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Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*)

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ABSTRACT

Effective conservation and management of natural resources requires accurate predictions of ecosystem responses to future climate change, but environmental science has largely failed to produce these reliable forecasts. The future response of Pacific salmon (*Oncorhynchus* spp.) to a changing environment and continued anthropogenic disturbance is of particular interest to the public because of their high economic, social, and cultural value. While numerous retrospective analyses show a strong correlation between past changes in the ocean environment and salmon production within the north Pacific, these correlations rarely make good predictions. Using a Bayesian time-series model to make successive 1-yr-ahead forecasts, we predicted changes in the ocean survival of Snake River spring/summer chinook salmon (*O. tshawytscha*) from indices of coastal ocean upwelling with a high degree of certainty ($R^2 = 0.71$). Furthermore, another form of the dynamic times-series model that used all of the available data indicated an even stronger coupling between smolt-to-adult survival and ocean upwelling in the spring and fall ($R^2 = 0.96$). This suggests that management policies directed at conserving this threatened stock of salmon need to explicitly address the important role of the ocean in driving future salmon survival.

Key words: climate, forecast, prediction, salmon, Snake River, time series, upwelling

INTRODUCTION

The ability to forecast future effects of global change on ecosystems and the services that they provide to human society represents an emerging imperative for environmental science (Clark *et al.*, 2001). This becomes more essential as climate change, alteration of nutrient cycles, species introductions and extinctions, the spread of disease, and pollution increasingly threaten the natural resources on which we rely for food, fiber, and freshwater (Carpenter, 2002). In marine ecosystems, historical overfishing by humans and changes in the ocean environment interacted to drastically reduce invertebrate, fish, and marine mammal populations around the globe (Jackson *et al.*, 2001). As we continue to heavily exploit fish stocks (Pauly *et al.*, 1998) while altering the earth's ecosystems (Vitousek *et al.*, 1997), effective conservation and management will require a forward-looking perspective that explicitly addresses the role of an uncertain global environment.

Throughout their range, Pacific salmon (*Oncorhynchus* spp.) hold enormous social, economic, and cultural value, and therefore society places paramount importance on predicting the response of salmon populations to future anthropogenic disturbances and natural changes in the environment (Ruckelshaus *et al.*, 2002). Nevertheless, current predictions of the response of salmon to future climate change are not specific enough (Melack *et al.*, 1997) to aid in the development of management actions to ensure sustainable fisheries, or even population existence. The Columbia River of the northwest United States historically produced the greatest runs of chinook salmon (*O. tshawytscha*) in the world. By the 1990s however, >90% declines in their abundance led to the listing of five evolutionarily significant units under the Endangered Species Act, two within the largest tributary, the Snake River (Fig. 1). Much of the debate surrounding the cause of their decline centers on the '4 Hs': habitat degradation, harvest, hydroelectric and other dams, and hatchery production (Ruckelshaus *et al.*, 2002), but Snake River chinook salmon are not currently exploited to the degree they once were (Schaller *et al.*, 1999). Recent analyses point to the 4 Hs as important drivers of salmon declines in this region, but they also identify the ocean as a source of unexplained variance

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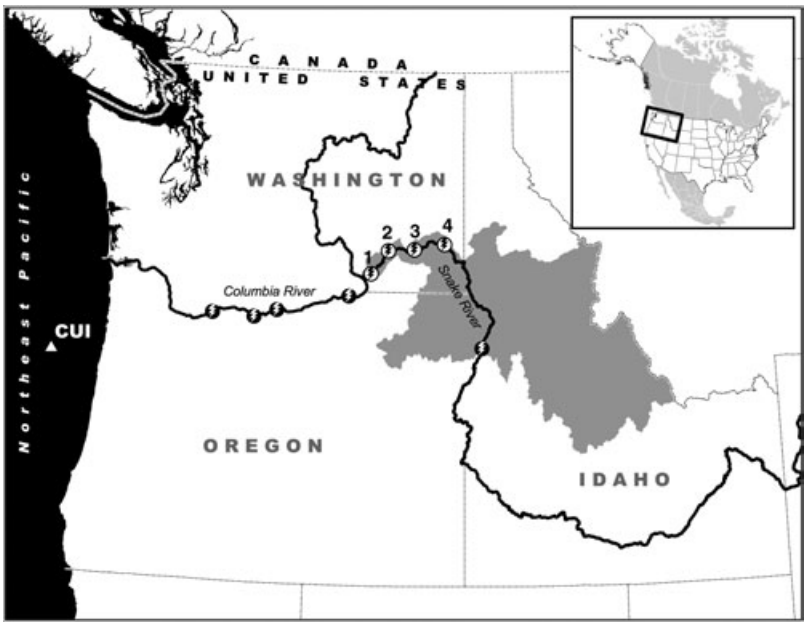


Figure 1. Map of the study area showing the Snake River basin (gray shading), the four hydroelectric dams on the lower Snake River used to enumerate juvenile and adult salmon for estimating smolt-to-adult survival (open symbols numbered 1–4), and the location of the coastal upwelling index at 45°N 125°W. The fifth hydroelectric dam shown on the upper Snake River denotes Hells Canyon Dam (solid symbol), a barrier to anadromous fish.

(Kareiva *et al.*, 2000; Deriso *et al.*, 2001; Levin *et al.*, 2001; Wilson, 2003). While numerous retrospective analyses show a strong correlation between past changes in the ocean environment and salmon production within this region (Mantua *et al.*, 1997; Beamish *et al.*, 1999b; Hare *et al.*, 1999; Levin *et al.*, 2001), these correlations rarely make good predictions because they tend to break down over time without any apparent cause (Nickelson, 1986; Gargett, 1997).

Here we explore the role of ocean-climate conditions in predicting the marine survival of Snake River spring/summer (SRSS) chinook salmon using extensive time series of its smolt-to-adult survival rate (SAR). Traditional quantitative approaches to fisheries management that rely solely on the numbers of spawning fish to predict future returns have largely proven inadequate, as they typically ignore the other environmental processes that affect salmon throughout their complex life history (Botsford *et al.*, 1997; Hare and Mantua, 2000). We adopted another approach using formal time-series analyses to explicitly predict how a changing ocean environment affects the marine survival of salmon. We use seasonal changes in coastal upwelling of the northeast Pacific to make successive 1-yr-ahead forecasts of the SAR of SRSS chinook salmon and compare those to the observed survival.

METHODS

Ocean-climate data

We chose the Pacific Coastal Upwelling Index (CUI), otherwise known as the Bakun Index, as our measure of ocean-climate conditions. Coastal upwelling is thought to influence salmon during their ocean residence through bottom-up forcing of the marine food web (Nickelson, 1986; Gargett, 1997), and has been used by others to compare the ocean environment to catches of Pacific salmon and Dungeness crab in this region (Botsford and Lawrence, 2002). We obtained the CUI from the National Marine Fisheries Service Pacific Fisheries Environmental Lab (PFEL, http://www.pfeg.noaa.gov, last accessed 1 July 2004). On a monthly basis, PFEL generates indices of the intensity of large-scale, wind-induced coastal upwelling at 15 standard locations along the west coast of North America (each 3° of latitude from 21°N to 60°N). Following Botsford and Lawrence (2002), we chose the CUI for 45°N latitude 125°W longitude (Fig. 1) to compare with ocean survival of chinook salmon from the Columbia River Basin. This area of the north Pacific represents a region that salmon from the Columbia River move into after reaching the ocean (Miller *et al.*, 1983). Previous studies suggest that the primary influence of the ocean on salmon survival occurs within the first year that juveniles occupy coastal waters (Pearcy, 1992). Rather than test all 12 months as predictor variables in the time-series model, we first conducted a backward stepwise regression using all 12 months as predictors of the observed SAR. We used the year of ocean entry for March through December, but shifted it 1 yr ahead for January and February to reflect the salmon's first winter at sea. The multiple regression analysis identified April, September, and October as significant

Table 1. Results of the backward-stepwise regression analysis to identify appropriate months of upwelling to use as predictor variables for the survival of wild Snake River spring-summer chinook salmon in the time-series model. Results are based on $N = 37$ yr of data (1964–2000) with an overall model fit of $R^2 = 0.39$.

Source	SS	df	MS	F	P-value
Regression	30.7	3	10.2	6.92	<0.001
Residual	48.8	33	1.48		
Total	79.5	36			

Effect	Coefficient	SE	t	P-value
Intercept	0.776	0.296	2.62	0.013
April	0.016	0.0091	1.80	0.081
September	0.027	0.0100	2.68	0.011
October	−0.027	0.0112	−2.44	0.020

predictors (Table 1), and therefore we tested all eight combinations of those 1–3 months as predictor variables in the time-series model (see below).

Salmon data

We used 37 yr of data on wild SRSS chinook salmon to analyze the effect of ocean-climate conditions on SAR. Because SRSS chinook salmon typically spend 1–3 yr in the ocean (but sometimes 4 yr), we calculated ocean survival as the percent of smolts migrating to the ocean in a given year that returned as adults 1, 2, 3, and 4 yr later. We thus required estimates of smolt abundance from outmigration years 1964 to 2000 and the corresponding adult returns for years 1965 through 2003. Counts of juvenile and adult chinook salmon passing the uppermost dam on the Snake River provide the basis for estimating smolt and adult salmon abundance (Fig. 1). During the time period examined here, the number of dams on the lower Snake River increased from one to four (numbered 1–4 on Fig. 1), such that our fish counts come from the following dams: Ice Harbor (pre-1969), Lower Monumental (1969), Little Goose (1970–74), and Lower Granite (1975–present). The actual method of counting fish at each of these dams, however, did not change over time.

All of the smolt and adult data plus the SARs are provided in Appendix A. We direct readers interested in the details of these methods to Williams *et al.* (2005). We used estimates of wild smolts for the period 1964–84 reported by Raymond (1988). We derived estimates for wild smolts from 1993 to 2003 by expanding the daily counts of wild smolts at Lower Granite Dam (http://www.fpc.org, last accessed 1 July 2004), by the daily estimates of their detection probability at the dam as described by Sandford and Smith (2002). For smolt years 1995–2003, we adjusted smolt estimates by an estimated percentage of non-clipped hatchery fish arriving at the dam not identified as of hatchery origin. From 1985 to 1993 direct counts of smolt abundance were not available and therefore we based smolt abundance on a Beverton–Holt curve ($R^2 = 0.62$, Zabel *et al.*, 2005) generated from the number of smolts from 1964 to 1984 and 1994 to 2003, and the number of wild spawners passing the uppermost Snake River dam 2 yr earlier corrected for any in-river harvest above the dam (derived from Petrosky *et al.*, 2001; Williams *et al.*, 2005).

The counts of adults include both wild and hatchery fish and, for the period between 1964 and 1992, we used the estimated annual adult returns of wild spring-summer chinook salmon to the upper dam on the Snake River from Petrosky *et al.* (2001). From 1993 to 1996 we used the age-4 and age-5 wild adult returns from Petrosky *et al.* (2001), but recalculated the wild age-3 returns to account for fish enumerated in Oregon rivers (R.C.P. Beamsderfer, Oregon Department of Fish and Wildlife, Salem, OR, USA, unpublished data). Fish counters assigned fish to either a group with adipose fins (ostensibly wild fish) or a group without adipose fins (known hatchery fish with fins clipped as juveniles). For the period between 1997 and 2002, we derived the annual number of wild fish by adjusting counts of non-adipose-fin-clipped adults passing the counting window at the uppermost Snake River dam by the estimated proportion of non-clipped hatchery fish in the return (fish with an adipose fin, but possibly with other clipped fins). We then subtracted the corrected hatchery count from the total adult return to derive the wild fish estimate.

For the period between 1964 and 1999, we used age-class distributions calculated from age-of-return data in Petrosky *et al.* (2001) to assign fish in a return year to the year in which they migrated as smolts to the ocean. Beginning in 1997, we estimated age-class data based on returns of adults that were implanted with Passive Integrated Transponder (PIT) tags as juveniles (for details see Achord *et al.*, 1996). Finally, to account for Columbia River harvest rates that varied between 0 and 40%, we expanded adult returns to the uppermost Snake River dam for the period between 1964 and 1999 based on estimated Columbia River harvest rates by Petrosky *et al.* (2001). We expanded adult returns for 2000–03 based on unpublished harvest rates (Peter Dygert, NOAA Fisheries, Seattle, Washington, personal communication). As we do not yet have complete returns of adult salmon from

the 2001 and 2002 outmigrations, we made preliminary estimates of the SAR for 2001 based on expansions of the age-3 and age-4 returns and for 2002 based on expansions of the age-3 adults, using the average age-composition from the 1964–2000 outmigrations.

Time-series analyses

We modeled the effect of ocean-climate conditions on salmon survival using a class of Bayesian time-series models known as dynamic linear models (DLMs), a form of the more general Kalman filter (Pole *et al.*, 1994). This technique has been applied effectively to ecological data, and the methodology has been described in detail elsewhere (Lamon *et al.*, 1998; Scheuerell *et al.*, 2002), so we only describe it briefly here. At each time step t the observed response variable (Y_t, a scalar) is sequentially fitted to the $1 \times m$ vector of predictor variables ($\boldsymbol{X}_t$), with the $m \times 1$ regression parameter vector (θ_t) plus an error term (v_t, a scalar) according to the observation equation

$$Y_t = \mathbf{X}_t \boldsymbol{\theta}_t + v_t \qquad v_t \sim N[0, V_t]. \tag{1}$$

The observation errors v_t have a variance V_t that is time dependent and is usually not known well enough to approximate it with a fixed value. Therefore, as the analysis proceeds through time, V_t is estimated from all of the prior data. The discounting scheme described below also applies to V_t. The size of m equals the total number of parameters used in forecasting (i.e. any level, slope, and regression parameters).

The DLM makes use of changes in the parameter set over time through a system equation. Using prior information from Bayesian learning, the $m \times 1$ vector of regression parameters (θ_t) evolves through time according to the first-order Markov process

$$\boldsymbol{\theta}_t = \mathbf{G}\boldsymbol{\theta}_{t-1} + \boldsymbol{\omega}_t \qquad \boldsymbol{\omega}_t \sim N[\mathbf{0}, \mathbf{W}_t]. \tag{2}$$

The $m \times m$ system evolution matrix $\mathbf{G}$ dictates how the parameters change systematically through time while the $m \times 1$ variance vector ω_t describes the stochastic change in each of the parameter estimates (θ_t) over time. In this case, $\mathbf{G}$ is simply the identity matrix, but could take a more complex form in other ecological applications. The system variance matrix ($\mathbf{W}_t$) has the variance in ω_t along the diagonal and zeros elsewhere. $\mathbf{W}_t$ is determined by the component discount factors applied to the posterior covariance matrix of the previous time step (Pole *et al.*, 1994).

One-year-ahead forecasts are generated at each time step, and the parameters are updated as new information becomes incorporated into the model. Through the use of discounting, priors are given weights that determine how influential the prior data are when updating the parameter estimates. These discounts essentially represent the rate of exponential decay of useful information such that when the discount is 1 (its maximum value), all of the prior information is retained, whereas a discount near 0 means no prior information is used at all. In general, the lower the discount value, the faster a parameter can change through time, but at the cost of decreased precision of the estimate. We selected the discounts by varying them systematically and then minimizing the negative log-likelihood of the overall model. Our final discounts were 0.9, 0.95, and 0.9 for the trend, regression, and variance blocks, respectively.

Assessing the likelihood of the observed data given a particular model is the straightforward case using normally distributed errors as defined by Hilborn and Mangel (1997), where the negative log-likelihood (L) for the forecast model is given by

$$L = n\left[\frac{1}{2}\log(2\pi) + \ln(\sqrt{V_t|D_{t-1}})\right] + \sum_{t=1}^{n} \frac{(Y_t - X_t\theta_t|D_{t-1})^2}{2(V_t|D_{t-1})}, \tag{3}$$

where the forecast variance (V_t) depends on the data only through the previous time step (D_{t-1}). By using all of the available data including the observation in the current year (D_t), we can derive the best statistical fit of the model to the observed time series. In this case, the estimates of both the parameter vector ($\theta_t \mid D_t$) and the observation variance ($V_t \mid D_t$) benefit from the increased knowledge gained by observing the current data point.

We used several metrics for assessing the performance of our time-series models for predicting the SAR of SRSS chinook salmon. First, we ranked all competing models according to their posterior negative log-likelihood (L), such that the lowest negative log-likelihood ($L_{\min}$) was the best. Next, we compared alternative models through the use of cumulative Bayes factors (H), which essentially represent the odds of one model in comparison with another (Jeffries, 1961; Kass and Raftery, 1995; Lamon *et al.*, 1998). We did this for two cases: to compare any specific climate model to its reference model ($H_{\mathrm{ref},i}$) and to compare the best overall model to all others ($H_{\min,i}$). Because we used the negative log-likelihood, the Bayes factor for the first case becomes the difference in log-likelihood between the reference model (L_{ref}) and any other model (L_i),

$$H_{\mathrm{ref},i} = L_{\mathrm{ref}} - L_i, \tag{4a}$$

or for the second case, the overall best model ($L_{\min}$) and any other model (L_i):

$$H_{\min,i} = L_{\min} - L_i. \quad (4b)$$

According to Kass and Raftery (1995), when $2H_{\mathrm{ref},i}$ is 0 to 2, the evidence favoring model i over its reference model is 'not worth more than a bare mention'; 2–6 indicates 'positive', 6–10 offers 'strong', and >10 provides 'very strong' evidence for the model over its reference. The criteria are the same for $2H_{\min,i}$, but with opposite sign, effectively indicating the 'weight of evidence' against the lower ranked model compared to the best overall model.

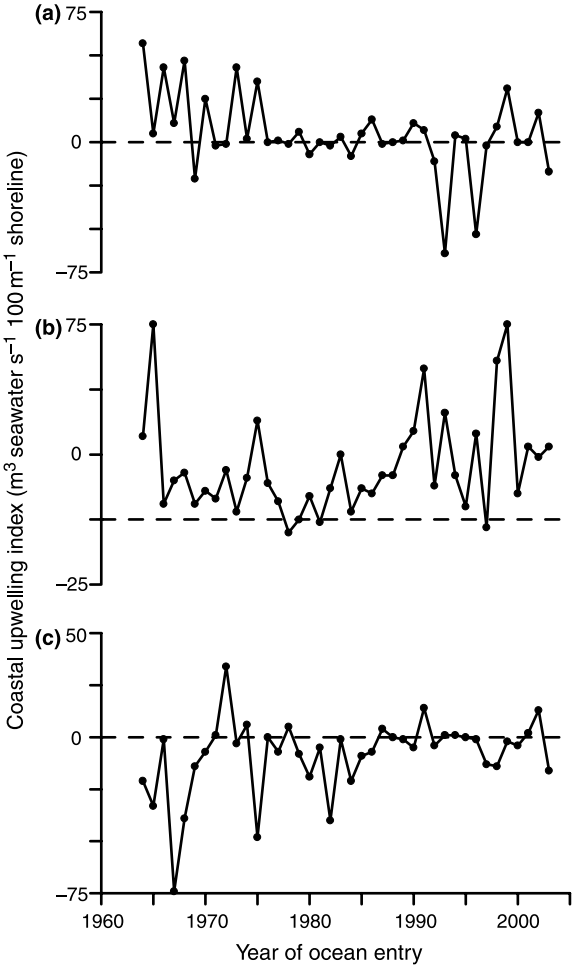
RESULTS

The magnitude of the CUI showed considerable variation over the duration of our study (Fig. 2). During April, the CUI was generally positive until 1975, when it remained near zero with the exception of a few strong downwelling years in 1993 and 1996 (Fig. 2a). During September, we observed predominantly positive CUI values (upwelling), with particularly strong upwelling in 1965 and after 1990 (Fig. 2b). In October, the CUI indicated strong downwelling in the late 1960s, but the intensity weakened through the mid 1980s until it fluctuated around zero for the remainder of the time series (Fig. 2c).

We observed a dramatic decrease in the SAR of wild SRSS chinook salmon during the late 1960s and early 1970s (Fig. 3), followed by a relatively flat period until the 1992 and 1993 outmigrations, when we observed the lowest SAR on record. Beginning with the 1994 outmigration however, the survival of salmon in the ocean started to climb again through 1999, when we observed SARs near the highest on record. The preliminary estimates of SAR for the 2001 and 2002 outmigrations also suggest continued high marine survival near 4% (Fig. 3).

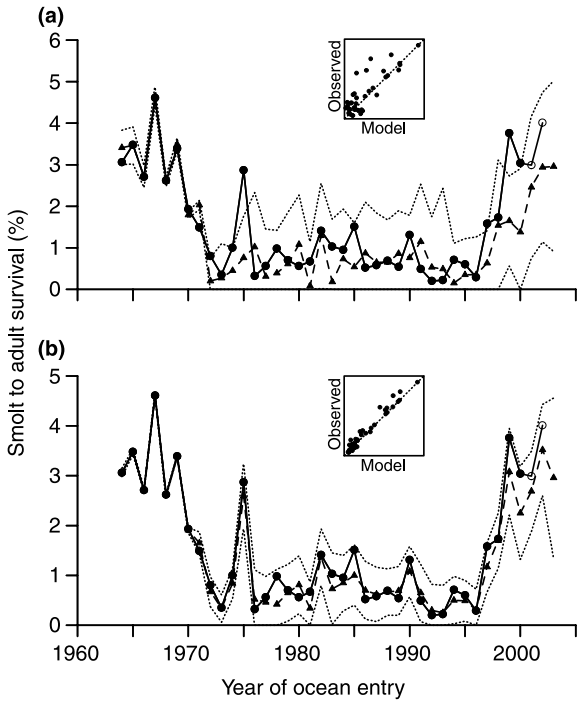
The overall best model for predicting SAR included a linear trend term plus all 3 months (April, September, October) of the CUI (Table 2). Of the 14 upwelling-related models that we examined, 12 of them performed significantly better than their respective reference models based on an autocorrelated random walk. In general, models including the October CUI performed better than those with the other months. Similarly, models incorporating a linear trend also tended to predict SAR better than those without a trend term. All of the models met the necessary condition of no serial autocorrelation of the residuals.

Figure 2. Time series of the Pacific coastal upwelling index calculated for (a) April, (b) September, and (c) October from 1964 to 2003 at 45°N 125°W.



The forecasts of the top-ranked CUI model including all 3 months matched observed survival rates reasonably well over the duration of the time series ($R^2 = 0.71$) and, with few exceptions, the observed data fell within the 90% uncertainty limits of the model forecasts (Fig. 3a). The wider prediction limits surrounding some of the forecasts reflected greater model uncertainty resulting from relatively poor predictions in prior years; the prediction errors decreased in magnitude as more data became incorporated into the analysis. However, the forecasting model only relies on prior data up to, but not including, the observation in the current year. When we fit the time-series model using all data up to, and including, the observation in the current year (Fig. 3b), we found a much better fit ($R^2 = 0.96$). This so-called 'online' fit essentially represents our best statistical description of the temporal dynamics in SAR.

Figure 3. Time series of the smolt-to-adult survival (SAR) for wild Snake River spring-summer chinook salmon (solid circles) from 1964–2002 compared to (a) the 1-yr-ahead model forecasts (triangles), and (b) the best-fit model based on all of the available data (triangles). Dotted lines in each panel represent the 90% credible limits around the (a) forecast and (b) best-fit models. Inset plots show the fit between the modeled and observed SAR (scale is 0–5% for both axes) for the (a) forecast ($R^2 = 0.71$), and (b) best-fit models ($R^2 = 0.96$). Note that the estimates of SAR for the 2001 and 2002 outmigrations (open circles) are preliminary in that they are based on age-3 (jack) returns in 2002 and 2003. The forecast of the SAR for the 2003 outmigration is also shown.



DISCUSSION

Interannual variation in environmental indices is usually quite high, and therefore, analyses of ocean-climate effects on salmon survival benefit from long time series (Gargett, 1997; Mantua *et al.*, 1997; Beamish *et al.*, 1999a; Hare *et al.*, 1999). Using 37 yr of data on wild SRSS chinook salmon, we found interesting patterns in their SAR (Fig. 3). The observed decline in survival during the late 1960s and early 1970s predated the oft-cited effect of the ocean 'regime shift' that occurred in 1977 (Mantua *et al.*, 1997; Beamish *et al.*, 1999b), but did coincide with the construction of four additional dams on the lower Snake and Columbia Rivers through which migrants must pass (Schaller *et al.*, 1999; Levin and Tolimieri, 2001). Furthermore, hatchery operations and habitat modifications have also negatively affected these salmon (Ruckelshaus *et al.*, 2002). Most likely, the aforementioned anthropogenic activities interacted with a shift toward poor ocean conditions to drive the observed decline in SAR (Anderson, 2000; Deriso *et al.*, 2001; Wilson, 2003). Since the mid-1990s however, the SAR of this threatened fish stock has increased, apparently resulting from combined improvements to fish passage through the hydropower system and better ocean conditions. Here we concentrated on the important role of the ocean environment in driving the observed patterns in SAR.

We hypothesized that the CUI limits salmon survival through bottom-up forcing of the marine food web. During the spring and summer months, coastal upwelling events supply cool, nutrient-rich water to phytoplankton, increasing primary production and subsequent zooplankton production (Brodeur and Ware, 1992). This, in turn, should translate into better foraging conditions for juvenile salmon (Pearcy, 1992; Gargett, 1997) that generally enter the ocean from April through June (Miller *et al.*, 1983). Furthermore, the seasonal effects of the ocean environment may persist for over a year with varying amplitude and frequency (McGowan *et al.*, 1998), leading to the conditions that largely control salmon mortality during their first year in the ocean (Pearcy, 1992). In support of this hypothesis, we found that stronger upwelling in April and September led to increased SARs (Tables 1 and 2).

During the fall transition, the upwelling conditions normally subside, resulting in decreased zooplankton production. However, stronger downwelling in the fall could increase food supply to salmon through two mechanisms. First, strong fall downwelling appears to counteract the loss of zooplankton from this region through advective currents typically observed under the conditions that favor upwelling (Mackas *et al.*, 2001). Secondly, the poleward currents associated with downwelling events also tend to bring in southerly species of copepods and euphausiids from the California Current, increasing the overall biomass of zooplankton during the fall (Mackas *et al.*, 2001). These arguments therefore support our negative relationship between October downwelling (i.e. negative upwelling) and SAR (Tables 1 and 2). Furthermore, the transition between downwelling and upwelling (April) and then between upwelling and downwelling (October) is thought to be an important time of year for salmon in the ocean as it represents larger shifts in the physical environment and biological production (Ware and McFarlane, 1989; Logerwell *et al.*, 2003).

Table 2. Dynamic linear model results for predicting smolt-to-adult survival (SAR) for wild Snake River spring-summer chinook salmon from the monthly coastal upwelling index indices identified in Table 1. Trend refers to either a linear (slope + intercept) or constant (intercept only) trend term. Within each trend group, models are ranked in order of increasing predictive performance (i.e. lowest posterior negative log-likelihood [L_i]). The sign of the regression coefficient for each month is given in parentheses. The value $2H_{\mathrm{ref},i}$ provides evidence in favor of a model compared to its reference model, and $2H_{\mathrm{min},i}$ provides evidence against any model i relative to the best overall model L_{min}. Values of $2H$ equal to 2 (−2) and 6 (−6) represent 'positive' evidence for (against), and 'strong' evidence for (against) any model i, respectively. See Methods section for details.

		Predictors				Bayes factors	
Trend	Rank	X_1	X_2	X_3	L_i	$2H_{\mathrm{ref},i}$	$2H_{\mathrm{min},i}$
Linear	1	Apr (+)	Sept (+)	Oct (−)	51.8*	22.4	0.0
	2	Apr (+)	Oct (−)		54.7	16.6	−5.8
	3	Oct (−)			54.8	16.4	−6.0
	4	Sept (+)	Oct (−)		56.0	14.0	−8.4
	5	Sept (+)			62.9	0.2	−22.2
	6				63.0†	0.0	−22.4
	7	Apr (+)			63.6	−1.2	−23.6
	8	Apr (+)	Sept (+)		63.8	−1.6	−24.0
Constant	1	Sept (+)	Oct (−)		55.4	16.2	−7.2
	2	Oct (−)			56.4	14.2	−9.2
	3	Apr (+)	Oct (−)		56.7	13.6	−9.8
	4	Apr (+)	Sept (+)	Oct (−)	57.7	11.6	−11.8
	5	Sept (+)			62.2	2.6	−20.8
	6	Apr (+)	Sept (+)		63.3	0.4	−23.0
	7				63.5‡	0.0	−23.4
	8	Apr (+)			63.7	−0.4	−23.8

*The minimum negative log-likelihood (L_{min}) for the entire set of models.
†The reference negative log-likelihood (L_{ref}) for the set of models including a linear trend.
‡The reference negative log-likelihood (L_{ref}) for the set of models including a constant trend.

Strong summer upwelling followed by weak downwelling may help to retain northerly species of zooplankton and thereby provide additional food to salmon (Mackas *et al.*, 2001).

Our modeling approach relied on a Bayesian framework with prior data for predicting SAR. This might lead one to wonder whether the improved SAR that we predicted in recent years was simply driven by strong influence of the priors from the 1960s. To verify that this was not the case, we also ran our analysis beginning in 2000 and moving backwards through time to 1964. The results differed slightly in the details, but the general pattern was the same ($R^2 = 0.69$ for the forecast model; $R^2 = 0.92$ for the online model). Therefore, we conclude that the improved survival in recent years is a function of ocean-climate conditions, but acknowledge that even if ocean-climate conditions improve dramatically, combined effects of the '4 Hs' on this, and other life stages, may suppress adult returns to levels below those observed in the 1960s (Kareiva *et al.*, 2000; Wilson, 2003). Therefore, management policies directed at mitigating the effects of the '4 Hs' on this threatened stock of fish should explicitly address the important role of the ocean in driving future salmon survival (Lawson, 1993; Botsford *et al.*, 1997; Deriso *et al.*, 2001).

We acknowledge that SAR is a function of ocean conditions over the entire time period that salmon spend at sea, but the literature certainly suggests that the first year at sea is the most critical and largely determines the year-class strength (Pearcy, 1992; Gargett, 1997; Beamish and Mahnken, 2001). Thus, we concentrated on this critical time in the life history of salmon. Furthermore, shifts in the age at maturity of salmon and the subsequent timing of adult returns to freshwater could change the SAR without any changes in ocean survival. In this case, however, the age composition of SRSS chinook salmon has shown very little systematic variation over time with nearly equal proportions of age-4 and age-5 adults (Appendix A).

Previous investigations have used commercial catches of salmon to illustrate a coupling between salmon survival and ocean-climate 'regimes' (e.g. Mantua *et al.*, 1997; Beamish *et al.*, 1999b), but they

are largely correlative or based on visual inspection (Botsford and Lawrence, 2002). While these types of analyses offer insights into general patterns, they also tend to lose any predictive power during climate regime shifts and therefore require another set of new data to derive a new relationship after the fact (Nickelson, 1986; Gargett, 1997). On the contrary, our analysis using actual estimates of SAR appeared robust to the three regime shifts that occurred in the northeast Pacific during 1977, 1989 (Hare and Mantua, 2000), and 1998 (Peterson and Schwing, 2003). This encouraging result might reflect our use of a relatively small-scale ocean-climate index. Other researchers calculate regime shifts from large-scale basin-wide indices such as the Pacific decadal oscillation (Mantua *et al.*, 1997), but correlations between environmental variables and salmon survival do not generally hold at large spatial scales (Mueter *et al.*, 2002). For example, Logerwell *et al.* (2003) recently highlighted the importance of using small-scale oceanographic features to predict the SAR of Oregon coastal coho salmon (*O. kisutch*), and found a much stronger model fit ($R^2 = 0.75$ versus 0.47) than Koslow *et al.* (2002), who relied on a large-scale multivariate index of ocean conditions. Certainly the possibility exists that the environmental indices we used are not, in fact, the true causative agents driving the SAR of SRSS chinook salmon, but are instead autocorrelated with some other variable.

When SRSS chinook salmon were listed as threatened under the Endangered Species Act in 1992, their SAR was at an all-time low and many researchers feared that negative anthropogenic activities (e.g. the '4 Hs') would never allow the stock to recover (Kareiva *et al.*, 2000). However, the SAR has improved dramatically in recent years, and our predictions for the 2001–03 outmigrations are also quite optimistic (Fig. 3). Given the ability of our forecast model to capture nearly 70% of the variation in SAR, these optimistic forecasts should assist managers in recovery planning as they develop policies to address an uncertain future. Furthermore, the ocean conditions that favor salmon survival will likely decrease again in the future given the cyclic nature of the NE Pacific ecosystem (Mantua *et al.*, 1997; Beamish *et al.*, 1999b). When they do, we will be able to predict the decrease in SAR of SRSS chinook salmon 1–3 yr in advance as the changes occur in the ocean rather than waiting for enough data to become available and relying on retrospective hindcasts. These forecasts in particular should help identify necessary management actions to ensure the persistence of this important fish stock.

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APPENDIX

Appendix A. The number of smolts indexed by their year of ocean entry, the total number of those smolts that returned as adults (adjusted for any harvest), the proportion of adults in each age class, and the subsequent smolt-to-adult survival rate (SAR).

			Proportion by age class				
Year	Smolts	Adults	Age 3	Age 4	Age 5	Age 6	SAR (%)
1964	2900000	88732	0.049	0.399	0.552	0.000	3.06
1965	2200000	76559	0.089	0.455	0.456	0.000	3.48
1966	2800000	75882	0.086	0.530	0.384	0.000	2.71
1967	2000000	92101	0.068	0.600	0.332	0.000	4.61
1968	2100000	55093	0.087	0.614	0.299	0.000	2.62
1969	2100000	71109	0.040	0.496	0.464	0.000	3.39
1970	3200000	61813	0.073	0.372	0.555	0.000	1.93
1971	2300000	34345	0.044	0.662	0.294	0.000	1.49
1972	3200000	25670	0.029	0.428	0.543	0.000	0.80
1973	2900000	10194	0.055	0.377	0.568	0.000	0.35
1974	2100000	20953	0.007	0.415	0.578	0.000	1.00
1975	2200000	63195	0.019	0.364	0.617	0.000	2.87
1976	2500000	7972	0.113	0.465	0.422	0.000	0.32
1977	800000	4484	0.003	0.471	0.526	0.000	0.56
1978	1000000	9823	0.041	0.410	0.549	0.000	0.98
1979	1800000	12612	0.035	0.520	0.445	0.000	0.70
1980	2800000	15651	0.039	0.417	0.544	0.000	0.56
1981	1000000	6683	0.094	0.313	0.593	0.000	0.67
1982	600000	8448	0.030	0.495	0.475	0.000	1.41
1983	1200000	12374	0.034	0.434	0.532	0.000	1.03
1984	1200000	11371	0.026	0.477	0.497	0.000	0.95
1985	1158323	17528	0.032	0.350	0.618	0.000	1.51
1986	954172	4945	0.037	0.375	0.588	0.000	0.52
1987	1062161	6198	0.032	0.473	0.495	0.000	0.58

Appendix A. (Continued).

			Proportion by age class				
Year	Smolts	Adults	Age 3	Age 4	Age 5	Age 6	SAR (%)
1988	1267371	8769	0.042	0.491	0.467	0.000	0.69
1989	1239684	6636	0.012	0.241	0.747	0.000	0.54
1990	1284358	16875	0.017	0.414	0.569	0.000	1.31
1991	737063	3596	0.096	0.497	0.407	0.000	0.49
1992	527424	1046	0.121	0.334	0.545	0.000	0.20
1993	633564	1379	0.009	0.465	0.526	0.000	0.22
1994	692262	4910	0.025	0.589	0.317	0.069	0.71
1995	1432823	8632	0.029	0.428	0.535	0.008	0.60
1996	356326	1032	0.048	0.556	0.396	0.000	0.29
1997	162131	2561	0.054	0.749	0.180	0.017	1.58
1998	570109	9881	0.058	0.796	0.119	0.027	1.73
1999	1482893	55725	0.041	0.729	0.219	0.011	3.76
2000	1276133	38852	0.050	0.369	0.581	0.000	3.04
2001	480634	7584[1]	0.17	0.83			2.99[2]
2002	970821	1978[3]	1.0				4.01[4]
2003	1332333						
Lower 95% CI			0.037	0.430	0.425	0.000	
Mean			0.048	0.475	0.474	0.004	
Upper 95% CI			0.059	0.520	0.523	0.008	

[1]The total return for the 2001 outmigration does not contain any age-5 adults that returned in 2004.

[2]The SAR for 2001 is preliminary and based on extrapolated returns of age-3 and age-4 adults applied to the average proportion of those age classes.

[3]The total return for the 2002 outmigration does not contain any age-4 adults that returned in 2004 or any age-5 adults that will return in 2005.

[4]The SAR for 2002 is preliminary and based on extrapolated returns of age-3 adults applied to the average proportion of those age classes.