Transactions of the American Fisheries Society 134:1562–1581, 2005
© Copyright by the American Fisheries Society 2005
DOI: 10.1577/T05-037.1

[Article]

Effects of Environmental Conditions during Stream, Estuary, and Ocean Residency on Chinook Salmon Return Rates in the Skagit River, Washington

CORREIGH M. GREENE,* DAVID W. JENSEN, GEORGE R. PESS, AND E. ASHLEY STEEL

National Oceanic and Atmospheric Administration Fisheries, Northwest Fisheries Science Center, Division of Environmental Conservation, 2725 Montlake Boulevard East, Seattle, Washington 98112-2097, USA

ERIC BEAMER

Skagit System Cooperative, Post Office Box 368, La Conner, Washington 98257, USA

Abstract.—We predicted 22 years of return rates for wild Chinook salmon *Oncorhynchus tshawytscha* as a function of environmental conditions experienced during residency in freshwater, tidal delta, bay, and ocean habitats as well as as an indicator of density dependence (based on egg production) across life stages. The best predictors of return rate included the magnitude of floods experienced during incubation, a principal components factor describing environmental conditions during bay residency, a similar factor describing conditions experienced during the third ocean year, and an estimate of egg production. Our models explained up to 90% of the variation in return rate and had a very high forecasting precision, yet environmental conditions experienced during ocean residency explained only 5% of the variation. Our results suggest that returns of wild Chinook salmon can be predicted with high precision by incorporating habitat residency and that freshwater and nearshore environmental conditions strongly influence the survival of Skagit River Chinook salmon.

Accurately predicting population dynamics has been a continual challenge for fisheries biologists (Rothschild 2000; Ruckelshaus et al. 2003). Adult returns in any year are determined by survival across multiple life stages, each of which occurs in a particular type of habitat (e.g., tributary, main stem, estuary, ocean) and during a unique set of environmental conditions. Efforts to examine the relative importance of habitat conditions experienced during each life stage on overall survival have been complicated by measurement problems and insufficient information at appropriate life stages (Zabel and Williams 2002; Fausch et al. 2002). These problems have had the unfortunate effect of clouding the debate about how best to approach population management (Kareiva et al. 2000; Zabel and Williams 2002; Ruckelshaus et al. 2003). In this paper, we describe a statistical approach for assessing the importance of multiple life stages on the population dynamics of Chinook salmon *Oncorhynchus tshawytscha* and for combining environmental effects at multiple life stages into a predictive model of spawner returns.

Quantifying the influence of environmental conditions on survival has often been attempted by correlating the survival of a particular life stage in a particular habitat with environmental conditions experienced within that habitat. For example, some researchers have argued that freshwater conditions strongly constrain salmonid productivity because stream flooding during incubation increases mortality through streambed scour and fill, and fine sediment deposition (Seegrist and Gard 1972; Lisle and Lewis 1992; DeVries 1997). Other authors have stressed the importance of environmental variation in estuarine habitats (tidal delta and nearshore habitats such as bays and inlets) by correlating measures of growth and survival to seasonal changes in temperature (Reimers 1973) or trends in habitat availability (Magnuson and Hilborn 2003). In addition, a growing volume of research has identified the influence of climatic and marine environmental variation on large fluctuations in the abundance of anadromous salmonids that appear synchronized at large spatial scales (Coronado and Hilborn 1998; Hare et al. 1999; Mueter et al. 2002a). However, the degree

* Corresponding author: correigh.greene@noaa.gov.

Received January 31, 2005; accepted June 27, 2005
Published online November 3, 2005

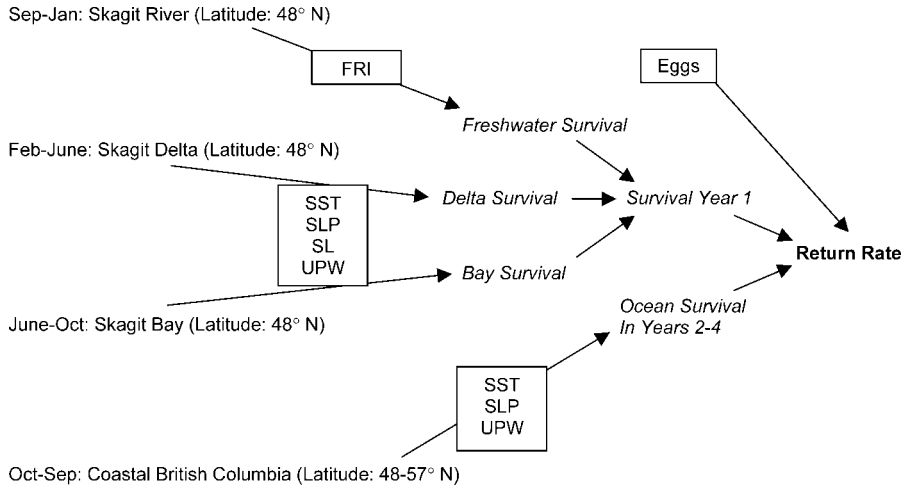

FIGURE 1.—Conceptual framework for the statistical models used in this paper. Boxed parameters are measured at the temporal and spatial scale of residency in different habitats and are predicted to be correlates of italicized population parameters, which are not measured. Bold parameters are measured population parameters. Abbreviations are as follows: FRI = flood recurrence interval; SST = sea surface temperature; SLP = sea level pressure; UPW = coastal upwelling; and SL = sea level (see text for additional details).

to which population fluctuations reflect changes in estuarine or ocean environmental conditions has been particularly difficult to quantify due to our inability to partition overall marine mortality into habitat-specific mortality.

Despite clear documentation of the effects of environmental processes at multiple life stages, we know little about the relative impact of these processes on population dynamics. This is because habitat effects on life stage specific survival rates have yet to be systematically combined throughout the life cycle to explain overall population dynamics. Such assessments are critical for predicting population trends and for assessing which habitats might be best targeted for protection and recovery. To estimate the relative importance of different habitats upon survival, we would ideally be able to measure survival rates directly in freshwater, estuarine, and ocean habitats, and to compare over multiple years the effects of their variation on a population. However, given the difficulty of measuring survival rates of juvenile salmon, especially through estuarine habitats, an alternative approach is to ask how particular environmental factors measured during periods of residency in these habitats influence return rate (Figure 1; see also Lawson et al. 2004). In this paper, we examine the relationship between the return rates of Chinook salmon (spawners per spawner or recruits per spawner) and a suite of environmental variables measured during residency in streams, tidal delta, bay, and ocean habitats. Our approach is novel in that it quantifies the relative importance of habitat conditions experienced during multiple life stages on return rate in a given year, and results in surprisingly strong power for predicting return rates.

Methods

We examined environmental predictors of return rates of ocean-type Chinook salmon inhabiting the Skagit River basin, a 8,544-km^2 watershed on the western slope of the Cascade Range in northern Washington (Figure 2). Chinook salmon use multiple habitats during their life cycle (Figure 1). In the Skagit River, Chinook salmon are primarily of wild stock, with two relatively small and fully marked indicator broodstocks existing to provide data for harvest managers. Fish spawn between July and October, with the peak occurring during low flow in September. Eggs incubate in redds for approximately 5 months. After hatching, juveniles migrate downstream usually within a month and spend 1 or 2 months in the delta before migrating to the tidally dominated fjord systems of Skagit Bay. Extensive field surveys indicate that habitat use of the delta ranges from February to June, and bay habitat use ranges from June through October (E. Beamer, unpublished data). From Skagit Bay, fish migrate north into the Pacific Ocean, where most remain for 3 to 5 years. We tested the relative influence of environmental conditions experienced during the above periods of residency in four

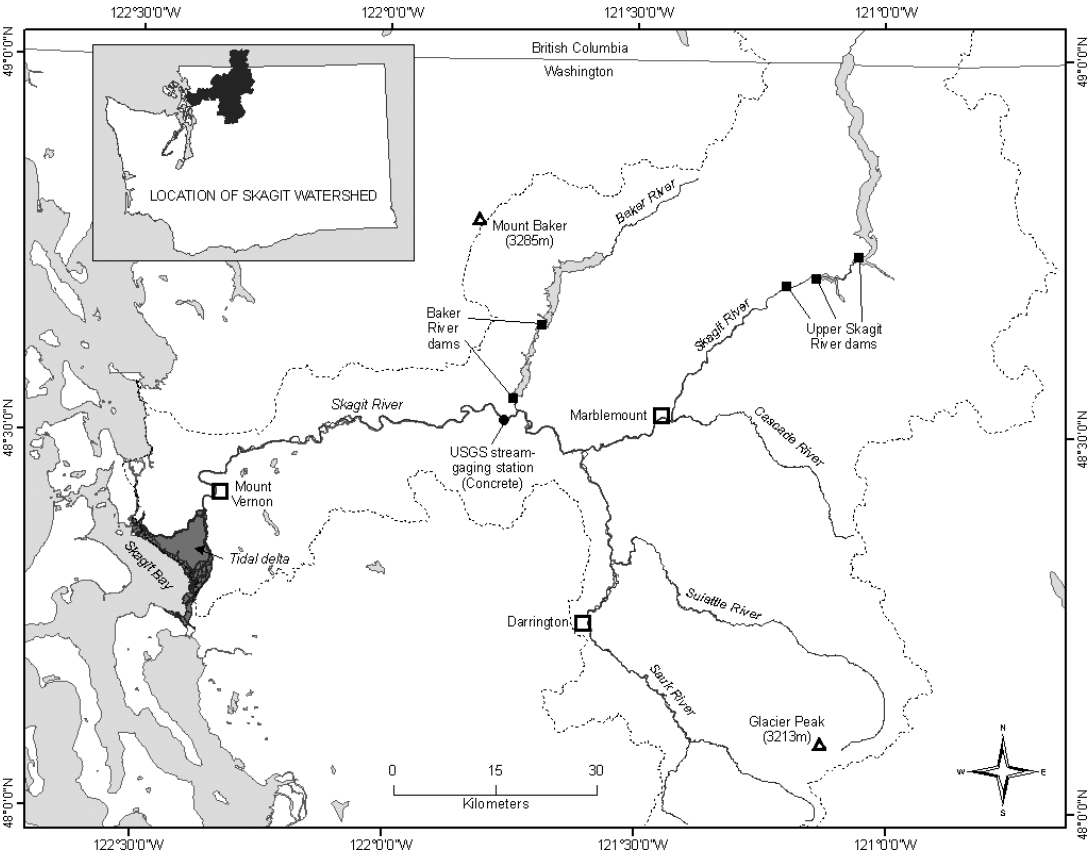

FIGURE 2.—Map of the Skagit River basin, with major tributaries and relevant habitat types delineated.

habitat-classes (freshwater, delta, bay, ocean) upon return rates over the course of 17 brood years (Figure 1). We used an additional four brood years as a forecast to test the ability of our regression models to predict the future.

Environmental Data

Freshwater data.—We determined flood recurrence interval (FRI), the estimated frequency in years at which a flood of a given magnitude will occur, for the single largest annual peak flow event during the intragravel stage of development. For each year from 1974 to 1995 we fit the annual maximum peak discharge data to a log-Pearson type III distribution using a method of moments approach (U.S. Water Resources Council 1981; Sumioka et al. 1998). We based FRI for the entire Skagit River upon data obtained from the U.S. Geological Survey (USGS) stream gauge near Concrete, Washington (Figure 2; 48°31′28″N, 121°46′11″W; available at http://waterdata.usgs.gov/nwis/peak/). Larger FRI values indicate larger flows.

Delta, bay, and ocean data.—No continuous long-term monitoring program of habitat conditions in the Skagit River delta and Skagit Bay existed during the years of this study. Therefore, the putative effects of delta and bay habitat conditions on return rates had to be inferred from regional marine and atmospheric data collected during the periods of residency in delta and bay habitats. We identified four marine variables that might influence survival during delta and bay residency based on previous studies (e.g., Koslow et al. 2002): sea surface temperature (SST), sea level pressure (SLP), coastal upwelling (UPW), and sea level (SL). We obtained mean SST and SLP from the Comprehensive Ocean–Atmosphere Data Set (COADS), which is based on data collected from ship traffic in the region (Koslow et al. 2002; Mueter et al. 2002b). To obtain habitat-specific information for the Skagit, we used data collected be-

TABLE 1.—Factor loadings of principal components for environmental conditions experienced during delta, bay, and ocean residency; SST = sea surface temperature; SLP = sea level pressure; UPW = coastal upwelling; and SL = sea level.

Variable	Source	Delta (Feb–Jun)		Bay (Jun–Oct)		Ocean (Oct–Sep; Factor 1)
		Factor 1	Factor 2	Factor 1	Factor 2	
SST	COADS[a]	0.027	0.981	0.0725	0.896	−0.524
SLP	COADS[a]	0.769	−0.235	0.607	0.396	0.783
UPW	PFEL[b]	0.786	0.063	0.876	0.052	0.800
SL	University of Hawaii[c]	−0.872	−0.119	−0.774	0.453	
Percent of variance explained		49.266	25.906	43.486	29.166	50.933

[a] Comprehensive Ocean–Atmosphere Data Set (http://dss.ucar.edu/pub/coads/).
[b] Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/).
[c] University of Hawaii Sea Level Center (http://uhslc.soest.hawaii.edu/).

tween 48.5°N and 49.5°N and 122–123°W during juvenile residency in either the delta (February–June) or the bay (June–October). The coastal upwelling index and sea level were based on coastal data measured at Neah Bay, Washington (48°22.1′N, 124°37.0′W).

Ocean-type Chinook salmon from the Skagit River migrate from bay habitats to the ocean primarily in the fall, traveling as far north as Southeast Alaska (Myers et al. 1997). To describe conditions during ocean residence, we averaged data for latitudes between 48°N and 57°N yearly from October to the following September. Sea surface temperature and SLP were based on COADS data within the region between 48°N and 57°N and 122–137°W, screened to include only coastal and inland passage locations. Upwelling was calculated across the same time period using the mean index value from four coastal sites in Washington and British Columbia (48°N, 125°W; 51°N, 131°W; 54°N, 134°W; and 57°N, 137°W). Because SST, SLP, UPW, and SL are intercorrelated, we calculated a habitat ''factor'' for delta, for bay, and for ocean habitats using principal components analysis (PCA; Rencher 1998). In all three cases, the first principal component accounted for 43–50% of the variance of the ocean variables. We concluded that the principal components described similar environmental conditions for each habitat and that the first principal component was sufficient as an environmental indicator in delta and bay habitats (Table 1). For conditions experienced during delta and bay residency, the first component loaded positively on SLP and upwelling, and negatively on sea level. The only principal component describing conditions experienced during ocean years loaded positively on SLP and upwelling, and negatively on SST.

Biological Data

Our sample consisted of 22 brood years from 1974 through 1995 (Table 2). The first 17 years were used to develop models, and the final four or five brood years were reserved to test model predictions. We used return rates based on both spawners per spawner and recruits per spawner for six populations spawning in hydrologically distinct regions of the Skagit River watershed as our response variables, and each brood year's number of eggs as a measure of density dependence. Both variables were based on escapement estimates for each spawning population and age composition data derived from fisheries in the bay and lower river.

Population-specific escapement was based on annual Chinook salmon redd counts of the Skagit River's six genetically distinct spawning populations (Myers et al. 1997), performed by the Washington State Department of Fisheries and Wildlife (WDFW) from 1977 to 2000 (brood years 1974–1997; Washington Department of Fisheries and Wildlife and Western Washington Treaty Indian Tribes 1992). Escapement estimates based on redd counts are sometimes criticized due to variation in interobserver reliability, failure to control for environmental effects on counts, and biases produced by assumptions of constant demographic rates (e.g., spawner-to-redd ratio) used in population expansions (Walters and Ludwig 1981; Hilborn et al. 1999). However, redds are surveyed in the Skagit using a combination of aerial and ground surveys during periods of low flow and precipitation that optimize redd counting. In 1998, two techniques for estimating escapement based on multiple aerial or ground surveys were compared with WDFW's method. The comparison revealed that coefficients of variation (CV = 100 × SD/mean) based on

TABLE 2.—Escapement, egg production, harvest rates, and spawners per spawner (S_t) and recruits per spawner (R_t) for the six Skagit River spawning populations across the 22 brood years used in the study. Egg production is summed across spawning populations, while other variables are averaged.

Brood year	Escapement contributing to brood	Eggs (millions)	Mixed-stock harvest (%)	Terminal harvest (%)	S_t	R_t
1974	12,808	12.360	0.556	0.125	1.568	7.316
1975	11,837	11.296	0.577	0.106	0.942	4.349
1976	14,638	14.218	0.532	0.145	1.822	7.316
1977	9,966	9.626	0.527	0.168	1.492	7.691
1978	13,798	12.737	0.509	0.206	1.271	3.065
1979	13,904	13.125	0.608	0.159	0.787	3.743
1980	21,654	20.379	0.594	0.119	0.361	1.323
1981	9,283	8.623	0.605	0.080	2.746	8.085
1982	10,466	9.919	0.601	0.157	1.994	8.248
1983	9,109	8.453	0.552	0.166	1.297	6.172
1984	13,022	11.410	0.555	0.235	1.916	7.099
1985	18,405	17.022	0.518	0.162	0.560	1.751
1986	19,295	18.812	0.507	0.119	0.961	2.664
1987	10,713	9.821	0.532	0.089	0.677	1.804
1988	12,900	12.237	0.563	0.080	0.923	2.664
1989	7,637	7.060	0.559	0.058	0.795	2.270
1990	17,763	16.685	0.526	0.042	0.492	1.051
1991	6,866	6.517	0.426	0.055	1.297	2.535
1992	7,654	6.990	0.414	0.037	1.419	2.560
1993	6,084	5.666	0.512	0.032	1.462	2.974
1994	5,924	5.127	0.394	0.034	2.226	4.221
1995	8,562	8.040	0.566	0.041	0.600	1.197

multiple aerial surveys and estimates of sex ratios ranged from 6.6% to 29.2% for different spawning populations, and were often biased due to sampling variation in the sex ratios. The authors concluded that WDFW's means of estimating escapement was the best estimate for five of the six Skagit spawning populations (Hahn et al. 2001).

We determined age composition for each brood year using scale samples collected from wild Chinook salmon. Scale samples were collected from commercial gill net and test gill-net fisheries conducted in the Lower Skagit River and the Skagit River mouth. Both fisheries hang nets in folds, a technique that catches a wider size distribution than the gill-net mesh size would allow if hung flat and therefore reduces biases in estimating age composition. Because scale samples were not collected at the spawning grounds, we assumed that the age composition was the same for all spawning populations. Samples were analyzed and ages were determined by WDFW using the same scale collection method each year.

The number of fish used to determine age-class composition for the Skagit River averaged 857 per year (SE, 148). To maximize the number of brood years in our analysis, we used only 3–5-year-old recruits for populations from the Skagit River. Two- and six-year-old recruits were a minor part of the Skagit River return, averaging 0.9% and 0.2% of the return, respectively, from 1965 to 1995. Age-class composition data were not available for Skagit Chinook salmon in 1979. To estimate a 1979 Skagit Chinook salmon age distribution, we used the average proportion of 5-year-olds from 1965 to 1995 (16.5%), and regression estimates for 3- and 4-year-olds (13.7% and 69.0%, respectively) because the proportions of 3- and 4-year-olds shifted over time.

Using these estimates of escapement and age structure, we calculated return rate using two methods: the number of spawners produced per spawner in the previous cohort, and the number of recruits per spawner. The age-adjusted spawners per spawner (S_t) based on a particular brood year t is

$$S_t = \sum_{x=3}^{5} \frac{p_{x,t+x} N_{t+x}}{N_t}, \qquad (1)$$

where N_t is the adult escapement in year t, and $p_{x,t}$ is the proportion of adults of age x in the return in year t. As the fundamental structure of S_t is N_{t+x}/N_t, S_t is also a measure of the population growth rate λ (Caswell 2001).

The main problem with using S_t is that it does not account for individuals lost to harvest. We therefore calculated a second measure of return rate based on recruits per spawner (R_t), which ad-

justs for age-specific terminal and nonterminal harvest:

$$R_t = \frac{\sum_{x=3}^{5} p_{x,t+x} N_{t+x}}{1 - \sum_{x=3}^{5} \mu_{x,t} - \sum_{x=3}^{5} h_{x,t}} \Big/ N_t, \qquad (2)$$

where $\mu_{x,t}$ and $h_{x,t}$ are age-specific estimates of terminal and nonterminal exploitation for fish of age x, respectively. Estimates of terminal and nonterminal harvest rates (Table 2) were based on age-specific analysis of coded wire tag recoveries of North Puget Sound Chinook salmon index stocks (N. Sands, Northwest Fisheries Science Center, personal communication). The summing of both terminal and nonterminal age-specific exploitation rates in equation (2) reflects the lack of certainty in the age-specific estimates.

We calculated the number of eggs E_t produced in year t as

$$E_t = \mathrm{FN}_t \sum_{x=3}^{5} m_x p_{x,t}, \qquad (3)$$

where F is the average proportion of females (0.45) and m_x is the age-specific fecundity (4,830, 5,832, and 6,155 for fish aged 3, 4, and 5 years, respectively). These values were determined from adults in two Skagit River index stocks averaged over 9 years (1994–2002; Henderson and Hayman 2002).

Although spawning populations within the Skagit River are segregated somewhat by spawning location and run timing (Washington Department of Fisheries and Wildlife and Western Washington Treaty Indian Tribes 1992), biological data significantly covary among spawning populations, and FRI covaries among river basins each year. Therefore, we used the average return rate and total egg production for the six spawning populations to represent the biological response for each brood year (Table 2).

Statistical Analysis

In the Puget Sound region, most ocean-type Chinook salmon leave freshwater as subyearlings and return as 4-year-olds (i.e., four ocean years; Healey 1991). The relative influence of different aquatic habitats on recruitment for this age-class could be defined as

$$N_{t+4} = N_t m f_t d_t b_t o_{t+1} o_{t+2} o_{t+3} e_t, \qquad (4)$$

where N_{t+4} is the number of spawners returning in year $t + 4$ from a previous cohort of N_t adults, m is the mean fecundity, f_t is freshwater (egg-to-smolt) survival, d_t is survival in the tidal delta, b_t is survival in bay habitats, o_{t+x} is ocean survival in year $t + x$, and e_t is a density-dependent adjustment to survival based on the number of eggs laid in year t. This equation assumes that density dependence is not habitat-specific and accrues across several different types of habitats. Similar equations could be used to calculate the change in numbers for 3-year-olds and 5-year-olds by adding or removing an additional ocean parameter. Note that equation (4) can be used to calculate total survival by dividing both sides by mN_t.

An analogous model that allows us to examine statistically the relevance of these parameters to mean adult returns is

$$\begin{aligned}\log_e(N_{t+x}/N_t) = {} & \omega + \alpha \log_e(f_t) + \beta \log_e(d_t) \\ & + \delta \log_e(b_t) + \phi_1 \log_e(o_{t+1}) \\ & + \phi_2 \log_e(o_{t+2}) + \phi_3 \log_e(o_{t+3}) \\ & + \phi_4 \log_e(o_{t+4}) + \tau \log_e(E_t), \qquad (5)\end{aligned}$$

where f_t, d_t, n_t, and o are now environmental variables in freshwater and ocean, respectively, that correlate with survival (Figure 1). The coefficients α, β, δ, ϕ_x, and τ describe the influence of environmental conditions during freshwater, delta, subtidal, and ocean residency as well as the number of eggs (equation 3) upon return rate, and ω is a constant. We substituted equation (1) or (2) for N_{t+x}/N_t to obtain an age-structured estimate of return rate and used multiple linear regression to estimate the importance of these variables.

Using standard multiple linear regression analyses to predict return rate from this model requires several assumptions. We assume that residuals from the model above are normally distributed with constant variance and that samples are independent. These assumptions were validated using standard tests for homogeneity of variance and normality (Neter et al. 1996). To test for sample independence, we plotted sample autocorrelation and partial autocorrelation functions for return rate. These plots revealed no significant temporal autocorrelation in the response. We calculated condition indices to determine the degree of collinearity among predictors (Belsley 1991). Even though significant bivariate correlations among predictors were nonexistent (Table 2), collinearity did exist among the entire set of predictors and was due almost entirely to correlations of multiple predictors with eggs. Because the pattern of col-

linearity was the same for the years used in model fitting (1974–1990) and in the full data set (1974–1994), the predictions used for validation (1991–1994) were not affected (Harrell 2001). We also examined Cook's distance and leverage values (McCullagh and Nelder 1989; Neter et al. 1996) for any particularly influential observations. An additional assumption for models that include eggs as one of the predictors is that the population exhibits Ricker population dynamics because E depends directly upon the number of spawners (equation 3).

We used this general model to consider which predictors best explained the effects of environmental conditions on recruitment (Table 2). We evaluated which variables to include in the model using two methods. The first method was based on model selection using information theory and Akaike's information criterion (AIC) of all possible models derived from the eight predictors. Akaike's information criterion takes into account how well the model fits the data but penalizes for the number of parameters in the model (Burnham and Anderson 2002). In this first method, all subsets of the eight predictor variables (256 combinations) were regressed on each measure of return rate. These models were ranked by AIC, and the best model was the one with the lowest AIC. This model, calibrated with the first 17 years of data, was used to predict returns for years 18–21 of the time series. In addition, we obtained predictions from the full set of 256 models and from the set of models where the AIC differed from the best AIC model by less than seven ($\Delta\text{AIC} \leq 7$). The cutoff of ΔAIC less than or equal to 7 was chosen for a second model-averaged prediction because Burnham and Anderson (2002) suggest that an AIC difference between a given model and the AIC best model of greater than 7 suggests that the model is not a highly plausible explanation for the data. The predictions from both all subsets and those with ΔAIC less than or equal to 7 were adjusted by their Akaike weights (Burnham and Anderson 2002); thus predictions from models with a smaller AIC contribute more weight to the final model-averaged prediction. Based on results from model averages (see below), we also examined a four-parameter model incorporating eggs, FRI, bay factor, and the third ocean year factor. The accuracy of the predictions from each of these sources was compared by calculating the root mean squared prediction error (RMSE) for both the 17-year model calibration data set and the following 4-year prediction.

The full set of models was also used to evaluate the importance of each predictor by summing the Akaike weights for all of the models in which a given predictor occurs (Burnham and Anderson 2002). The importance of variable j is defined as

$$\sum_{i=1}^{R} w_i I_j(M_i), \tag{6}$$

where w_i is a model's Akaike weight and $I_j(M_i)$ is equal to 1 if variable j is in model i and 0 otherwise. Thus, if a given variable is consistently included in the models with the low AIC, its importance will be much larger than a variable that is not associated with good fitting models.

The second method of model selection was a forward selection procedure that used the AIC as the criterion to pick candidate models. To use AIC in a stepwise procedure, we first determined the AIC for each univariate regression. The model with the lowest AIC was chosen as the best candidate for that step. In the following step, AICs for bivariate regressions were computed, each of which included the best variable from step 1. This process was continued further steps as long as AIC continued to decrease.

Results

We found that both measures of return rate were significantly correlated with eggs, FRI, and bay factor score (Table 3). These correlations indicate that return rate was strongly related to conditions experienced during several early life history stages, although potential interactions among predictors could not be ruled out. In particular, we found that interactions that included the eggs parameter tended to result in higher collinearity of other parameters, particularly FRI and other variables. However, significant bivariate covariation among potential predictor variables was nonexistent.

A total of 256 models could be specified from the eight parameters available in our model framework. Examination of AICs of all these models and their respective model weights revealed several patterns. First, the best models ($\Delta\text{AIC} \leq 7$) all included negative effects of both FRI and the bay factor. This was true regardless of whether R_t or S_t were used as a measure of return rate. Second, improvements in AIC across models for both dependent variables (as represented by the cumulative AIC weight) were convex functions of model rank, indicating that the 10 best models provided 50% of the overall model weight and that many of the other models with ΔAIC less than or equal

TABLE 3.—Correlations of parameters used in this study (below diagonal) and sample size of each comparison (above diagonal). Ocean factors are the same data shifted for the appropriate brood year. Asterisks indicate significant correlations ($P < 0.05$).

Data item	S_t	R_t	Eggs	FRI	DEL	BAY	O1	O2	O3	O4
Spawners per spawner (S_t)		24	24	24	24	24	24	23	22	21
Recruits per spawner (R_t)	0.970*		24	24	24	24	24	23	22	21
Eggs	−0.582*	−0.532*		26	24	24	24	23	22	21
Flood recurrence interval (FRI)	−0.563*	−0.499*	0.280		27	27	27	26	25	24
Delta factor score (DEL)	−0.223	−0.154	0.097	0.300		27	27	26	25	24
Bay factor score (BAY)	−0.642*	−0.623*	0.280	−0.090	0.061		27	26	25	24
1st ocean year factor score (O1)	−0.047	−0.068	0.140	−0.342	0.008	0.206		26	25	24
2nd ocean year factor score (O2)	−0.206	−0.139	−0.059	−0.048	−0.118	0.194	0.120		25	24
3rd ocean year factor score (O3)	0.201	0.334	0.138	−0.256	0.231	0.141	0.231	0.072		24
4th ocean year factor score (O4)	−0.174	−0.252	0.261	−0.061	−0.053	0.031	0.395	0.211	0.045	

to 7 did not provide much more explanatory power (Figure 3). These results indicate that some models were much better at predicting return rate than others, but also that no one model stood out as the best.

Analyses of the parameters resulting from the full-model weighting procedure revealed that both R_t and S_t measures were very similarly correlated with environmental factors (Table 3). Regardless of how it was measured, return rate was negatively correlated with all environmental factors but the third ocean year factor (O3). Importance values derived from weighting of models containing particular parameters (equation 6) revealed that while some differences in importance values existed between the R_t and S_t models, they shared four environmental factors with the highest importance values (>0.5): eggs, FRI, and the bay and third ocean year factors.

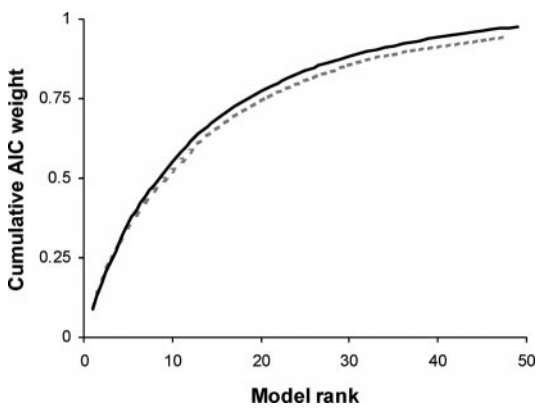

FIGURE 3.—Cumulative Akaike information criterion (AIC) weights as a function of model rank (the lowest weight indicates the best model) for age-adjusted spawners per spawner in brood year t (S_t; solid line) and recruits per spawner in brood year t (R_t; dashed line) for all models in which ΔAIC is less than or equal to 7.

In addition to using model averaging, other techniques for model selection that use information theory include selecting the best model from competing alternatives (Fujiwara and Caswell 2001) and using stepwise selection procedures that have AIC as the selection criterion (Logerwell et al. 2003). When we applied both of these techniques to the R_t data (Table 4), the best model was the same in both cases (eggs, FRI, delta, bay, O1, O3, and O4). For S_t, the best model was different for the two techniques. The forward selection procedure resulted in a four-parameter model (eggs, FRI, bay, and O3), while the best AIC model had an additional two parameters (delta and O2). All three models had similar parameter values as the model average and were highly significant, although in some cases analysis of variances failed to rank some of the included parameters as significantly different from zero (Table 4). Each of

TABLE 4.—Estimates of parameters for several types of models predicting return rate. Model-averaged estimates based on all model subsets are included for both measures of return rate. Parameter estimates and their resulting F- and R^2_{adj}-statistics are also provided for models with the best Akaike information criterion score obtained in either the forward selection procedure, the full model set, or both. Standarized betas (Std B) indicate the standardized slope of the regression line when other parameters are held constant (asterisks indicate $P < 0.05$). See Table 3 for an explanation of data items.

	Model average		Best AIC		
Data item	S_t	R_t	S_t (Full set)	S_t (Forward selection)	R_t (Both)
Constant	5.458[a]	7.441[a]	7.646	6.370	10.105
Eggs (Std B)	−0.393	−0.516	−0.438 (−0.234)	−0.358 (−0.190)	−0.508 (−0.215)
FRI (Std B)	−0.262	−0.272	−0.232* (−0.464)*	−0.254* (−0.508)*	−0.267* (−0.428)*
Delta (Std B)	−0.064	−0.099	−0.082 (−0.170)		−0.095 (−0.158)
Bay (Std B)	−0.377	−0.491	−0.346* (−0.578)*	−0.385* (−0.645)*	−0.479* (−0.638)*
O1 (Std B)	−0.051	−0.143			−0.127 (−0.190)
O2 (Std B)	−0.064	−0.002	−0.080 (−0.149)		
O3 (Std B)	0.128	0.205	0.138* (0.252)*	0.115 (0.211)	0.222* (0.327)*
O4 (Std B)	−0.025	−0.158			−0.137 (−0.197)
F (error df)			15.157* (10)	20.509* (12)	7.976* (9)
R^2 (R^2_{adj})			0.901 (0.841)	0.872 (0.830)	0.862 (0.754)

[a] Because constants for model averages do not necessarily represent any particular model, they should not be used for building predictive models.

the three models explained large portions of the total variation in return rate ($R^2 > 0.85$), even when adjusted for the number of model parameters ($R^2_{adj} > 0.75$).

For both R_t and S_t, the forward-selection procedure picked the same parameters that were ranked of high importance via model averaging (Figure 4). In addition, the forward selection procedure chose parameters in the same general order for both R_t and S_t, indicating strong correspondence of the variance structure between these two variables (Table 5). Comparison of R^2 values across models revealed that the bay factor explained 40–45% of the variation in both R_t and S_t, FRI explained another 16–33%, and the remainder of the variables explained 7–18%, depending upon which measure of return rate and which R^2 value was used. Examination of the standardized betas (the slope of the relationship between return rate and an environmental variable, holding all other variables constant; Table 5) revealed that for all three models, the bay factor had the strongest effect on return rate, closely followed by FRI. The third ocean year factor (O3) was next strongest, followed by eggs, and then by all other variables.

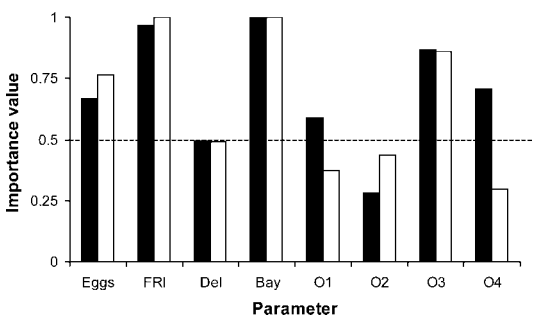

FIGURE 4.—Importance values of the eight parameters used in this study, as determined from the all-subsets model average for age-adjusted spawners per spawner in brood year t (S_t; open bars) and recruits per spawner in brood year t (R_t; solid bars). Abbreviations are as follows: FRI = flood recurrence interval; Del = tidal delta habitat factor score; Bay = bay habitat factor score; and O1–O4 = 1st–4th ocean year factor scores. See text for full explanations of importance values and the parameters.

To assess the predictive power of particular models or model sets, we compared the root mean square errors (RMSEs) of predicted values for both model calibration and forecasting data sets. For the 17-year model calibration data set, the model with the best AIC had the lowest (best) RMSE, followed by the two-model averaged prediction sets, and then by the four-parameter model that included the four consensus parameters identified in Figure 3 (eggs, FRI, bay, and O3). However, these trends were reversed for the 4-year forecasting data set. In this case, the model with the best AIC had the highest (worst) RMSE, followed by model averages composed of all possible models or with those with ΔAIC less than or equal to 7 (Figure 5). The lowest RMSE resulted from the four-parameter model. These patterns held true for both R_t and S_t models.

These results indicated that predictions from the best AIC and the four-parameter model (a subset of the best AIC models) were both comparable to those from model averaging. We further compared

TABLE 5.—Results of the forward selection procedure of S_t and R_t models and the relative explanatory power of the models based on their Akaike information criterion (AIC), R^2, and R^2_{adj} (i.e., adjusted for the number of parameters). See Table 3 for abbreviations.

Model	Parameters	AIC	R^2	R^2_{adj}
	S_t			
1	Constant, bay	−27.791	0.462	0.426
2	Constant, bay, FRI	−42.326	0.796	0.767
3	Constant, bay, FRI, O3	−44.555	0.841	0.804
4	Constant, bay, FRI, O3, eggs[a]	−46.222	0.872	0.830
5	Constant, bay, FRI, O3, eggs, delta	−46.014	0.885	0.833
6	Constant, bay, FRI, O3, eggs, delta, O2[b]	−46.497	0.901	0.841
	R_t			
1	Constant, bay	−20.164	0.463	0.427
2	Constant, bay, FRI	−24.973	0.640	0.589
3	Constant, bay, FRI, O4	−27.092	0.718	0.653
4	Constant, bay, FRI, O4, O3	−28.887	0.774	0.699
5	Constant, bay, FRI, O4, O3, eggs	−30.015	0.812	0.727
6	Constant, bay, FRI, O4, O3, eggs, O1	−30.932	0.842	0.747
7	Constant, bay, FRI, O4, O3, eggs, O1, delta	−31.241	0.862	0.754

[a] Best model chosen by the forward selection procedure. Models 5 and 6 that follow are based on improvements in R^2_{adj} and AIC.
[b] Model with best AIC.

these models by combining model calibration and prediction data sets and computing new regressions. We then compared each model's predictive power for the entire data set by calculating predicted residual sum of squares (PRESS), the squared sum of residuals after removing each brood year from the analysis. This technique assesses how well a model predicts each data point (Neter et al. 1996). The four-parameter models

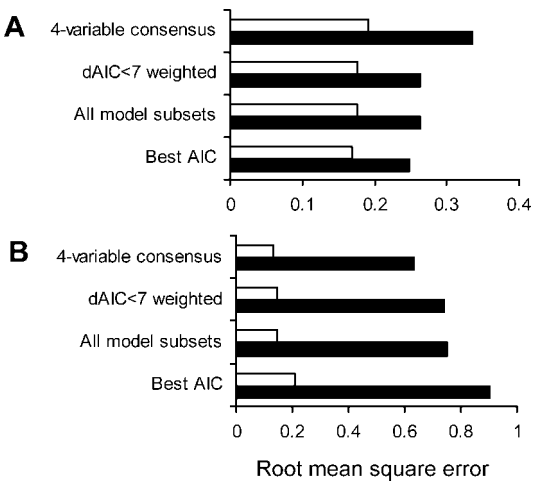

FIGURE 5.—Root mean square errors of **(A)** model calibration and **(B)** forecast data sets for four models of age-adjusted spawners per spawner in brood year t (S_t; open bars) and recruits per spawner in brood year t (R_t; solid bars). The abbreviation AIC stands for Akaike information criterion; see text for more information on the data sets.

(Figures 6A, 6D) predicted both S_t and R_t slightly better than the best AIC models (Figures 6C, 6F), resulting in PRESS scores of 1.12 and 1.28 for the S_t under the four-parameter and best AIC models, respectively, and 3.91 and 3.66 for R_t models. The four-parameter models also compared well with the model averages (Figures 6B, 6E), which were 1.17 and 3.64 for S_t and R_t models, respectively. All models tended to overestimate the most recent data for R_t, although the four-parameter model had the lowest error and was able to precisely predict a fifth year unavailable to other models.

Given that the four-parameter models were equivalent to or slightly outperformed the more complex best AIC models, we focused on the relationships of predictors and return rate for just the four-parameter models. The two measures of return rate showed both similarities and differences to changes in the variables included in the four-parameter model. Both S_t and R_t models were highly significant (S_t: $F_{4,21} = 33.347$; R_t: $F_{4,21} = 11.027$; $P < 0.0001$), and explained most of the variation in Skagit River Chinook salmon return rate from 1974 to 1995 (S_t: $R^2 = 0.89$; R_t: $R^2 = 0.72$; Figure 6). Parameter coefficients from both models of the entire 22-year data set differed little from those of the model using only the original 17 years (compare Tables 4, 6). In addition, both response variables showed strong significant negative relationships with FRI and the bay factor, and a significant positive relationship with the third ocean year factor (Table 6; Figures 7, 8). Flood

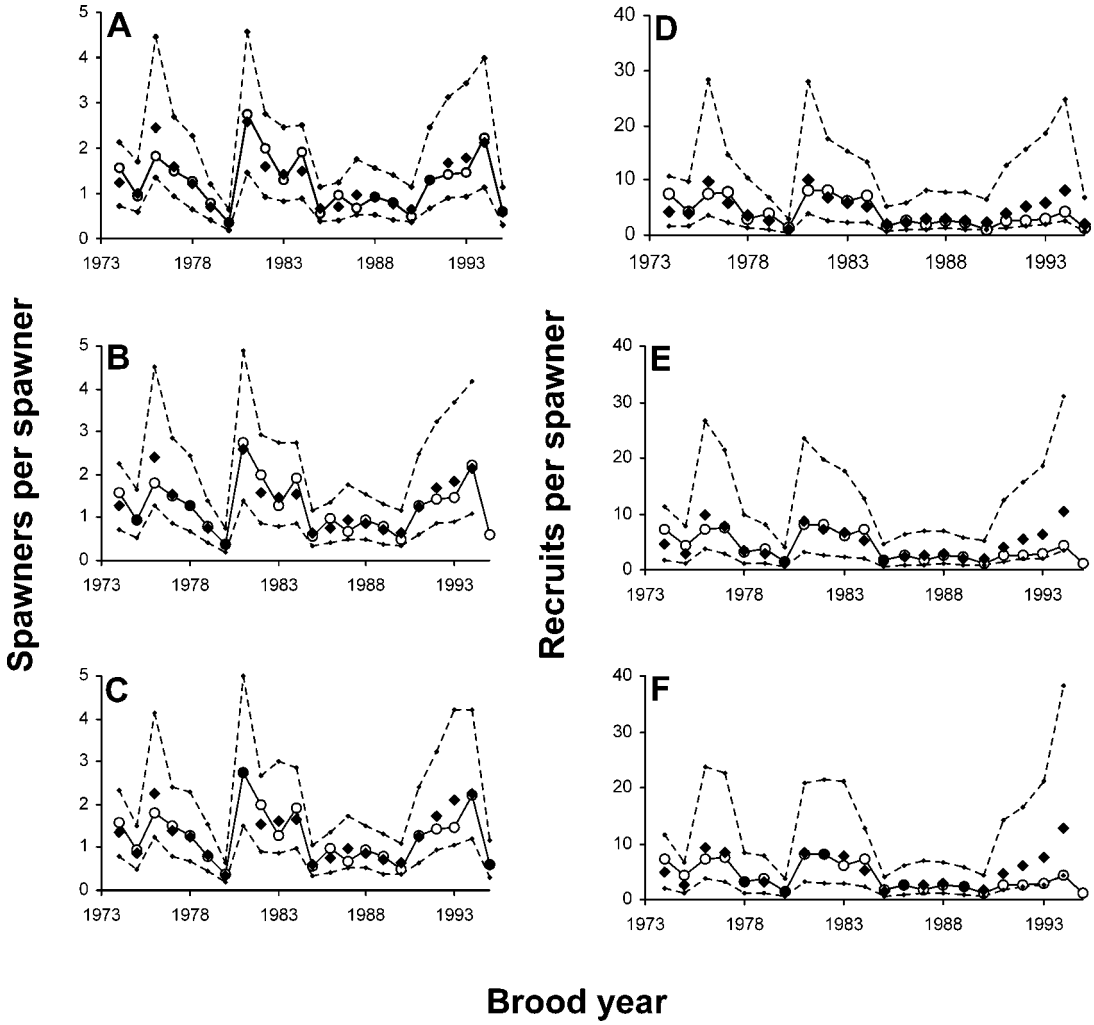

FIGURE 6.—Mean observed and predicted return rates as measured by spawners per spawner (S_t) or recruits per spawner (R_t) in the Skagit River computed with the full 22-year data set for three models: **(A, D)** the four-parameter model (eggs, flood recurrence interval, bay habitat factor score, and third ocean year factor score), **(B, E)** the ΔAIC ≤ 7 model average, and **(C, F)** the best AIC model. Actual observations are indicated by circles connected by lines, while predicted values are indicated by diamonds. The dashed lines indicate the 95% confidence intervals of the prediction. Note that final data point in the time series (1995) can be predicted only for the four-parameter and best AIC models for S_t and only for the four-parameter model for R_t. However, this brood year was not used in the quantitative comparisons of the models.

recurrence interval and the bay factor were the two most important parameters in the model, as determined by standardized beta coefficients (the standardized slopes of each parameter upon return rate) and partial correlations with return rate (Table 6). However, S_t and R_t models differed in their response to eggs, with S_t but not R_t showing a significant negative relationship (Figures 7C, 8C). Consequently, parameter rankings of eggs as judged by standardized betas differed between models (Table 6). For S_t, eggs was the third strongest relationship, followed by the third ocean year factor. Rankings of these two parameters were reversed for R_t. Given the high degree of collinearity that eggs has with other variables (FRI in particular), these relationships are not surprising.

Discussion

Our extensive analysis of multiple models that account for changing environmental conditions

TABLE 6.—Unstandardized and standardized parameter estimates and their standard error and significance for the four-parameter models computed with the full 22-year data set. Unstandardized coefficients indicate the actual values in the regression equation, while standarized coefficients indicate the slopes corrected for the variation in other parameters; $P < 0.05$*, $P < 0.01$**.

Data item	Unstandardized coefficients		Standardized beta	Partial correlation with return rate
	Beta	SE		
		S_t		
Constant*	5.925	2.077		
Eggs*	−0.332	0.130	−0.239	−0.527
FRI**	−0.238	0.039	−0.589	−0.831
Bay factor**	−0.398	0.051	−0.659	−0.884
Third ocean year factor*	0.119	0.045	0.230	0.541
		R_t		
Constant	2.082	4.032		
Eggs	−0.025	0.252	−0.015	−0.024
FRI*	−0.199	0.075	−0.399	−0.542
Bay factor**	−0.560	0.099	−0.749	−0.808
Third ocean year factor*	0.238	0.087	0.371	0.551

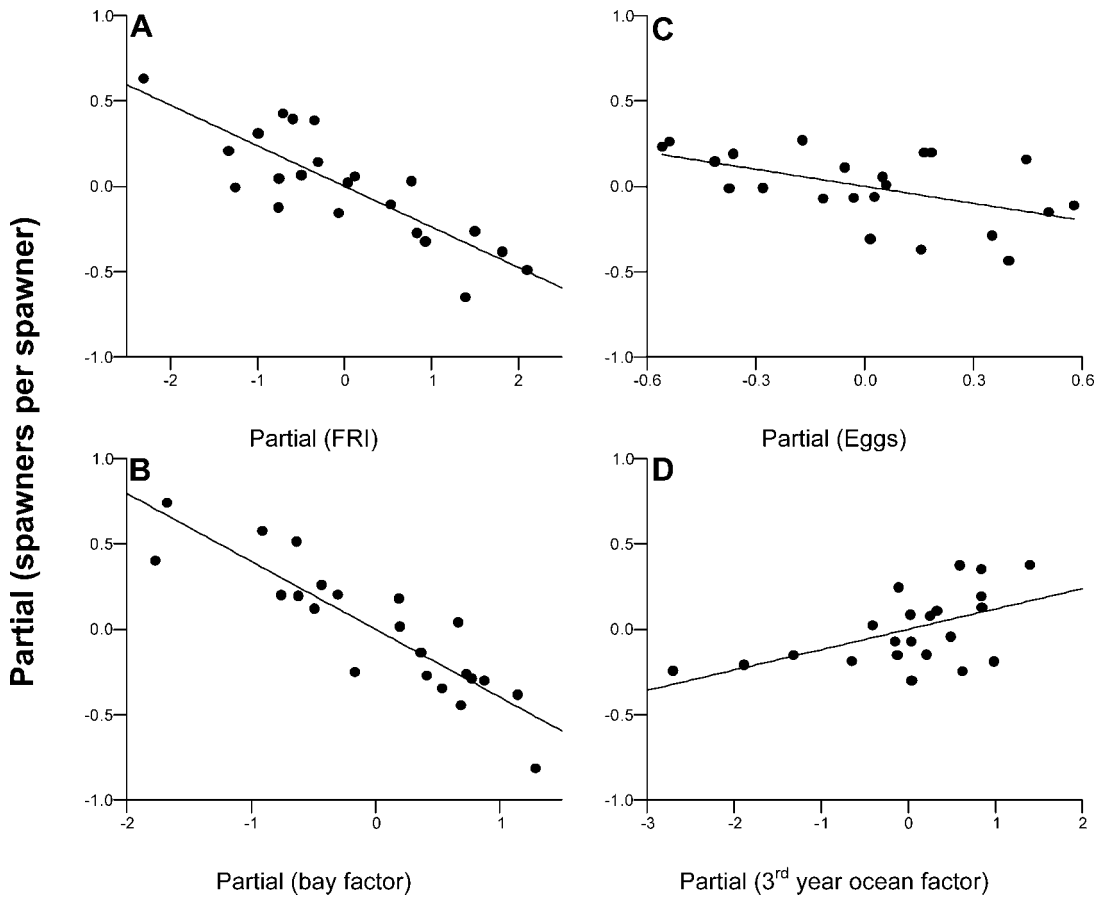

FIGURE 7.—Partial regression plots of spawners per spawner as a function of **(A)** flood recurrence interval (FRI), **(B)** bay habitat factor score, **(C)** egg production, and **(D)** third ocean year factor score included in the four-parameter model computed with the full 22-year data set. Slopes of plotted lines are the standardized betas in Table 5.

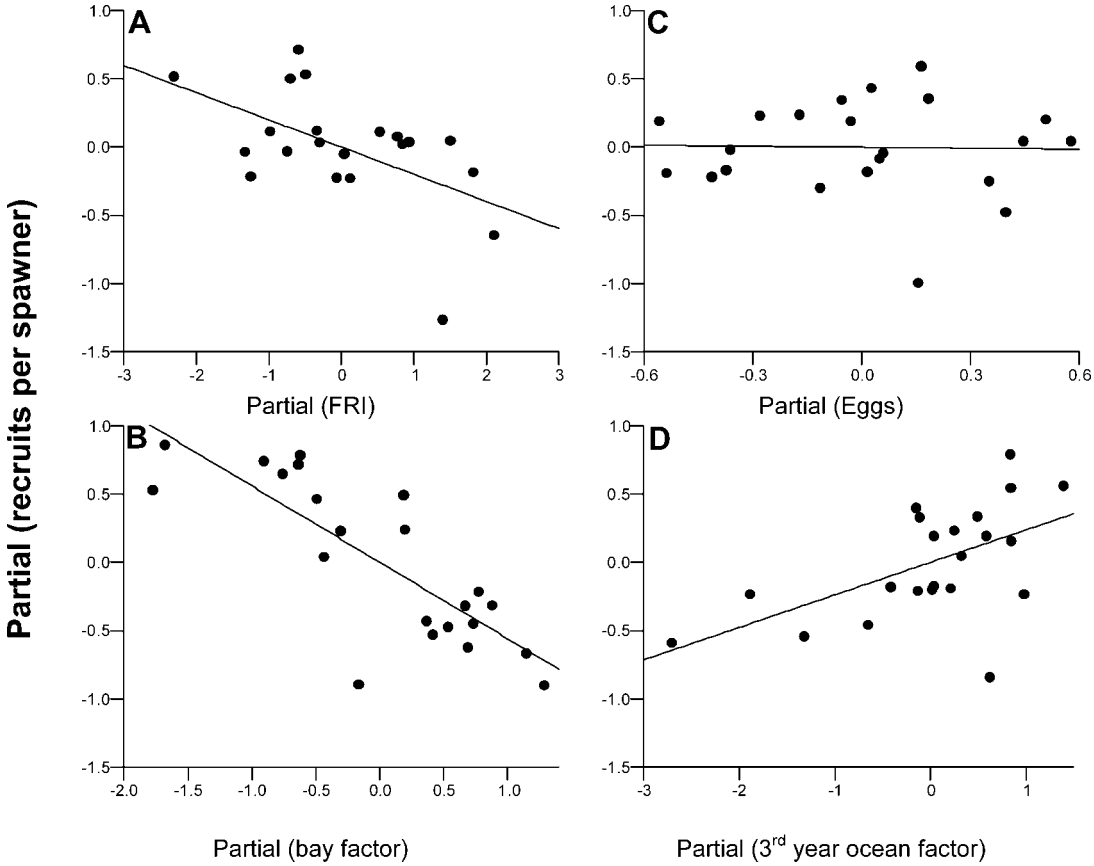

FIGURE 8.—Partial regression plots of recruits per spawner as a function of **(A)** flood recurrence interval (FRI), **(B)** bay habitat factor score, **(C)** egg production, and **(D)** third ocean year factor score included in the four-parameter model computed with the full 22-year data set. Slopes of plotted lines are the standardized betas in Table 5.

during several life stage transitions in Chinook salmon indicates that we can successfully predict return rates with a handful of variables. Our model averaging analysis revealed strong patterns of convergence in two measures of return rate, and indicated that both freshwater and marine processes strongly correlate with survival. Our results also suggest that much of the mortality occurs early in the life cycle of Chinook salmon, a pattern consistent with other salmonids (Beamish et al. 2000; Friedland et al. 2003). A simple four-parameter model (eggs, FRI, bay factor, and third ocean year factor), identified from a consensus analysis of the model averaging, performed surprisingly well and had better forecasting power than more complex models. Therefore, while our analysis should be viewed as preliminary due to the relatively small data set and limitations of both the environmental and fisheries data, it indicates that this relatively simple model should be a robust forecasting tool, especially for wild stocks of ocean-type Chinook salmon.

Much research in recent years has been devoted to seeking correlations between salmon abundance, survival, or return rate and freshwater or ocean conditions (e.g., Bradford 1995; Peterman et al. 1998; Botsford and Paulsen 2000), and many of these findings are characterized by uncertainty in predictions of population dynamics. Three main innovations in our approach may account for its higher precision. First, we focused our efforts on wild salmon. Second, we integrated information about environmental conditions experienced at multiple life stages. Third, we utilized detailed information on residence time for each habitat included in the model. Residence time allowed us to estimate when an environmental variable could influence survival. We believe this to be the most important factor in providing the explanatory and predictive power of our models.

Given the variable nature of escapement data, the explanatory power and predictive precision of our models are surprisingly strong and should generate strong scientific interest and a set of testable hypotheses that can improve our understanding of Chinook salmon population dynamics. Two important types of mechanisms may exist if the patterns we have identified reflect causal relationships. Habitat conditions at particular life stages may directly affect mortality during that particular life stage, or they may reduce growth or body condition, resulting in changes in mortality at later stages. Some combination of both explanations is possible. For example, high floods might destroy eggs in redds, but they also might reduce growth opportunities for parr migrating downstream, thereby indirectly increasing predation risk as fish enter the tidal delta and Skagit Bay. Below we examine some of these hypotheses in more detail.

Effects of Environmental Conditions on Survival

Flood magnitude.—Flood magnitude was a strong predictor of return rate for Skagit River Chinook salmon, suggesting that large flow events may be a key factor in regulating Chinook salmon populations in the Skagit River basin. This result corroborates an entirely independent out-migrant trapping effort by WDFW (Seiler et al. 2003). Using 13 years of time-adjusted screw trap captures of out-migrants and egg estimates based on redd counts, Seiler et al. found a significant negative correlation ($R^2 = 0.8193$) of freshwater survival (f) with incubation flood magnitude (M, in m^3/s) following the relationship

$$f = -4.065\text{E} - 0.5 \cdot M + 0.190. \qquad (7)$$

Several possible mechanisms could explain such findings. Peak flows can have a direct negative effect on the earliest freshwater life stages by mobilizing the streambed to the depth of the egg pocket and removing or crushing the eggs (Holtby and Healey 1986; Montgomery et al. 1996; DeVries 1997). The active movement of streambed material during peak flows also can have an indirect effect on eggs and alevin by increasing fine deposition, reducing available oxygen (Lotspeich and Everest 1981) and increasing mortality, increasing downstream displacement (Latterell et al. 1998), or reducing growth and making fry less able to compete for resources and more susceptible to predation at later life stages (Koski 1966; Mason 1969; Thomas et al. 1969; Parker 1971). In addition, peak flows may displace age-0 salmonids downstream by reducing the availability of preferred or suitable slow water habitats and increasing competition for space (Seegrist and Gard 1972; Erman et al. 1988; Latterell et al. 1998).

Conditions in the tidal delta.—Researchers have long hypothesized that tidal delta habitat is a key rearing area for the subyearling Chinook salmon that dominate the Puget Sound region (Simenstad et al. 1982; Thorpe 1994). Our evidence for an estuarine signal based on the variables we measured was equivocal. Model averaging procedures indicated that the delta factor had a moderate importance weight for both measures of return rate. In addition, the models with the highest AIC included the delta factor, although the relationship was not significant for both measures of return rate. These findings indicate that the delta factor had some explanatory power but it was weak. This result may reflect that the input data are not spatially associated with the estuarine processes of the Skagit River delta. Alternately, the lack of a strong estuary signal may indicate that the effect of estuarine environmental processes on survival are not highly variable over years, and that the main large-scale influence of the tidal delta is a rearing limitation resulting from historical habitat loss (see below).

Bay conditions.—Our most consistent relationship was the negative correlation between return rates and the bay habitat factor score. Local biological processes in northwest estuaries often respond to large scale oceanographic processes (Hickey and Banas 2003; Ruesink et al. 2003; Thom et al. 2003); therefore, it is plausible that processes occurring along the Washington coast influence processes in Skagit Bay, which, in turn, impact juvenile salmon during their residence there. One such process that might mediate mortality of juveniles is variation in salinity. Levels of salinity in the Strait of Juan de Fuca correlate with sea level (Cannon et al. 1990) and upwelling (Thomson 1994), both of which are components of the bay factor. Researchers have alternatively hypothesized high levels of salinity to be a growth challenge for juvenile salmon due to osmoregulation challenges (Handeland et al. 1998; Boeuf and Payan 2001; Morita et al. 2001), or as a growth benefit due to higher primary productivity in saline waters (Gargett 1997). Alternately, changes in salinity may facilitate influxes of marine predators (De Ben et al. 1990; Bravender et al. 1999; Mortensen et al. 2000; Willette et al. 2001), in which case higher values of salinity would correlate with higher mortality.

Ocean conditions.—Ocean conditions are an important factor affecting the dynamics of salmonid populations (Hare et al. 1999; Mueter et al. 2002a; Logerwell et al. 2003). Specifically, Pacific Decadal Oscillation (PDO), El Nino–Southern Oscillation (ENSO), and regional variability can affect upwelling, sea surface temperature, and sea level pressure. These environmental conditions determine, at least in part, growth rates, prey availability, and predation rates that directly affect salmonid survival during the ocean life stage (Hare et al. 1999; Mueter et al. 2002a). Although our analysis revealed that ocean conditions were a significant predictor of return rates, three lines of evidence from our research suggest that ocean conditions may not be the primary source of variation in survival. First, we found that flood recurrence interval during incubation explained 16–33% of the variation in return rate, second only to the bay factor. Second, the ocean factor scores in our models explained no more than 5% of the variation in return rate. Third, much of the variation in marine or ocean conditions suggested by other researchers appears explicable by conditions experienced during bay residency in our model. Undoubtedly, ocean conditions are responsible for some of the variation in conditions experienced during bay residency. Nevertheless, there was a stronger temporal association between environmental conditions experienced during bay residency and spawner return rates compared with conditions experienced during the longer ocean life stage.

We did find a small but significant proportion of the variation in return rates explained by the third ocean year factor. As data collected for this factor precede the dominant returning cohort of spawners, this effect may reflect the consequences of environmental conditions upon migration. For example, cold temperatures and strong north winds might facilitate survival as a result of reduced energetic demands on returning migrants. Testing this intriguing possibility would require a detailed multiyear analysis of size and condition of fish during adult migrations and information on locations of fish during their migration.

Density dependence.—Density dependence describes the compensatory effects of population size at various life stages on population dynamics (Ricker 1954; Rothschild 2000; Myers 2001). The number of eggs was a relatively important parameter across models for both measures of return rate, was included in the best AIC models, and had a significant negative effect on S_t. These findings point to the existence of compensatory processes during the juvenile life stages, when we would expect such a coarse predictor of density dependence to provide any sort of signal. Other work strongly suggests that density-dependent interactions control the timing, abundance, and size distribution of juveniles using tidal delta habitats (Neilson et al. 1985; Korman et al. 1997). One hypothesized mechanism of density dependence is density-dependent migration (Reimers 1973; Greene and Beechie 2004). A possible outcome of density-dependent migration is an influx of juveniles of poor condition or small size into Skagit Bay during large out-migrations. This mechanism may be particularly pronounced in the Skagit River delta where an estimated 80% habitat loss has occurred since the mid-1800s due to agricultural conversion (Collins et al. 2003). Data on seasonal changes in size distributions in Skagit Bay support this hypothesis (E. Beamer, unpublished data). This interpretation might also explain why we detected a much weaker relationship of return rate with environmental conditions experienced during tidal delta residency, compared with eggs and conditions experienced during bay residency.

Recently, Ruggerone and Goetz (2004) postulated an altogether different mechanism of density dependence for Chinook salmon in Puget Sound based on competition for food with pink salmon *O. gorbuscha*. They found a large difference in Chinook salmon marine survival based on coded wire tag data between years with and without pink salmon out-migrations. As the Skagit River is one of the largest sources of pink salmon in Puget Sound, this interspecific mechanism of density dependence should apply most strongly to Skagit River Chinook salmon. However, we were unable to detect a similar effect in our data based on two types of analyses. First, there was no strong autocorrelation in the residuals of our analysis as would be expected if the pink salmon population size were an unexplained source of the variation in return rate. Secondly, we could find no odd–even year difference in return rate. This pattern persisted even after we converted our return rate data to smolt–adult survival by rearranging equation (4) and by factoring out both exploitation using harvest rates and freshwater survival using the relationship of Seiler et al. (2003). The mean difference in survival between even brood years (high numbers of juvenile pink salmon) versus odd years was about 1%, and this difference was much less than the overall level of variation (CV = 14–15%). In the context of the conclusions drawn by Ruggerone and Goetz (2004), our findings suggest that

hatchery Chinook salmon compete much more with pink salmon than wild Chinook salmon. This premise is consistent with differences in the timing of estuarine entry and length of residency among pink salmon, wild Chinook salmon, and hatchery Chinook salmon (E. Beamer, unpublished data).

Management Implications

The modeling approach we have advocated should be extremely useful for managers because it utilizes information that can be obtained before Chinook salmon start to return to the Skagit River basin to spawn. Unlike other forecasting tools (e.g., coded wire tags from returning hatchery fish), it does not rely on information that can be utilized only after fish have already returned and applies specifically to wild fish (Bradford 1995; Friedland 1998; Petrosky et al. 2001). The data we used in our models are collected on a regular basis and widely available. Our approach is therefore repeatable in the Skagit River basin and in other watersheds, as long as data on habitat-specific residency and age-specific return rates are collected.

We used available redd count data to estimate spawner returns in a given year and egg populations in the following year. As explained in the methods, data like these have been criticized for their lack of accuracy. Given the possibility of developing precise predictions of population changes from escapement data, managers would stand to benefit from improved estimates of spawner returns using repeated redd counts over the period of peak spawning and combinations of redd count methods (snorkel surveys, foot surveys, aerial surveys) in the context of a carefully constructed monitoring design. These methods could enable managers to quantify false redds, spawners per redd, observer variability, and redd density. Potential inaccuracies in these measures likely serve to mute estimates of population size, with overreporting in low population years and underreporting in high population years. More accurate data may enable predictions that better track population extremes.

Another human-related bias affecting the precision of our modeling is variation in exploitation. Estimating exploitation rates (usually based on expansions of coded wire tag recoveries) has its own challenges, including inaccuracies based on low recoveries (Zhou 2002) and misapplication of survival data from hatchery stocks to wild populations (Nickelson 1986). We found a strong correspondence of S_t and R_t models, indicating that the ecological relationships largely overshadowed

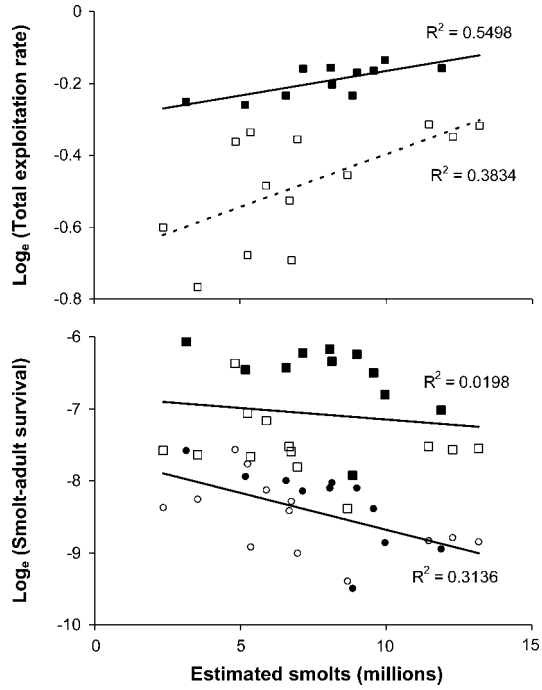

FIGURE 9.—**(A)** Log-transformed total exploitation rates (mixed stock plus terminal harvest) as a function of the estimated number of smolts (eggs adjusted by estimated freshwater survival) for brood years before 1985 (filled squares) and thereafter (open squares); **(B)** log-transformed smolt–adult survival (return rate data modified using a transformation of equation 4 and incorporating estimated freshwater survival) as a function of the estimated number of smolts based on recruits per spawner (squares) and spawners per spawner (circles) for brood years before 1985 (filled symbols) and thereafter (open symbols).

variation introduced by harvest estimation and suggesting that exploitation rates were relatively constant over time, in contrast to the estimates reported in Table 2. Furthermore, there were differences between S_t and R_t models, including lower overall explanatory power and lack of a significant density-dependent signal for the best R_t models.

To explore why these differences might arise, we examined exploitation rates and our estimated smolt–adult survival rate (survival rates adjusted by f) as a function of smolts (eggs adjusted by f). As shown in Figure 9A, exploitation rates were positively correlated with smolt abundance as would be expected if harvest were based on principles of maximum sustainable yield (Quinn and Deriso 1999). However, different relationships between exploitation rate and population size arose before and after the 1985 brood year, correspond-

ing to a large change in the Pacific Decadal Oscillation (PDO; Hare et al. 1999). When exploitation rate was not accounted for in smolt–adult survival (i.e., based on S_t), a density-dependent relationship emerged despite the suggestion of a regime difference (Figure 9B). When exploitation was incorporated into overall survival (using R_t), the temporal change in the pattern of exploitation both magnified the overall variation in survival rate and obscured the density-dependent relationship (Figure 9B). However, the compensatory relationship was still evident within each regime. These findings are important for several reasons. First, these findings illustrate that S_t and R_t models did strongly correspond within regimes despite changes in harvest over time. Second, they highlight why the density-dependent relationship was less strong in the R_t models: changes in the pattern of exploitation between regimes muted the overall density-dependent relationship, above and beyond the possible moderating effect of density-dependent harvest rates upon compensatory processes. Third, they indicate that harvest did not nullify density-dependent processes within regimes, supporting the conclusion that compensatory processes occur primarily during juvenile life history stages. These findings argue for comparisons of S_t and R_t models when extracting environmental relationships from fisheries data.

If our model correctly captures both ecological mechanisms driving Chinook salmon population performance and biases in its estimation, it should be useful to investigate predicted population responses to the intercorrelated processes of climate change such as the El Nino–Southern Oscillation (ENSO), the PDO, or global warming. We should expect climate to affect salmonid populations via simultaneous effects on both freshwater and marine systems. For example, flood magnitude is positively associated with air temperature (Redmond and Koch 1991; Kiffney et al. 2002), and we might therefore expect ENSO years to be associated with stronger floods and lower freshwater survival. However, warmer sea surface temperatures, lower atmospheric sea level pressure, and lower upwelling activity are also associated with ENSO events (Hare et al. 1999). These characteristics are positively correlated with higher return rates if incurred during bay residency, and negatively correlated with return rate if incurred during the third ocean year (see also Kope and Botsford 1990). Overall survival is the composite of survival across multiple life stages, each of which occurs in a unique habitat and during a unique set of environmental conditions. These potentially complex interactions may help explain the difficulty researchers have had in accurately predicting return rates, and call for models like ours that integrate the entire life cycle.

Acknowledgments

We thank Mary Ruckelshaus, Pete Lawson, Robert Kope, Jonathan Hoekstra, Chris Jordan, and three anonymous reviewers for helpful comments on the manuscript. Nate Mantua, Bob Dattore, and Steve Worley helped direct us to marine data sources. Reference to trade names does not imply endorsement by the U.S. Government.

References

Beamish, R. J., D. J. Noakes, G. A. McFarlane, W. Pinnix, R. Sweeting, and J. King. 2000. Trends in coho marine survival in relation to the regime concept. Fisheries Oceanography 9:114–119.

Belsley, D. A. 1991. Conditioning diagnostics: collinearity and weak data in regression. Wiley, New York.

Boeuf, G., and P. Payan. 2001. How should salinity influence fish growth? Comparative Biochemistry and Physiology 130C:411–423.

Botsford, L. W., and C. M. Paulsen. 2000. Assessing covariability among populations in the presence of intraseries correlation: Columbia River spring–summer Chinook salmon (*Oncorhynchus tshawytscha*) stocks. Canadian Journal of Fisheries and Aquatic Sciences 57:616–627.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1327–1338.

Bravender, B. A., S. S. Anderson, and J. Van Tine. 1999. Distribution and abundance of juvenile salmon in Discovery Harbour Marina and surrounding area, Campbell River, B. C., during 1996. Canadian Technical Report of Fisheries and Aquatic Sciences 2292:1–45.

Burnham, K. P., and D. R. Anderson 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Cannon, G. A., J. R. Holbrook, and D. J. Pashinski. 1990. Variations in the onset of bottom-water intrusions over the entrance sill of a fjord. Estuaries 13:31–42.

Caswell, H. 2001. Matrix population models. Sinauer Associates, Sunderland, Massachusetts.

Collins, B. D., D. R. Montgomery, and A. J. Sheikh. 2003. Reconstructing the historical riverine landscape of the Puget lowland. Pages 79–128 *in* D. R. Montgomery, S. Bolton, D. B. Booth, and L. Wall, editors. Restoration of Puget Sound rivers. University of Washington Press, Seattle.

Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho and fall Chi-

nook salmon in the Pacific Northwest. Bulletin of Marine Science 62:409–425.

De Ben, W. A., W. D. Clothier, G. R. Ditsworth, and D. J. Baumgartner. 1990. Spatiotemporal fluctuations in the distribution and abundance of demersal fish and epibenthic crustaceans in Yaquina Bay, Oregon. Estuaries 13:469–478.

DeVries, P. E. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Canadian Journal of Fisheries and Aquatic Sciences 54:1685–1698.

Erman, D. C., E. D. Andrews, and M. Yoder Williams. 1988. Effects of winter floods on fishes in the Sierra Nevada. Canadian Journal of Fisheries and Aquatic Sciences 45:2195–2200.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.

Friedland, K. D. 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. Canadian Journal of Fisheries and Aquatic Sciences 55:119–130.

Friedland, K. D., D. G. Reddin, J. R. McMenemy, and K. F. Drinkwater. 2003. Multidecadal trends in North American Atlantic salmon (*Salmo salar*) stocks and climate trends relevant to juvenile survival. Canadian Journal of Fisheries and Aquatic Sciences 60:563–583.

Fujiwara, M., and H. Caswell. 2001. Demography of the endangered North Atlantic right whale. Nature (London) 414:537–541.

Gargett, A. 1997. The optimal stability ''window'': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? Fisheries Oceanography 6: 109–117.

Greene, C. M., and T. J. Beechie. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 61:590–602.

Hahn, P., C. Kraemer, D. Hendrick, P. Castle, and L. Wood. 2001. Washington State Chinook salmon spawning escapement assessment in the Stilliguamish and Skagit Rivers, 1998. Report of Washington Department of Fish and Wildlife to Pacific Salmon Commission, Olympia, Washington.

Handeland, S. O., A. Berge, B. T. Bjornsson, and S. O. Stefansson. 1998. Effects of temperature and salinity on osmoregulation and growth of Atlantic salmon (*Salmo salar* L.) smolts in seawater. Aquaculture 168:289–302.

Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries 24(1):6–14.

Harrell, F. E., Jr. 2001. Regression modeling strategies with application to linear models, logistic regression, and survival analysis. Springer-Verlag, New York.

Healey, M. C. 1991. Life history of Chinook salmon *Oncorhynchus-tshawytscha*. Pages 313–394 *in* C. Groot, and L. Margolis, editors. Pacific salmon life histories. UBC Press, Vancouver.

Henderson, R., and R. A. Hayman. 2002. FY 2002 Skagit summer Chinook indicator stock study. Report of Skagit System Cooperative to Northwest Indian Fisheries Commission, La Connor, Washington.

Hickey, B. M., and N. S. Banas. 2003. Oceanography of the U.S. Pacific Northwest coastal ocean and estuaries with application to coastal ecology. Estuaries 26:1010–1031.

Hilborn, R., B. G. Bue, and S. Sharr. 1999. Estimating spawning escapement from periodic counts: a comparison of methods. Canadian Journal of Fisheries and Aquatic Sciences 56:888–896.

Holtby, L. B., and M. C. Healey. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 43:1946–1959.

Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring–summer Chinook salmon in the Columbia River basin. Science 290:977–979.

Kiffney, P. M., J. P. Bull, and M. C. Feller. 2002. Climatic and hydrologic variability in a coastal watershed of southwestern British Columbia. Journal of the American Water Resources Association 38: 1437–1451.

Kope, R. G., and L. W. Botsford. 1990. Determination of factors affecting recruitment of Chinook salmon *Oncorhynchus tshawytscha* in central California. Fishery Bulletin 88:257–269.

Korman, J., B. Bravender, and C. D. Levings. 1997. Utilization of the Campbell River estuary by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in 1994. Canadian Technical Report of Fisheries and Aquatic Sciences 2169:1–45.

Koski, K. V. 1966. The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams. Master's thesis. Oregon State University, Corvallis.

Koslow, J. A., A. J. Hobday, and G. W. Boehlert. 2002. Climate variability and marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. Fisheries Oceanography 11:65–77.

Latterell, J. J., K. D. Fausch, C. Gowan, and S. C. Riley. 1998. Relationship of trout recruitment to snowmelt runoff flows and adult trout abundance in six Colorado mountain streams. Rivers 6:240–250.

Lawson, P. W., E. A. Logerwell, N. J. Mantua, R. C. Francis, and V. N. Agostini. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 61:360–373.

Lisle, T. E., and J. Lewis. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream: a simulation approach. Canadian Journal of Fisheries and Aquatic Sciences 49:2337–2344.

Logerwell, E. A., N. J. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for under-

standing and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554–568.

Lotspeich, F. B., and F. H. Everest. 1981. A new method for reporting and interpreting textural composition of spawning gravel. U.S. Forest Service Research Note PNW-369.

Magnuson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. Estuaries 26:1094–1103.

Mason, J. C. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26:63–91.

McCullagh, P., and J. A. Nelder 1989. Generalized linear models. Chapman and Hall, London.

Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Schuett Hames, and T. P. Quinn. 1996. Streambed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061–1070.

Morita, S. H., K. Morita, and H. Sakano. 2001. Growth of chum salmon (*Oncorhynchus keta*) correlated with sea-surface salinity in the North Pacific. ICES Journal of Marine Science 58:1335–1339.

Mortensen, D., A. Wertheimer, S. Taylor, and J. Landingham. 2000. The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. Fishery Bulletin 98: 319–335.

Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002a. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 59:456–463.

Mueter, F. J., D. M. Ware, and R. M. Peterman. 2002b. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the northeast Pacific Ocean. Fisheries Oceanography 11: 205–218.

Myers, J. M., R. G. Kope, G. J. Bryant, D. J. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. Lindley, and R. S. Waples. 1997. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NEFSC-35.

Myers, R. A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. ICES Journal of Marine Science 58:937–951.

Neilson, J. D., G. H. Geen, and D. Bottom. 1985. Estuarine growth of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences 42:899–908.

Neter, J., M. H. Kutner, C. J. Nachtscheim, and W. Wasserman. 1996. Applied linear regression models. Irwin, Homewood, Illinois.

Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Canadian Journal of Fisheries and Aquatic Sciences 43:527–535.

Parker, R. R. 1971. Size-selective predation among juvenile salmonid fishes in a British Columbia inlet. Journal of the Fisheries Research Board of Canada 28:1503–1510.

Peterman, R. M., B. J. Pyper, M. F. Lapointe, M. D. Adkison, and C. J. Walters. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. Canadian Journal of Fisheries and Aquatic Sciences 55:2503–2517.

Petrosky, C. E., H. A. Schaller, and P. Budy. 2001. Productivity and survival rate trends in the freshwater spawning and rearing stage of Snake River Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 58:1196–1207.

Quinn, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Redmond, K. T., and R. W. Koch. 1991. Surface climate and streamflow variability in the western United States and their relationship to large-scale circulation indices. Water Resources Research 27:2381–2399.

Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Research Reports of the Fish Commission of Oregon 4:1–42.

Rencher, A. C. 1998. Multivariate statistical inference and applications. Wiley, New York.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559–623.

Rothschild, B. J. 2000. ''Fish stocks and recruitment'': the past thirty years. ICES Journal of Marine Science 57:191–201.

Ruckelshaus, M. H., P. S. Levin, J. B. Johnson, and P. Kareiva. 2003. The Pacific salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33: 665–706.

Ruesink, J. L., G. C. Roegner, B. R. Dumbauld, and J. A. Newton. 2003. Contributions of coastal and watershed energy sources to secondary production in a northeastern Pacific estuary. Estuaries 26:1079–1093.

Ruggerone, G. T., and F. A. Goetz. 2004. Survival of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*). Canadian Journal of Fisheries and Aquatic Sciences 61:1756–1770.

Seegrist, D. W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101:478–482.

Seiler, D., S. Neuhauser, and L. Kishimoto. 2003. 2002 Skagit River wild 0+ Chinook production evalua-

tion annual report. Washington Department of Fish and Wildlife, Olympia.

Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343–364 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Sumioka, S. S., D. L. Kresch, and K. D. Kasnick. 1998. Magnitude and frequency of floods in Washington. U.S. Geological Survey, Water Resources Investigations Report 97-4277, Denver.

Thom, R. M., A. B. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. A. Southard, and S. L. Sargeant. 2003. Factors influencing spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Willapa Bay, Washington, and Coos Bay, Oregon, estuaries. Estuaries 26:1117–1129.

Thomas, A. E., J. L. Banks, and D. C. Greenland. 1969. Effect of yolk sac absorption on the swimming ability of fall Chinook salmon. Transactions of the American Fisheries Society 98:406–410.

Thomson, R. E. 1994. Physical oceanography of the Strait of Georgia–Puget Sound–Juan de Fuca Strait system. Review of the marine environment and biota of Strait of Georgia, Puget Sound, and Juan de Fuca Strait. Canadian Technical Report of Fisheries and Aquatic Sciences 1948:36–100.

Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17:76–93.

U.S. Water Resources Council. 1981. Guidelines for determining flood flow frequency. U.S. Water Resources Council, Bulletin 17B, Washington D.C.

Walters, C. J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock–recruitment relationships. Canadian Journal of Fisheries and Aquatic Sciences 38:704–710.

Washington Department of Fisheries and Wildlife and Western Washington Treaty Indian Tribes. 1992. Washington State salmon and steelhead stock inventory (SASSI). Washington Department of Fisheries and Wildlife, Olympia.

Willette, T. M., R. T. Cooney, V. Patric, D. M. Mason, G. L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fisheries Oceanography 10: 14–41.

Zabel, R. W., and J. G. Williams. 2002. Selective mortality in Chinook salmon: what is the role of human disturbance? Ecological Applications 12:173–183.

Zhou, S. J. 2002. Uncertainties in estimating fishing mortality in unmarked salmon in mark-selective fisheries using double-index-tagging methods. North American Journal of Fisheries Management 22:480–493.

Transactions of the American Fisheries Society 135:456, 2006
© Copyright by the American Fisheries Society 2006
DOI 10.1577/T05-037e.1

ERRATUM

Erratum: Effects of Environmental Conditions during Stream, Estuary, and Ocean Residency on Chinook Salmon Return Rates in the Skagit River, Washington

C. M. Greene, D. W. Jensen, G. R. Pess, E. A. Steel, and E. Beamer

Volume 134(6), November 2005: 1562–1581.
Page 1575, Equation 7 should read as follows:

$$f = -4.065\mathrm{E} - 05 \cdot M + 0.190.$$