are important results for two reasons. First, the similarities in response across most of the hatcheries strongly support the conclusion that curvilinear survival relationships exist. Second, this is the first time that quadratic survival relationships have been seen for a salmonid species. Simply looking at linear relationships can obscure or preclude the possibility of detecting important survival relationships.

Our analysis found three significant curvilinear relationships between environmental covariates and survival. In the

Fig. 3. Fitted curves from the quadratic PH model for spring transition data versus survivorship for hatcheries in the (a) Juan de Fuca Strait, (b) coastal, and (c) Lower Columbia River regions. Each line represents a different hatchery used in the CWT analysis.



survivorship curves for all three covariates, maximum survival was similar for each hatchery. For example, in the June SST survivorship curves, the maxima for all hatcheries in the coastal and Lower Columbia River regions occur between 13.07 and 13.71°C with a mean of 13.45°C (SE = 0.20°C). Survivorship curves show a consistent maximum

Table 6. Average regression coefficients estimated from the CWT analysis of cumulative upwelling at 48°N for the linear and quadratic models for each region and overall.

Model	Linear model coefficient	Quadratic model	
		Linear term	Quadratic term
Juan de Fuca Strait hatcheries			
$\hat{\beta}$	-0.0450	-2.6230	0.7830
SE($\hat{\beta}$)	0.0146	0.0032	0.0016
<i>p</i> value	0.2000	<0.001	0.001
Coastal hatcheries			
$\hat{\beta}$	-0.0798	-2.3136	0.6124
SE($\hat{\beta}$)	0.1039	0.3957	0.0156
<i>p</i> value	0.4770	0.0020	0.0040
Lower Columbia River hatcheries			
$\hat{\beta}$	-0.3344	-1.3166	0.1557
SE($\hat{\beta}$)	0.0614	0.5035	0.1295
<i>p</i> value	0.0020	0.0590	0.2950
Overall (across all hatcheries)			
$\hat{\beta}$	-0.1318	-1.7053	0.2572
SE($\hat{\beta}$)	0.0768	0.3805	0.1186
<i>p</i> value	0.1080	<0.001	0.0510

for survival at all hatcheries with a spring transition date around April 2 (SE = 7.25 days). The survivorship curves based on cumulative upwelling were somewhat more variable yet consistent in their interpretation. In all cases, survival of coho salmon to age 2 ranged from a low of less than 1% to a high of 6% under optimal conditions.

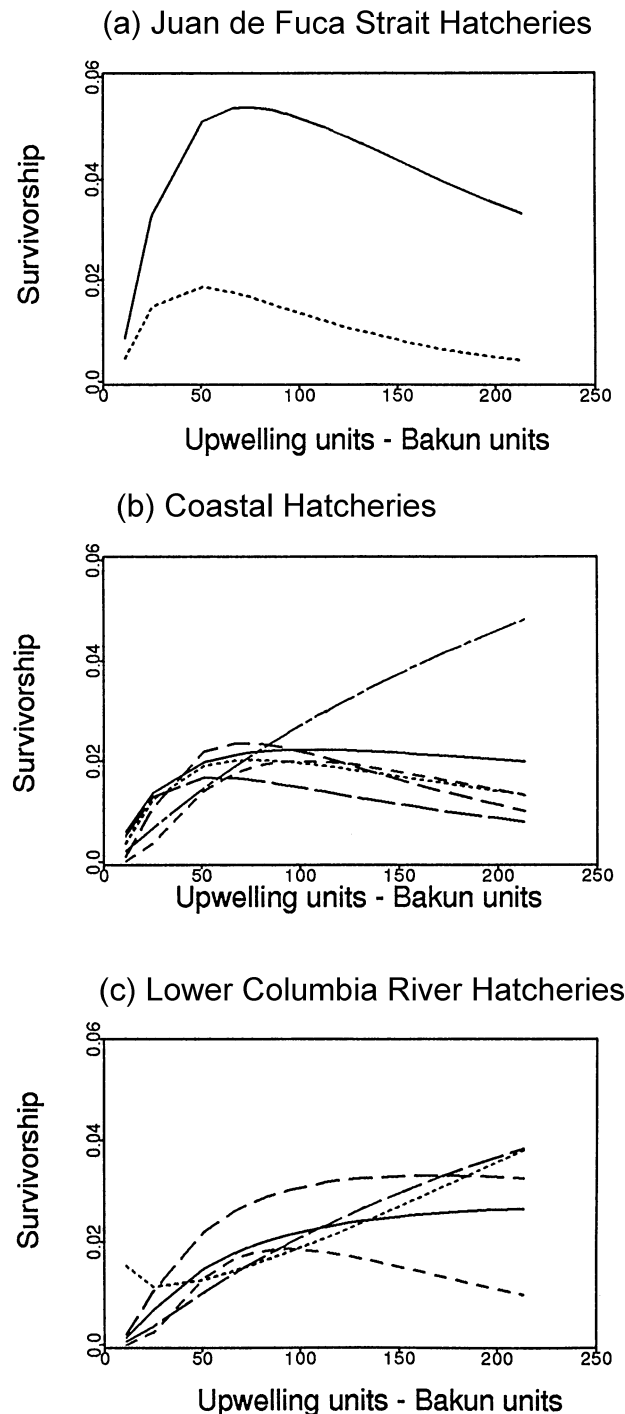
The results of the June SST, date of spring transition, and 48°N cumulative upwelling quadratic models seem to agree with the hypothesis for the existence of optimal environmental conditions put forth by Cury and Roy (1989) and Gargett (1997). Dome-shaped response curves are commonly found in ecology and population biology but until recently have not been widely found in fisheries literature (Sharp 1995). The important management implication is that regardless of hatchery practices, returns of salmonid adults may be governed by a narrow set of oceanographic conditions.

Possible survival mechanism

Both Cury and Roy (1989) and Gargett (1997) have suggested that optimal ocean conditions may exist for the survival of marine fish. They stated that these optimal conditions for survival are related to the water column stability of the ocean. However, these authors have differing opinions as to what environmental factors are responsible for the stability and mixing in the water column.

Using a yearly average of upwelling indices, Cury and Roy (1989) showed a "dome shaped" relationship between Pacific sardine (*Sardinops sagax caerulea*) recruitment and upwelling off the California coast, with upwelling units between 100 and 120 ($m^3 \cdot s \cdot 100 \text{ mi of coastline}^{-1}$) having the

Fig. 4. Fitted curves from the quadratic PH model for the cumulative upwelling at 48°N data versus survivorship for hatcheries in the (a) Juan de Fuca Strait, (b) coastal, and (c) Lower Columbia River regions. Each line represents a different hatchery used in the CWT analysis.



maximum recruitment. The reasoning behind the hypothesis has to do with the winds responsible for coastal upwelling. Upwelling indices are proportional to wind speed squared (Bakun 1973), with northerly alongshore winds inducing upwelling and bringing nutrients into the coastal upwelling region and enhancing primary production. However, when

wind speed becomes too high, mixing in the upper surface water layer starts to take place and begins to break up patches of phytoplankton (Demers et al. 1987). Cury and Roy (1989) suggested that turbulence as a result of high winds could limit recruitment in upwelling areas.

The quadratic relationship between June SST and survival that we found lends support to the upwelling hypothesis of Cury and Roy (1989). Eleven hatcheries from two regions all showed a maximum coho marine survival rate at a June SST of about 13.45°C (SE = 0.20°C). However, SST is affected by upwelling that brings cooler water into the surface layer (Knauss 1978). Increased upwelling reduces the effect of seasonal water warming and, as such, is negatively correlated with SST (Schwing and Mendelsohn 1997). On the other hand, higher June SST is indicative of weaker upwelling conditions because seasonal warming has taken place. Weaker upwelling conditions have a detrimental effect on primary production and subsequent food availability for young coho.

An additional hypothesis relating the effects of local winds on primary production was proposed by Huntsman and Barber (1977). They showed that sustained winds may negatively affect primary production and suggested that a relaxation in winds could slow the transport of nutrients offshore, allowing phytoplankton blooms to take place. Sustained higher wind speeds would increase the monthly average upwelling index, while months with more relaxation periods would tend to lower the monthly index. Whether the curvilinear relationships between upwelling and survival were due to the plankton patchiness or lack of phytoplankton blooms, the exact mechanism cannot be deduced without additional empirical data.

Gargett (1997) presented the idea of coastal water column stability being influenced by the strength of the winter Aleutian Low. In conditions of high water column stability, vertical movement of water that introduces nutrients into the upper layers of the water column is restricted, although light conditions remain optimal for phytoplankton production. When water column stability is low, nutrients are abundant, but the vertical movement of nutrients reduces the light levels required for phytoplankton growth. Gargett (1997) proposed the existence of conditions where upwelling is sufficient for nutrient input to the coastal waters and yet having enough stability to maintain light levels. The argument of Gargett (1997) for the existence of optimal conditions was used primarily to explain the variation in production between northern (Alaskan) and southern (to northern California) stocks of salmon.

In the water column stability hypothesis proposed by Gargett (1997), water column stability was driven by the strength of the Aleutian Low pressure system. Using the NPI (Trenberth and Hurrell 1994) as a measure of the strength of the Aleutian Low, a regression analysis between the NPI and hatchery data showed no relationship between the strength of the Aleutian Low pressure system and coho marine survival (Ryding 1998). Alternatively, Chelton et al. (1982) suggested that upwelling may be governed by variations in the California Current.

The relationship between spring transition and coho survival should also be emphasized. The significance of the date of spring transition implies that the conditions at ocean

entry dominate coho survival. In our analysis, optimum time for spring transition was calculated to be April 2 (SE = 7.25 days). This date would allow sufficient time for the establishment of smaller prey species to become abundant when smolts enter the ocean. The negative correlation between the other upwelling variables could indicate that spring transitions occurring earlier could be associated with stronger winds, which may hinder food production. Spring transitions occurring later in April may not allow enough time for the establishment of coho prey. Although water column stability is important, our data suggest that the timing of ocean entry by smolts relative to the date of spring transition may be a key factor affecting ocean survival.

Spatial replication

Replication and the ability to demonstrate reproducibility of effects is a cornerstone in statistical inference (Hurlbert 1984). In these analyses, hatcheries served as spatial replicates to assess reproducibility of observed survival relationships. Often, the analysis of CWT data from individual hatcheries resulted in statistically significant regression coefficients across brood years. However, when their relationships were assessed along with relationships estimated from other local hatcheries, no consistency could be found. The meta-analysis used in this study helped avoid spurious correlations that could have occurred from the analysis of return data from just one or a few hatcheries. The meta-analysis also helped identify regionally important factors that were consistently related to juvenile salmon survival. Demonstrating consistency of regression relationships across neighboring hatcheries is an important analytical technique in showing the reproducibility of results.

Acknowledgments

This study was funded by the Bonneville Power Administration, contract No. DE-BI79-87BP35885.

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