



# Marine environment-based forecasting of coho salmon (*Oncorhynchus kisutch*) adult recruitment

DAVID E. RUPP,<sup>1</sup>\* THOMAS C. WAINWRIGHT,<sup>2</sup> PETER W. LAWSON<sup>2</sup> AND WILLIAM T. PETERSON<sup>2</sup>

<sup>1</sup>Cooperative Institute for Marine Resources Studies, Hatfield Marine Science Center, Oregon State University, Newport, OR 97365, USA

<sup>2</sup>NOAA/NMFS, Northwest Fisheries Science Center, Hatfield Marine Science Center, Newport, OR 97365, USA

## ABSTRACT

Generalized additive models (GAMs) were used to investigate the relationships between annual recruitment of natural coho salmon (*Oncorhynchus kisutch*) from Oregon coastal rivers and indices of the physical ocean environment. Nine indices were examined, ranging from large-scale ocean indicators, e.g., Pacific Decadal Oscillation (PDO), to indicators of the local ecosystem (e.g., coastal water temperature near Charleston, OR). Generalized additive models with two and three predictor variables were evaluated using a set of performance metrics aimed at quantifying model skill in short-term (approximately 1 yr) forecasting. High explanatory power and promising forecast skill resulted when the spring/summer PDO averaged over the 4 yr prior to the return year was used to explain a low-frequency (multi-year) pattern in recruitment and one or two additional variables accounted for year-to-year deviations from the low-frequency pattern. More variance was explained when averaging the predictions from a set of models (i.e., taking the ensemble mean) than by any single model. Making multiple forecasts from a set of models also provided a range of possible outcomes that reflected, to some degree, the uncertainty in our understanding of how salmon productivity is driven by physical ocean conditions.

\*Correspondence. e-mail: david.rupp@oregonstate.edu  
Present address: Oregon Climate Change Research Institute  
College of Oceanic and Atmospheric Sciences, 326 Strand  
Ag Hall, Oregon State University, Corvallis, OR, 97331  
Received 10 March 2011  
Revised version accepted 29 August 2011

**Key words:** climate, coho salmon, forecast, generalized additive model, Pacific Decadal Oscillation

## INTRODUCTION

For thousands of years, Pacific Northwest salmon (*Oncorhynchus* spp.) have been a primary food source for native communities along the western coast of North America from California to Alaska. Since the late 1800s, Pacific salmon have been a major component of the region's commercial fishery (Magnuson *et al.*, 1996). However, Oregon coastal coho salmon (*Oncorhynchus kisutch*) populations, like many other salmon populations south of Alaska, have declined dramatically during the last few decades (Good *et al.*, 2005). Management of coastal salmon distinguishes natural fish from those produced in hatcheries; here we focus on the Oregon Coast Natural (OCN) stock that inhabits rivers along the Oregon coast, excluding the Columbia River. Adult OCN coho abundances were at historic lows throughout the 1990s, and concerns over the viability of these populations led to their listing as 'threatened' in 2008 under the Endangered Species Act (Good *et al.*, 2005; U.S. Federal Register, 2008).

Currently, short-term (1-yr) forecasts of fish abundance inform managers prior to placing restrictions on harvest to promote the rebuilding of salmon stocks such as OCN coho (e.g., Pacific Fishery Management Council (PFMC), 2003a). Forecasts for most stocks are based on stock-recruit relationships and/or regressions of older against younger age classes (sibling regressions), such as full-term adults against precocious males (known as 'jacks') that return after only a few months at sea. These techniques work well for many stocks, but fail when age-specific return data are inaccurate or lacking, or when there are strong environmental effects on either maturation or mortality rates. In the case of Pacific salmon (*Oncorhynchus* spp.) in the northwestern United States, there have been several efforts to quantify environmental effects on recruitment by means of climate-related variables. For example, marine environment-based models have been developed that could be used to forecast future returns of OCN and Columbia River coho salmon (Koslow *et al.*, 2002; Logerwell *et al.*, 2003; Lawson *et al.*, 2004), Snake

River spring-run Chinook salmon (*Oncorhynchus tshawytscha*) (Scheuerell and Williams, 2005), and Skagit River fall-run Chinook salmon (Greene *et al.*, 2005). However, to date the only management forecast for west coast salmon stocks used by the PFMC that incorporates climate indicators is that for OCN river coho salmon. These coho rear in rivers only; other OCN coho rear predominantly in lakes.

In 1994, the Oregon Production Index Technical Team (OPITT) began forecasting adult recruitment of OCN river coho using coastal upwelling wind strength and sea surface temperature (chapter 3, PFMC, 2010). (We define ‘recruitment’ as the number of adult salmon returning to rivers to spawn, i.e., escapement, plus the number of salmon harvested at sea). Spring upwelling in the year of ocean entry had already been linked to adult coho recruitment (Nickelson, 1986; Percy, 1992; Lawson, 1993), whereas sea surface temperature in the winter before return to freshwater was found to be correlated to OCN coho adult recruits (Lawson, 1997). Together, spring upwelling winds and winter coastal sea surface temperature (SST) could explain 75% of the variability in adult recruitment from 1971 to 1995 (Lawson, 1997). Forecasts used a linear regression of log-transformed recruitment abundance against the spring (Bakun, 1973) upwelling wind index (UWI) at 42°N, 125°W, and winter SST at Charleston, OR, together with year (Table 1). Year was added as a third predictor to reflect the overall steady and approximately linear (on log-scale) decline in abundance during the preceding two and a half decades (Fig. 1).

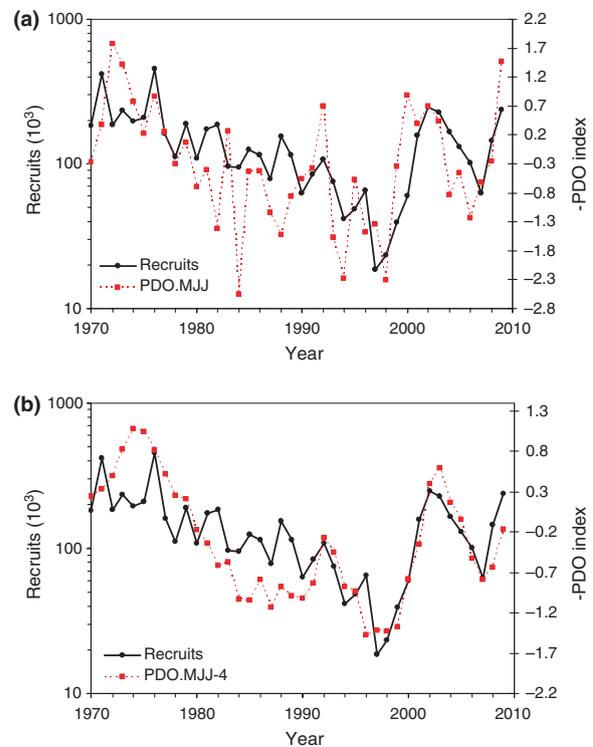
Recruitment of OCN river coho rebounded at the turn of the century, with larger numbers seen in 2002

**Table 1.** Chronology of linear regression models developed by OPITT for management-related forecasts of adult recruitment of OCN coho ( $R$ ) using as predictor variables the Bakun upwelling winds index averaged over April, May, and June of the smolt migration year (UWI.AMJ), mean sea surface temperature at Charleston, OR, in January of the spawner migration year (SST.J), year (Year) and a regime index (RI).

Years used	Model
1994–1995	$\log \hat{R} = b_0 + b_1 \text{UWI.AMJ} + b_1 \text{SST.J} + b_3 \text{Year}$
1996–1998	$\log \hat{R} = b_0 + b_1 \text{UWI.AMJ} + b_1 \text{SST.J}$
1999–2002	$\log \hat{R} = b_0 + b_1 \text{UWI.AMJ} + b_1 \text{SST.J} + b_3 \text{Year}$
2003–2007	$\log \hat{R} = b_0 + b_1 \text{UWI.AMJ} + b_1 \text{SST.J}$
2008	$\hat{R}_{2008} = R_{2007}$
2009–2010	$\log \hat{R} = b_0 + b_1 \text{UWI.AMJ} + b_1 \text{SST.J} + b_3 \text{RI}$

Source: Ch. 3, PFMC (Pacific Fishery Management Council) (2010).

**Figure 1.** Time series of OCN river coho recruits during year of return to freshwater with the mean May–June–July PDO index of the ocean entry year (PDO.MJJ) (a), and with the mean of the 4 yr of PDO.MJJ up to the ocean entry year (b). Note the sign of the PDO index has been reversed so that changes in recruits are in the same direction as changes in the PDO index.



than in any year since 1976. With the increase in abundance, year could no longer be used as a predictor of long-term trend. Lacking year, by 2003 the model using only upwelling and SST explained only 32% of the variability in abundance (chapter 3, PFMC, 2003b). Thus, while upwelling and SST together had once accounted for a large amount of the variability in annual adult recruitment (Lawson, 1997), by the turn of the century these two environmental indices were no longer reliable predictors.

In 2009, a variable called the ‘regime index’ (RI) was introduced to account for the period 1990–2000, when recruitment was at its lowest (Table 1) (PFMC, 2010). The regime index was set equal to 1 for 1990–2000 and to 0 for all other years. The regime index along with the upwelling wind index and SST explained 71% of the variability in recruitment from 1970 to 2009. Although the regime index proved to be a powerful explanatory variable, such an index can only be applied in retrospect once a regime change has been identified. This poses a problem for forecasting

unless we have a method for predicting when a regime transition will occur.

The need for a variable that explains low-frequency patterns in annual recruitment of OCN river coho was a primary motivation for this study. Although changes in freshwater habitat (e.g., terrestrial climate change and habitat degradation and restoration) will certainly affect freshwater productivity, our focus was on the marine environment and indices of ocean conditions that are likely to influence coho production. It has been shown that ocean environmental indices could explain 83% of the variability in OCN coho recruitment from 1970 to 2000 (Koslow *et al.*, 2002), although the extent to which this is due to a positive correlation among factors that promote both freshwater and marine survival is unknown (Lawson *et al.*, 2004).

We examined a suite of potential predictor variables that included the following indicators of large-scale ocean conditions: Multivariate El Niño-Southern Oscillation (ENSO) Index, North Pacific Gyre Oscillation index, North Pacific Index, Oceanic Niño Index, and Pacific Decadal Oscillation index. This suite also included the following indicators of local conditions: upwelling wind strength, timing of the upwelling spring transition, coastal sea surface temperature, and sea surface height. We considered which, if any, of these indices would serve as a proxy for a regime index, by comparing the lower frequency (i.e., multi-year) variability of the indices with variability in annual adult recruitment. We first examined each index individually to see how well it correlated with OCN recruitment. Secondly, we built generalized additive models (GAMs) using various combinations of indices and evaluated the models in terms of forecasting skill. We used GAMs because they have the powerful attribute of not imposing *a priori* a given functional relationship between the predictor(s) and the predictand. These models have been used previously to explore relationships between environmental variables and marine survival of Oregon hatchery coho (Logerwell *et al.*, 2003) and freshwater survival of OCN coho (Lawson *et al.*, 2004). Finally, we chose a subset of models that could be used in the February prior to the autumnal spawning migration to make forecasts of adult recruitment to meet annual harvest management decision deadlines.

## DATA AND METHODS

Data for salmon abundance and environmental indices were derived from a number of sources, which are described here. Sources for web-based datasets are given in Appendix A.

### *Oregon coastal natural coho salmon*

The Oregon Coast Natural (OCN) coho salmon stock consists of natural runs from rivers and lakes along the Oregon coast south of the Columbia River. This stock aggregate is a component of the greater Oregon Production Index area coho stock, which also includes hatchery and natural coho from the Columbia River and hatchery coho from the Oregon coast (though coastal hatchery coho have historically been a minor component and are currently at such low numbers as to be considered inconsequential).

The majority of coho have a 3-yr life cycle (Pearcy, 1992). Eggs hatch in the spring and coho spend their first year rearing in freshwater. Migration to the ocean as smolts occurs in the spring (March–June) of their second year. Oregon coho tend to remain in local, coastal waters during their first spring/summer at sea (Pearcy, 1992). Afterwards, migration routes of Oregon coho extend from the northern end of Vancouver Island to just south of San Francisco Bay (Wright, 1968; Weitkamp and Neely, 2002), although a small number (approximately 10%; Oregon Department of Fish and Wildlife, unpublished data) of jacks return early to freshwater in the fall of the same year they migrated to the ocean. Most coho adults return to spawn in their natal rivers during the fall of their third year.

For the period 1970–2009, annual time series of aggregate OCN coho pre-harvest adult recruitment were generated from estimates of spawner escapement and harvest-related mortality (table III-2, chapter 3, PFMC, 2010). Recruitment was calculated as  $R = S/(1 - H)$ , where  $R$  and  $S$  are the number of recruits and escaped spawners in the same year, respectively, and  $H$  is the proportion of recruits that are harvested or lost to harvest-related activities. Spawner escapement (the number of adults that return to freshwater spawning grounds) was estimated by statistical expansion of counts in selected stream reaches. The sampling design and statistical methods have changed over time, beginning with sampling only in a few streams in the 1950s, then expanding until the 1990s when a full stratified-random sampling method was instituted, covering all coho salmon spawning habitat along the Oregon coast. A history of sampling methods can be found in Jacobs and Nickelson (1998) and Lewis *et al.* (2009). River and lake data were kept separate because it is believed that population dynamics differ markedly between river and lake runs (Lawson *et al.*, 2004). This paper focuses exclusively on the OCN river estimates. Because the published reports combine river and lake runs together, the

**Table 2.** Estimated annual adult recruitment (in thousands) of Oregon Coast Natural river coho salmon by year of return to freshwater.

Year	Recruits	Year	Recruits	Year	Recruits
1970	183.1	1984	94.7	1998	23.2
1971	416.3	1985	124.9	1999	39.2
1972	185.5	1986	114.6	2000	60.2
1973	235.0	1987	78.1	2001	157.6
1974	196.4	1988	154.3	2002	246.8
1975	208.4	1989	115.1	2003	227.8
1976	451.7	1990	63.0	2004	165.9
1977	161.2	1991	84.0	2005	130.5
1978	111.6	1992	107.5	2006	101.1
1979	188.8	1993	75.0	2007	62.8
1980	108.3	1994	41.6	2008	144.7
1981	174.5	1995	48.7	2009	237.8
1982	185.7	1996	65.4		
1983	96.0	1997	18.7		

OCN river recruitment estimates are provided in Table 2.

#### *Multivariate El Niño-Southern Oscillation Index*

The Multivariate ENSO Index (MEI) is the first principal component of six variables over the tropical Pacific: sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky (Wolter and Timlin, 1993). High values of the MEI indicate El Niño events. The unexpectedly low survival of some hatchery coho stocks in the years from 1983 to 1985 has been attributed to the very strong El Niño event of 1982–1983 (Percy, 1992). Others have pointed out that the extended El Niño period from 1990 to 1998 (with a brief La Niña from mid-1995 through 1996) coincided with the period of lowest-recorded marine survival rates of Oregon hatchery coho and poorest returns of OCN adults (Peterson *et al.*, 2006).

#### *North Pacific Gyre Oscillation index*

The North Pacific Gyre Oscillation (NPGO) index is defined as the second principal component of sea surface height anomalies over the region 25–62°N, 180–110°W (Di Lorenzo *et al.*, 2008). The NPGO index has recently been shown to be positively correlated with nutrient concentrations and salinity both along Line P of the Alaskan Gyre and in the Southern California Current System (Di Lorenzo *et al.*, 2008, 2009), which lie north and south, respectively, of the Oregon Production Index area. We hypothesized, therefore, that the mean monthly NPGO index serves

as an indicator of productivity, and therefore of marine survival (with higher values of the index implying higher survival), in the greater California Current System, which encompasses the domain of OCN coho.

#### *North Pacific Index*

The North Pacific Index (NPI) signals the strength of the Aleutian Low and is calculated as the average sea level pressure over the region spanning 30°–65°N and 160°E–140°W (Trenberth and Hurrell, 1994). A higher NPI signifies a weaker low, with cooler air being advected to the western coast of the USA and weaker winter downwelling. It has been suggested that winter ocean environment affects water column stratification, and thus productivity, the following spring (Polovina *et al.*, 1995; Gargett, 1997; Logerwell *et al.*, 2003). We hypothesized, therefore, that high values of the NPI imply greater productivity and higher coho survival.

#### *Oceanic Niño Index*

The Oceanic Niño Index (ONI, Kousky and Higgins, 2007) is the 3-month running mean of the SST anomaly for the Niño 3.4 region (5°N–5°S, 120°–170°W). Like the MEI, high values of the ONI indicate El Niño events. We used the same rationale for investigating ONI as described above for MEI. Although the ONI and MEI are similar, we included the ONI to see if this much simpler index (based on one variable instead of six) would be at least as good as, if not a better than, MEI as a predictor variable.

#### *Pacific Decadal Oscillation index*

The Pacific Decadal Oscillation (PDO) index is defined as the first principal component of SST anomalies over the region spanning 25°–62°N and 180°–110°W (Di Lorenzo *et al.*, 2008). Variability in the PDO has been associated with variability in Northeast Pacific salmon catch (Mantua *et al.*, 1997; Hare *et al.*, 1999) and the PDO index has been correlated to marine survival of Oregon hatchery coho (Peterson and Schwing, 2003) and survival of Alaska/British Columbia pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon (Mueter *et al.*, 2005). Negative values of the PDO index (which signify cooler sea surface temperatures in the California Current) have been associated with higher survival of salmon stocks south of Alaska; therefore, we hypothesized that the same would be true for OCN coho.

#### *Spring transition date*

The date of spring transition (SPR) marks the shift between the winter season dominated by downwelling

to the summer season dominated by upwelling. The SPR generally occurs between early March and late May. Because coho smolts migrate to the ocean from March to June, the timing of the spring transition determines the upwelling conditions that most smolts first encounter when entering the marine environment. We therefore hypothesized that a late spring transition negatively affects early marine survival. Negative correlation has been observed between SPR and survival of hatchery coho smolts from Washington State and the Columbia River (Ryding and Skalski, 1999; Logerwell *et al.*, 2003). We relied on the method of Logerwell *et al.* (2003), based on an analysis of daily upwelling winds and sea level, to calculate the date of the spring transition.

#### Sea surface height

Sea surface height (SSH) is highly correlated with current structure and wind stress over the Oregon continental shelf (Huyer and Smith, 1978; Strub *et al.*, 1987). We therefore examined monthly SSH as an index of ocean conditions influencing OCN coho production. Long-term and frequently updated records of SSH were available for Neah Bay, WA, South Beach, OR, and Crescent City, CA. The data from South Beach, OR (44°37.5'N, 124°02.6'W) were chosen for this study because of the central location of the station. However, data from Neah Bay and Crescent City were used to fill gaps in the South Beach data by means of linear regression relationships after the following steps were taken to process the data.

Monthly SSH was adjusted for the inverse barometric effect (e.g., Strub *et al.*, 1987). This adjustment consisted of adding the atmospheric sea level pressure (SLP) anomaly to the unadjusted, or 'raw', SSH:

$$\text{SSH}_{\text{adj}} = \text{SSH}_{\text{raw}} + 9.948(\text{SLP} - 1013.3) \quad (1)$$

where  $\text{SSH}_{\text{adj}}$  is the adjusted sea level height in mm and SLP is in millibars. Monthly SLP for South Beach was obtained from surface grids (2.5° latitude × 2.5° longitude resolution) of monthly SLP (Kalnay *et al.*, 1996).

Long-term temporal trends in SSH exist for many stations along the coast. For example, at South Beach, sea level has increased by an average of 2.37 mm yr<sup>-1</sup> from 1969 to 2009 for a total of nearly 100 mm during that 41-yr period. This sea level increase amounts to nearly 20% of the total variability in SSH during the same period (data not shown). We removed this trend in SSH by regressing SSH linearly against time and

then taking the residuals of the fitted equation to be the final values of SSH. Thus, our SSH values were adjusted for the inverse barometric effect and for the long-term temporal trend.

#### Coastal sea surface temperature

Several studies have found sea surface temperature to be negatively correlated to Pacific Northwest coho survival (Lawson, 1997; Cole, 2000; Koslow *et al.*, 2002; Logerwell *et al.*, 2003). Furthermore, the mean SST for January of the adult return year has been used as a variable in linear models for short-term (approximately 1-yr) forecasting of adult recruitment of OCN river coho since 1994 (Table 1). We calculated monthly SST values as the mean of daily temperatures at higher high tide.

The coastal SST series we used began with a historical data set collected at the Oregon Institute of Marine Biology (OIMB) dock in Charleston, OR, from 1966 until 1997. For more recent temperature data, we used the Charleston tide gauge, which provides SSTs from 1993 to the present. The OIMB data were calibrated against the tide gauge data based on monthly regressions for the overlapping years 1993–1997 (adjusted  $R^2 = 0.876$ ;  $P < 0.001$ ), and were used for 1966 to 1993. Unfortunately, the tide gauge series had gaps in 2002–2003. The nearest comparable data we could obtain for these years was from the NOAA Stonewall Banks Buoy (Buoy 46050) and we used these data to fill missing values, again calibrated via linear monthly regressions (adjusted  $R^2 = 0.714$ ;  $P < 0.001$ ) for the overlapping period.

#### Upwelling wind index

Many studies have linked the strength of coastal upwelling winds to favorable conditions for marine survival of Pacific Northwest coho (Scarnecchia, 1981; Nickelson, 1986; Fisher and Percy, 1988; Holtby *et al.*, 1990). Coastal upwelling is arguably the key process driving plankton production, and therefore the food source for coho, in the California Current system (Peterson *et al.*, 2006). As our UWI, we used monthly mean values of Bakun's coastal upwelling index (Bakun, 1973) for 45°N, 125°W.

#### Data preparation

Data for each environmental variable were downloaded from the Internet (see Appendix A for the URL of each data source). Three-month running means were calculated for each environmental variable with the exception of MEI, which was left as a 2-month running mean (the condition in which it was obtained). The following format was used to label each

environmental variable: VVV.MMM, where VVV is the three-character abbreviation of the environmental variable, and MMM are the first letters of each of the months over which the mean of variable was calculated (e.g., MJJ for May, June, and July).

Twelve annual time series were created for each variable using each of the 12 3-month running means within the calendar year prior to the spawning return. In addition, for each variable, annual time series of December and January (of the return year) means were generated (except for MEI). We considered the January mean of the return year because mean January SST has been used in operational forecast models by OPITT. January is the latest month for which data potentially could be used in the management forecast, which is made in early February of the adult return year. In practice, however, SST is the only variable available in January by the time the forecast is made, so none of the other indices for January was considered during model selection. We therefore considered December a potential substitute for January for variables other than SST.

#### Statistical methods

**Correlation analysis** Pearson's correlation coefficient  $r$  was calculated for the logarithmic transformation of OCN river coho recruit abundance ( $\log R$ ) against each environmental variable during the year of ocean entry at each of 14 lags (12 3-month running means plus December and January of the return year). A test was conducted to determine whether  $r$  for a given environmental index was significantly different from zero. The effects of autocorrelation and multiple tests were considered in the test for statistical significance (Appendix B).

In our search for a lower frequency predictor variable, we also calculated the correlation between  $\log R$  and each index averaged over  $N$  years, for various values of  $N$ . To differentiate a multi-year average, we use the syntax VVV.MMM- $N$  to refer to the mean VVV.MMM of  $N$  calendar years prior to the return to freshwater. Multi-year averaged indices with high correlations were candidates for the low frequency variable.

**Generalized additive models (GAMs)** We used GAMs to build relationships between ocean environmental indices and OCN recruitment. For example, a GAM with three predictor variables can be expressed in the following general form:

$$Y = \hat{Y} + \varepsilon = f(X_1) + f(X_2) + f(X_3) + \varepsilon \quad (2)$$

where  $Y$  is the observed value,  $\hat{Y}$  is the predictand,  $X_1$  through  $X_3$  are the predictor variables, and  $\varepsilon$  is the deviation of  $\hat{Y}$  from  $Y$ . For our study,  $Y$  was the log-transformation of annual recruit abundance. The term  $f$  represents a smooth function, which in this case is a cubic spline. We limited the maximum number of knots in the spline to three to avoid over-fitting the data. The GAMs were fit using the R package *mgcv* (Wood, 2006) and ranked by their generalized cross-validation (GCV) score. Generalized cross-validation is a measure of predictive ability and is similar to ordinary cross-validation (OCV) but is much faster computationally (Wood, 2006).

We tested two-variable models that paired the selected low-frequency predictor (VVV.MMM- $N$ ) with every other environmental variable, including the logarithmic transformation of the number of parent spawners  $N_{\text{spawners}}$  (the number of spawners lagged by 3 yr). This amounted to 100 different models. We also tested three-variable models that combined VVV.MMM- $N$  with every other possible combination of two environmental variables for a total of 4950 models. To limit the effects of multi-collinearity, we rejected any models for which any pair of variables had  $r \geq 0.6$  (personal communication, Lorenzo Ciannelli, Oregon State University).

From the models ranked highest by GCV, we selected an initial subset of 18 models (nine two-variable and nine three-variable) using selection criteria aimed at having models that accounted for a wide range of processes as represented by our nine indices of year-to-year recruitment variability (eight environmental variables plus  $\log N_{\text{spawners}}$ ). On the two-variable models, we placed the restriction that no index was selected twice. On the three-variable models, we placed the restriction that no environmental index appeared twice within the same model, for example, spring sea surface temperature (SST.AMJ) with fall sea surface temperature (SST.OND), and that every index was represented at least once. Furthermore, we excluded sets of variables that we considered were too similar to be providing any new information: for example, SST.AMJ with summer upwelling (UWI.JAS) would be too similar to SST.MJJ with UWI.JAS. We also limited the NPGO index to no more than one model during the initial selection phase because currently the NPGO index is not calculated in time to make actual forecasts, although it may be in the future. Lastly, we excluded, with the exception of SST.J, all variables that included January of the return year because January data are typically not available in time for the forecasts made in February.

The 18 selected models were further evaluated based on the OCV score, the Akaike information criterion (AIC), and what we term the ‘historical forecast skill’ (HFS), defined below.

In OCV, one data point is removed from the data set, the model is refit from the remaining data points, and a prediction is made of the extracted data point. This is repeated for each data point, and the OCV score is the mean of the squares of the differences between predictions  $\hat{Y}_i$  and observations  $Y_i$ . Normalizing by the variance and subtracting from 1 gives us another way of expressing the OCV score, which we denote as  $OCV^*$ :

$$OCV^* = 1 - \frac{\sum_{i=1}^n (\hat{Y}_i - Y_i)^2}{\sum_{i=1}^n (\bar{Y} - Y_i)^2} \quad (3)$$

where  $\bar{Y}$  is the mean of the observations. Note that Eqn (3) is equivalent in form to the equation for calculating  $R^2$ ; only the methods of determining the  $\hat{Y}_i$  are different.

The HFS is similar to the OCV in that the score is evaluated using predictions for observations not included when fitting the model. However, the HFS mimics how a model would be applied operationally. We began by first fitting the model using the first half of the data set (1970–1989) and then making a forecast for the year 1990. Next, we included the year 1990 in the data set, refitted the model, and made a forecast for 1991. This procedure was repeated until a final forecast was made for 2009. The HFS was calculated the same way as is the  $OCV^*$  in Eqn (3), except  $\hat{Y}_i$  and  $Y_i$  were instead the 1-yr lead forecasts and observations, respectively, for the period when the forecasts were made (which, in this specific case, is 1990–2009). Note that the HFS of a perfect forecast is 1, while an HFS of 0 would arise from forecasting (correctly) the mean  $\bar{Y}$ , which can be poorly known, particularly for small data sets; there is no theoretical lower bound to the HFS.

From the 18 selected models, we proposed a subset to be used for forecasting by the management community. The final number of models was not predefined and was determined following the results of statistical analysis and model fitting. Forecasts were made from each model in the subset, providing a range of possible outcomes that reflected, to some degree, the uncertainty in our understanding of how salmon productivity is driven by ocean conditions.

Unfortunately, the current management system demands a single value of adult recruitment abun-

dance. Although this could be accomplished by selecting a single model, we instead generated from the subset of models an ‘ensemble’ of model forecasts, as it is commonly called in the climate modeling literature (e.g., Tebaldi and Knutti, 2007) and calculated a mean ensemble forecast. For simplicity and to avoid controversy regarding methods of weighting the individual forecasts in the ensemble, we chose not to calculate a weighted mean, although we recognize that weighted means have often been shown to perform better than un-weighted means (Tebaldi and Knutti, 2007). We evaluated the ensemble mean forecast using three performance metrics:  $R^2$ ,  $OCV^*$ , and HFS (note that the  $R^2$  here is not precisely the coefficient of determination of a regression, but is calculated similarly).

Prediction intervals for a given confidence level  $\alpha$  about an ensemble mean forecast were estimated with the assumption that forecast errors (in log-space) for each individual model were normally distributed. The variance of the forecast errors was calculated as the sum of the variance of the model residuals and the square of the standard error of the prediction as estimated by the GAM package (Wood, 2006). For a given year, we sampled  $10^6$  forecasts with random error from each of  $M$  models and combined the  $10^6 M$  randomized forecasts to generate a single frequency distribution. From the combined distribution, we extracted the  $100\alpha/2$ th and  $100(1-\alpha/2)$ th percentiles. This method was compared to non-parametric bootstrap methods and the bootstrapped prediction intervals were similar to those generated by the parametric method to an extent that did not justify the much greater computational cost of bootstrapping (results not shown).

## RESULTS

### Correlation analysis

Of the nine environmental indices examined, the PDO index was found to be the most highly correlated to OCN coho recruits, followed by SSH (Table 3). The highest correlations for these two indices occurred during the spring and early summer months of the ocean entry year (AMJ or MJJ) and were of negative sign, as hypothesized. Other variables that showed significant correlation in spring were sea surface temperature, upwelling index, and spring transition date. Consistent with Lawson (1997), SST during January of the return year was also significantly correlated with adult returns.

The North Pacific Gyre Oscillation (NPGO) showed the only significant correlation during autumn

**Table 3.** Correlation coefficients for log OCN river coho recruitment with environmental indices averaged over selected months.

Month	Environmental index								
	Multivariate ENSO	North Pacific Gyre Oscillation	North Pacific	Oceanic Niño	Pacific Decadal Oscillation	Sea surface height	Sea surface temperature	Upwelling	Spring transition date
	MEI	NPGO	NPI	ONI	PDO	SSH	SST	UWI	SPR
D*JF	-0.14	0.39	0.09	-0.06	-0.22	-0.24	-0.41	0.08	
JFM	-0.16	0.35	0.04	-0.08	-0.27	-0.33	-0.40	0.20	
FMA	-0.24	0.36	0.13	-0.13	-0.33	-0.43	-0.41	0.28	
MAM	-0.26	0.40	0.23	-0.22	-0.46	-0.54	-0.39	0.41	
AMJ	-0.35	0.43	0.36	-0.26	-0.56	-0.58	-0.34	0.34	
MJJ	-0.45	0.45	-0.04	-0.25	-0.60	-0.58	-0.12	0.02	
JJA	-0.40	0.45	-0.19	-0.20	-0.54	-0.51	-0.01	-0.05	
JAS	-0.35	0.46	-0.11	-0.20	-0.44	-0.41	-0.05	-0.19	
ASO	-0.36	0.48	-0.06	-0.19	-0.30	-0.37	-0.19	-0.16	
SON	-0.33	0.48	-0.13	-0.20	-0.22	-0.31	-0.27	-0.10	
OND	-0.32	0.47	-0.08	-0.20	-0.15	-0.25	-0.35	-0.07	
NDJ <sup>†</sup>	-0.29	0.40	0.01	-0.21	-0.16	-0.30	-0.43	0.05	
D	-0.29	0.41	0.06	-0.21	-0.11	-0.15	-0.38	0.05	
J <sup>†</sup>	-0.28	0.29	0.11	-0.20	-0.21	-0.36	-0.49	0.13	
N.A.									-0.47

Significant correlations are shaded in gray (see Appendix B). All months are for the calendar year of ocean entry, unless noted otherwise: \* year prior to ocean entry; <sup>†</sup> year of return to freshwater.

(SON), although a relatively high correlation was observed for nearly all months of the year. This persistence in cross-correlation with recruitment occurred because NPGO is also highly autocorrelated. The high autocorrelation explains why such a high correlation threshold was necessary to detect significance.

The Multivariate ENSO Index (MEI) was significantly correlated with recruits during late spring and summer, but the other ENSO Index, the Oceanic Niño Index, showed no significant correlation with recruitment. Another large-scale index, the North Pacific Index, was also uncorrelated with recruits.

After taking  $N$ -year averages of the PDO for each of 14 lags, we saw that  $r$  between PDO.MJJ and log recruits increased from 0.60 to 0.79 as  $N$  increased from 1 to 4, whereas  $r$  decreased when  $N$  increased from 4 to 5 yr (Table 4). It is important to note that taking the  $N$ -year average of the environmental time series increased the degree of autocorrelation and thus increased the critical  $r$  needed for rejection of the null hypothesis. Even so, the correlations remained significant for PDO.MJJ- $N$  up to at least  $N = 5$ . None of the other environmental indices averaged over  $N$ -years was as highly correlated to log-recruitment as was PDO.MJJ-4 (data not shown).

**Table 4.** Correlation coefficients for log OCN river coho recruits with the running mean of the PDO index taken over 1–5 yr prior to the freshwater return year, where the PDO index was first averaged over selected months.

Month	Years in running mean				
	1	2	3	4	5
D*JF	-0.22	-0.31	-0.36	-0.37	-0.36
JFM	-0.27	-0.38	-0.42	-0.42	-0.41
FMA	-0.33	-0.44	-0.48	-0.49	-0.47
MAM	-0.46	-0.55	-0.61	-0.63	-0.60
AMJ	-0.56	-0.65	-0.70	-0.73	-0.70
MJJ	-0.60	-0.70	-0.74	-0.79	-0.76
JJA	-0.54	-0.66	-0.72	-0.79	-0.77
JAS	-0.44	-0.58	-0.65	-0.74	-0.73
ASO	-0.30	-0.42	-0.52	-0.63	-0.64
SON	-0.22	-0.31	-0.40	-0.51	-0.54
OND	-0.15	-0.21	-0.28	-0.38	-0.42
NDJ <sup>†</sup>	-0.16	-0.23	-0.29	-0.36	-0.39
D	-0.11	-0.16	-0.19	-0.24	-0.28
J <sup>†</sup>	-0.21	-0.27	-0.33	-0.38	-0.40

Significant correlations are shaded in gray (see Appendix B). All months are for the calendar year of ocean entry, unless noted otherwise: \* year prior to ocean entry; <sup>†</sup> year of return to freshwater.

A closer examination of the time series of PDO.MJJ and adult recruitment together, indicated more inter-annual variability in the PDO signal than in adult recruitment. Furthermore, we observed a possible delayed response of adult recruitment to large sign-shifts in the PDO index between 1998 and 2000 and between 2003 and 2005 (Fig. 1a). The effect of averaging PDO.MJJ over 4 yr was to smooth the PDO signal and largely remove these apparent lags between the predictor variable and recruitment response (Fig. 1b).

#### Generalized additive models

Based on the correlation analysis above, we chose PDO.MJJ-4 to describe a low-frequency (multi-year) change in ocean conditions. In effect, it replaced those variables that had been used previously to achieve a similar purpose but were impractical predictors (i.e., year and regime index).

The model selection process described previously resulted in 11 distinct predictor variables (excluding PDO.MJJ-4) distributed among the 18 selected models (Table 5). Of these 11 variables, one (SSH.AMJ) was moderately but significantly correlated with PDO.MJJ-

4 ( $r = 0.51$ ). The 16 models without SSH.AMJ had no combinations of variables that were significantly correlated (Table 6), suggesting that collinearity in general was not an issue. Furthermore, residuals did not strongly violate the model assumption of a normal distribution: in no case was the null hypothesis of normality rejected using the Shapiro–Wilk test ( $\alpha = 0.05$ ).

Although there was not a strong correlation among variables within models, several of the 11 predictor variables were significantly correlated (Table 6). The consequence for making a multi-model forecasts in such cases is that the secondary (or tertiary) variable in each model provides limited independent information about the marine environment.

The GAM fitting resulted in non-linear relationships between annual log recruits and several predictor variables (variables with non-linear response functions are identified in Table 5). As an example, the additive effect of PDO.MJJ-4 to the prediction of log  $R$  based on the full period of record is illustrated in the lower right panel of Fig. 2, for the two-variable model where PDO.MJJ-4 was paired with the logarithm of the

**Table 5.** Performance statistics and 2010 recruitment forecast (in thousands) from selected two- and three-variable GAMs with PDO.MJJ-4 as the primary predictor variable.

Secondary variable	Performance statistics					2010 Forecast	
	GCV	AIC	$R^2$	OCV*	HFS		
SPR	0.149	38.9	0.74	0.67	0.64	213	
MEI.OND	0.158	41.2	0.72	0.65	0.56	170	
NPGO.OND <sup>†</sup>	0.160	41.6	0.73	0.64	0.57	NA	
ONI.OND <sup>†</sup>	0.161	41.9	0.73	0.62	0.55	168	
UWI.JAS <sup>†</sup>	0.162	42.2	0.73	0.64	0.42	206	
SSH.AMJ	0.166	43.1	0.71	0.63	0.56	199	
SST.J	0.172	44.8	0.70	0.61	0.50	169	
$\log N_{\text{spawners}}^{\dagger}$	0.180	46.3	0.70	0.59	0.49	212	
NPI.JFM	0.180	46.6	0.68	0.59	0.52	165	
Secondary and tertiary variables							
UWI.JAS <sup>†</sup>	NPGO.OND <sup>†</sup>	0.126	31.4	0.81	0.73	0.53	NA
SPR	$\log N_{\text{spawners}}$	0.136	35.1	0.77	0.70	0.67	206
MEI.OND	UWI.JAS <sup>†</sup>	0.140	36.1	0.78	0.69	0.50	180
SPR	NPI.JFM <sup>†</sup>	0.141	36.6	0.77	0.67	0.67	179
SPR	MEI.OND	0.142	36.7	0.77	0.69	0.63	189
UWI.JAS <sup>†</sup>	SST.AMJ	0.144	37.1	0.77	0.68	0.42	246
SPR	ONI.OND <sup>†</sup>	0.144	37.3	0.76	0.67	0.62	187
SSH.AMJ	UWI.JAS <sup>†</sup>	0.145	37.4	0.77	0.67	0.49	208
UWI.SON	SST.J	0.145	37.7	0.76	0.66	0.58	215
Ensemble mean (shaded models only)				0.81	0.74	0.61	206

The ensemble mean scores were calculated using only the models shaded in gray. Variables that were non-linearly related to the predictand are denoted with <sup>†</sup>, otherwise the relationship was linear. The NPGO index was not available in time to be used to make the 2010 forecast.

**Table 6.** Pearson's product moment correlation coefficient for all environmental variables used in the 18 selected models, 1970–1990.

	PDO.MJJ-4	UWI.JAS	NPGO.OND	SPR	log $N_{\text{spawners}}$	MEI.OND	NPI.JFM	SST.AMJ	ONI.OND	SSH.AMJ	UWI.SON
UWI.JAS	0.12 <sup>†</sup>										
NPGO.OND	-0.32 <sup>†</sup>	-0.10 <sup>†</sup>									
SPR	0.22 <sup>†</sup>	0.05	-0.43								
log $N_{\text{spawners}}$	-0.13 <sup>†</sup>	0.13	0.10	0.20 <sup>†</sup>							
MEI.OND	0.17 <sup>†</sup>	-0.10 <sup>†</sup>	-0.39	0.31 <sup>†</sup>	-0.08						
NPI.JFM	-0.23 <sup>†</sup>	0.02	0.01	-0.13 <sup>†</sup>	0.02	0.11					
SST.AMJ	0.22 <sup>†</sup>	0.08 <sup>†</sup>	-0.62	0.55	0.00	0.17	-0.31				
ONI.OND	0.02 <sup>†</sup>	-0.10	-0.27	0.28 <sup>†</sup>	-0.02	0.96	0.20	0.08			
SSH.AMJ	0.52 <sup>†</sup>	0.07 <sup>†</sup>	-0.57	0.73	0.00	0.30	-0.19	0.69	0.20		
UWI.SON	-0.09 <sup>†</sup>	0.07	-0.32	0.15	0.22	0.03	0.31	0.03	0.08	0.08	
SST.J	0.39 <sup>†</sup>	0.08	-0.19	0.33	-0.22	0.51	-0.13	0.20	0.47	0.35	-0.23 <sup>†</sup>

Shaded cells indicate pairs that are significantly correlated ( $P < 0.01$ ). Pairs that appear within the same model are denoted with †.

number of parent spawners ( $\log N_{\text{spawners}}$ ). Among the 18 models, the equivalent degrees of freedom (edf) for PDO ranged from 1.74 to 1.94 (as a reference, edf = 1 signifies a linear relationship and edf = 2 a quadratic-type relationship). The degree of non-linearity in the relationship between log recruits and several environmental indices argues for the use of non-linear model construction such as that provided by GAMs. The case is particularly strong for PDO.MJJ-4, which dominated the other variables in terms of explanatory power and showed the highest degree of non-linearity in response, along with UWI.JAS (as measured by the edf).

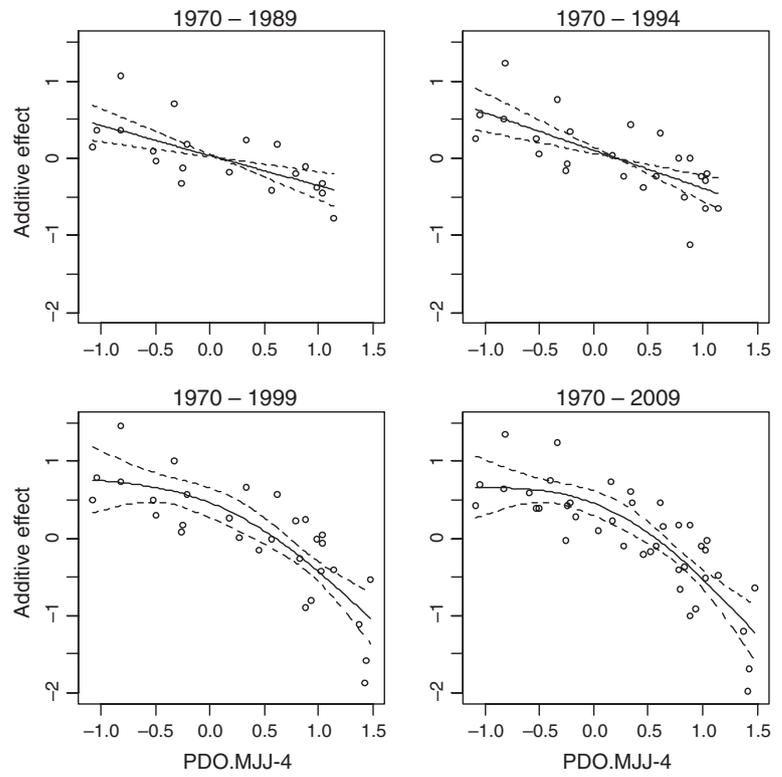
Among the selected two-variable models, PDO.MJJ-4 coupled with SPR scored best across all skill measures (GCV, AIC,  $R^2$ , OCV\*, and HFS) (Table 5). After SPR, the PDO index performed similarly when coupled with three of the other large-scale indices (MEI, NPGO, and ONI); all were in late fall/early winter. The next two best models included late spring–early summer SSH and winter return SST, in that order.

Log spawners and NPI were the weakest second variables. Furthermore, the relationship between log recruits and NPI was contrary to our hypothesis: the model assumed lower recruitment with higher values of NPI (Fig. 3).

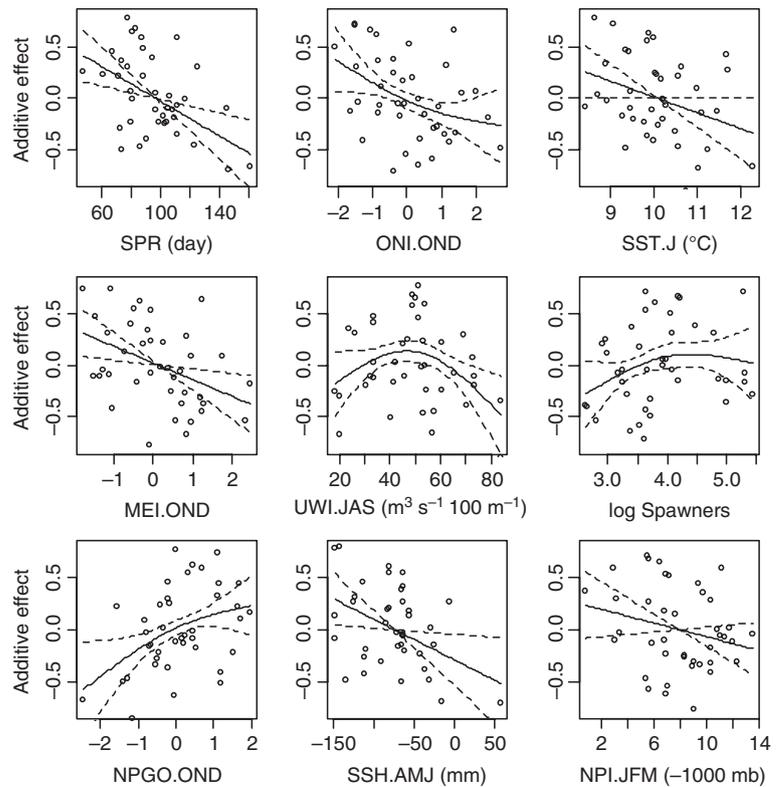
Of the two-variable models selected, the one with summer UWI provided the weakest forecast skill over the last two decades. The upwelling index (UWI.JAS) also showed the most striking non-monotonic relationship with log recruits (see Fig. 3). The trend between recruitment and upwelling wind strength was positive (as hypothesized) only up to a UWI of about  $50 \text{ m}^3 \text{ s}^{-1} 100 \text{ m}^{-1}$ , after which recruitment decreased with increasing UWI.

Time series of the predictions by the fitted two-variable models using the full time period 1970–2009 and time series of the forecasts in operational mode are shown in Fig. 4. As expected, predictions were less accurate and there was more variability among models when the models were applied operationally. However, there was also an undesirable increase in bias; most notably, all models overestimated abundance during the ‘bad’ years of the 1990s, except for 1996 (Fig. 4).

The addition of a third variable resulted in marked improvements in the standard performance metrics (GCV, AIC,  $R^2$ , and OCV\*) for all indices (Table 5). The three-variable model with the best scores (excepting HSF) included summer UWI and NPGO.OND. UWI.JAS was included in four models; however, these four models had the lowest historical

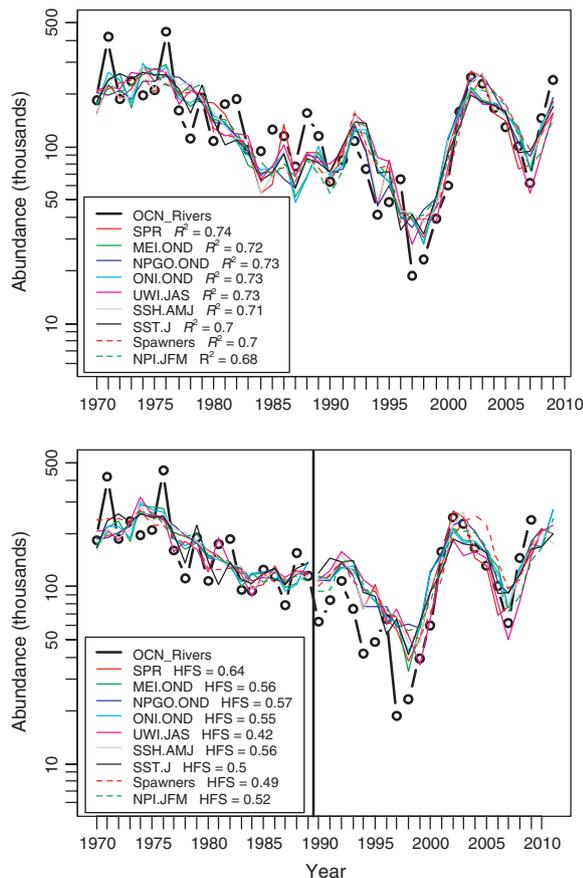


**Figure 2.** Partial regression plots of PDO.MJJ-4 paired with  $\log N_{\text{spawners}}$  in a two-variable GAM for different calibration periods. Confidence limits (95%; dashed lines) and partial residuals (open circles) around the fitted lines are shown. The ‘additive effect’ is the partial deviation from the mean in  $\log R$  for a given value of the predictor variable.



**Figure 3.** Partial regression plots for the second most explanatory variable in each of the selected two-variable GAMs listed in Table 5. In each case, PDO.MJJ-4 was the most explanatory variable. Confidence limits (95%; dashed lines) and partial residuals (open circles) around the fitted lines are shown. The ‘additive effect’ is the partial deviation from the mean of  $\log R$  for a given value of the predictor variable.

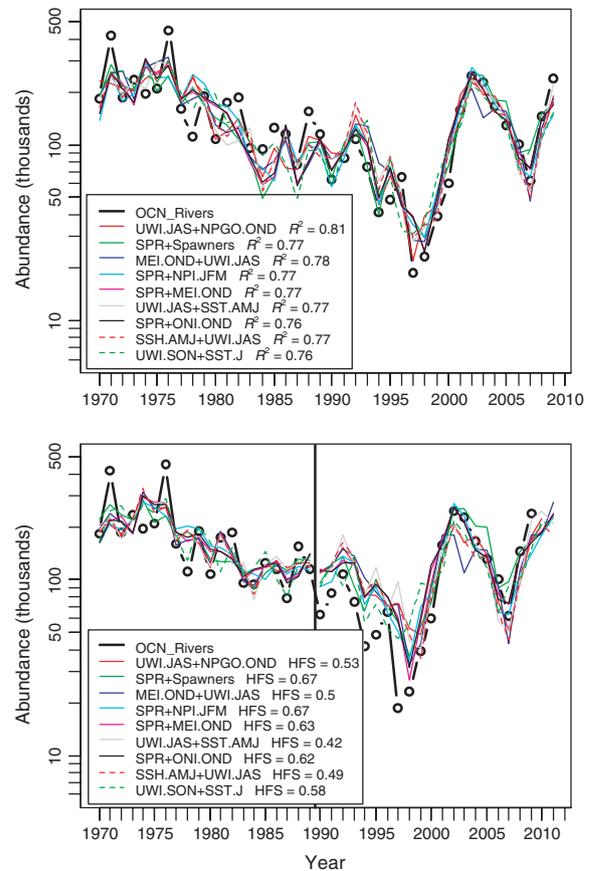
**Figure 4.** (Upper panel) Time series of modeled (thin lines) and observed (heavy line with circles) abundance of Oregon coastal natural river coho adult recruits. Predictions were made using PDO.MJJ-4 combined with a second predictor variable (as given in the legend along with  $R^2$ ). (Lower panel) Time series of predicted (pre-1990) and forecasted (post-1989) abundance using same models. Predictions shown prior to 1990 are from models fitted to 1970–89 data, whereas values for 1990 and after are 1-yr lead forecasts from models fitted to the data for all years prior to the forecast year. In the legend are values of the ‘historical forecast skill’ (HFS) for the period 1990–2009 (see text for details).



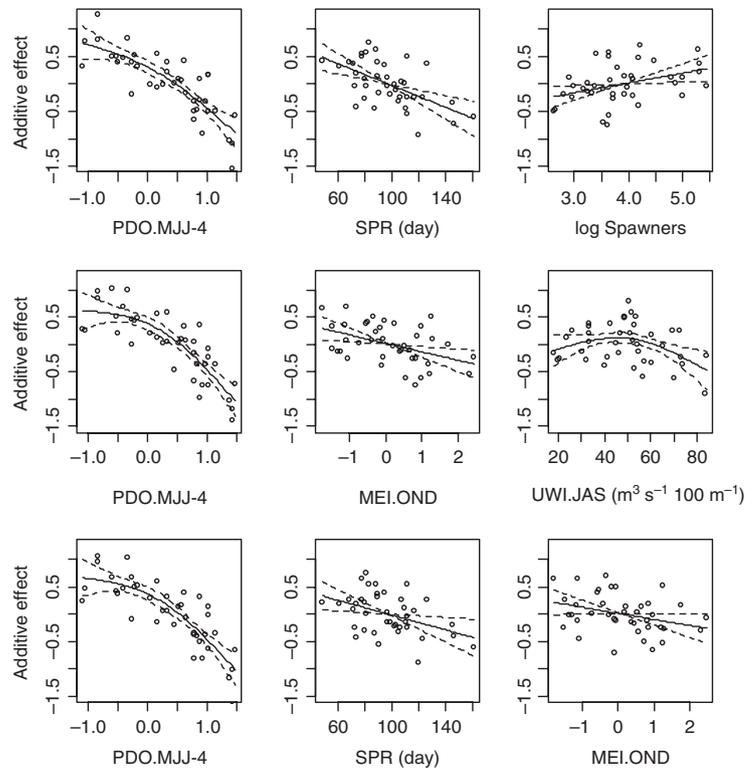
forecast skill. Moreover, the HFS scores of the three-variable models that included UWI.JAS were actually lower than several HFS scores of two-variable models. In contrast, the three-variable models with the highest HFS scores all included SPR.

Time series of the predictions by the fitted three-variable models using the full time period 1970–2009 and times series of model forecasts in operational mode are shown in Fig. 5. Although the HFS scores were higher overall for the three-variable models than for the two-variable models, the bias in the forecasts persists for the 1990s (Fig. 5).

**Figure 5.** Same as Fig. 4 but using models that combined PDO.MJJ-4 with two additional predictor variables.



For the forecast system we proposed to the management community, we chose a subset of the previously selected 18 models. All were three-variable models because the AIC was smaller for all the three-variable models over any two-variable model. We excluded models that contained the North Pacific Gyre Oscillation index, the North Pacific Index or the Oceanic Niño Index. The NPGO index was excluded because it currently is not calculated with sufficient lead time to be used in the annual management forecasts. The NPI was excluded because it was the weakest explanatory variable. Furthermore, the modeled relationship between NPI and log recruits was contrary to our hypothesis (the model assumed lower recruitment with higher values of winter NPI, or weaker Aleutian Low). The ONI was excluded because it provided a response very similar to that of Multivariate ENSO Index but scored slightly lower; MEI.OND and ONI.OND were highly correlated (Table 6) and we did not want two variables that were essentially providing the same information. Although the initially selected GAMs contain both autumn MEI



**Figure 6.** Partial regression plots for three of the selected three-variable GAMs listed in Table 5. Model variables are grouped by row and given in column order by explanatory power. Confidence limits (95%; dashed lines) and partial residuals (open circles) around the fitted lines are shown.

and ONI, it is interesting that summer MEI was correlated to annual recruitment, whereas summer ONI was not. It may be that the variables other than sea surface temperature that constitute the MEI (such as atmospheric pressure) give it a stronger teleconnection with conditions in the northeast Pacific.

The complete selection process left us with six three-variable models, which are shaded in gray in Table 5. The additive effects (as partial regression plots) of the variables in these six models are shown in Figs 6 and 7.

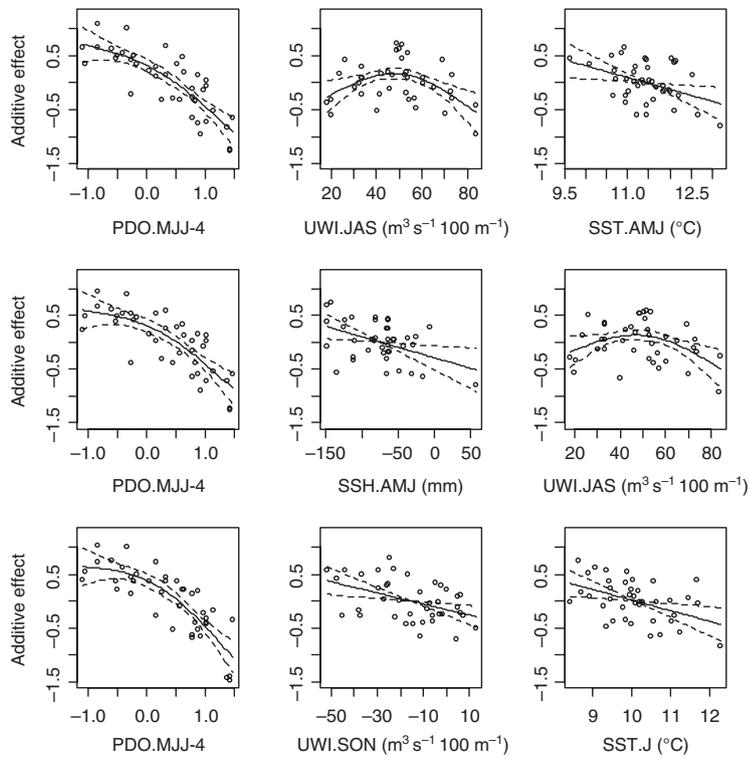
With respect to  $R^2$  and OCV\*, the ensemble mean forecasts scored as high or higher than any single-model forecasts within the ensemble (see Table 5). The HFS scores for the ensemble means were not as high as the highest-scoring individual models but were still higher than most (Table 5). Compared to past forecasts of adult OCN river coho recruitment, the ensemble mean forecast from the six three-variable GAMs performed very well (Fig. 8). The historical forecast skill score for the period 1990–2009 was 0.61 using the ensemble mean forecast from the models proposed here, whereas it was  $-0.11$  for the actual forecasts that were made.

## DISCUSSION

Our primary goal was to identify a set of environmental indices that would improve the short-term forecasts needed for harvest management of Oregon

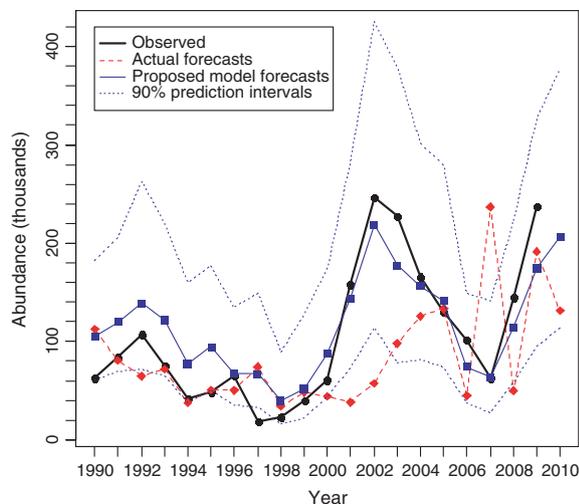
Coast Natural coho stocks. To accomplish this, we selected a number of potential indicators based on past research, in particular one (PDO) that appeared to provide a good representation of major persistent shifts in production that have been observed. We have shown that a number of two- and three-variable non-linear regression models individually provide higher forecast skill than the past forecast method, and that an ensemble combining the results of several individual forecasts performs even better than the individual forecasts, and provides a potentially more robust approach.

We have given special attention to estimating the forecast skill of models with the aim of avoiding artificial skill. A model may have artificial skill due to model complexity and due to the total number of models considered. Model complexity may lead to over-fitting to the sample data, which itself contains error. Because the GAMs we applied were based on cubic splines, they can be allowed to fit very complex patterns if given enough degrees of freedom. However, we limited the number of degrees by restricting the number of knots in the spline to a maximum of three. The fitting procedure assumed many relationships to be linear, whereas some were roughly quadratic (e.g., Fig. 3). This lack of wiggleness in the fitted relationships gives us confidence that over-fitting was minor with the selected models.



**Figure 7.** Partial regression plots for three of the selected three-variable GAMs listed in Table 5. Model variables are grouped by row and given in column order by explanatory power. Confidence limits (95%; dashed lines) and partial residuals (open circles) around the fitted lines are shown.

**Figure 8.** Observed and forecast abundance of Oregon coastal natural river coho salmon adult recruits for 1990–2009, with forecasts for 2010 included. The blue dashed line shows forecasts that would have been made using the proposed method, and the red dotted line shows actual forecasts made using the methods summarized in Table 1. Note the actual forecast for recruitment in 2008 was not based on a model but instead was equal to the ‘observed’ adult recruitment in 2007. (The slight discrepancy in the figure between the actual 2008 forecast and the observed 2007 recruitment is due to corrections made to the records of observed recruitment after 2007. The observed values shown in the figure were the most current estimates as of 2010.)



We did not avoid the problem associated with testing a large number of models (i.e., the increased probability of selecting a purely spurious association). Even the screening procedure we used to select the Pacific Decadal Oscillation index as the first predictor variable did not diminish the problem (DeSole and Shukla, 2009). However, by using a set of models in place of merely a single best model, we may have compensated for the eventual failure of any particular model built on spurious relationships. With time and experience, we can remove poorly performing models from the selected set and replace them with models with a stronger biophysical basis.

We also ranked the models based on their GCV score, which, unlike the  $R^2$ , was a measure of the error of predictions from excluded data points. This in itself should have reduced the probability of artificial skill. Furthermore, for the selected models we calculated an additional measure meant to help us estimate the forecast skill of the model: the historical forecast skill score. The HFS score can be a useful measure in that it arises from mimicking the actual forecast procedure through time and thus reflects what the management community would experience, and as a consequence, provides more realistic expectations of model performance.

We chose potential environmental variables with thought given to plausible mechanisms promoting

adult recruitment. However, to increase confidence that the particular modeled relationships are ecologically meaningful, these relationships should be investigated further. For one thing, the apparent lag in the time series between the recruitment pattern and PDO pattern led us to speculate that coho production was linked not only to the ocean conditions in the year of ocean entry, but also to multi-year persistence of good (or poor) ocean conditions. It is reasonable to assume that multiple years of consecutive 'good' ocean conditions are required to see a sizable recovery in salmon productivity following a period of low productivity. However, it could be argued that a single 'bad' ocean year could cause salmon recruitment to plummet.

Another relationship that merits further examination is the response to upwelling. A dome-shaped relationship between recruitment and upwelling strength has been previously hypothesized for pelagic fish in Ekman-type upwelling systems (Cury and Roy, 1989). In the case of Pacific salmon, Ryding and Skalski (1999) observed a dome-shaped response of survival with upwelling for coho from nine hatcheries in the Juan de Fuca Strait, Washington coast, and lower Columbia River. Most of these stocks responded with maximum survival occurring at March–September cumulative upwelling values of 50–80  $\text{m}^3 \text{s}^{-1} (100 \text{ m})^{-1}$ . In comparison, Cury and Roy (1989) found a maximum in the response curve for Pacific sardine (*Sardinops sagax caerulea*) at 100–120  $\text{m}^3 \text{s}^{-1} (100 \text{ m})^{-1}$  (calculated as the annual average upwelling index), which corresponds to wind speeds of 5–6  $\text{m s}^{-1}$ . Similarly, Ware and Thompson (1991) observed a maximum at 7–8  $\text{m s}^{-1}$  in the response curve of both diatom abundance and Pacific sardine recruitment to May–June wind speed.

Wind-driven turbulence in the upper ocean layer has been given as an explanation for these observed dome-shaped responses to upwelling strength and/or wind speed: turbulence breaks up patches of phytoplankton, resulting in greater energy expenditure by phytoplankton predators (Cury and Roy, 1989; Ware and Thompson, 1991; Ryding and Skalski, 1999). Although Oregon coho salmon do not feed on phytoplankton while in the ocean but rather mainly on fish even soon after migrating to sea (Brodeur *et al.*, 2007; Daly *et al.*, 2009), the assumption is that the turbulence effect indirectly impacts higher trophic levels. In our case, the apparent optimal upwelling index of approximately 50  $\text{m}^3 \text{s}^{-1} (100 \text{ m})^{-1}$  corresponds to a wind speed of just under 4  $\text{m s}^{-1}$  when using the reported monthly average UWI (Schwing *et al.*, 1996). This wind speed is lower than what would be expected to cause turbulent mixing (Pe-

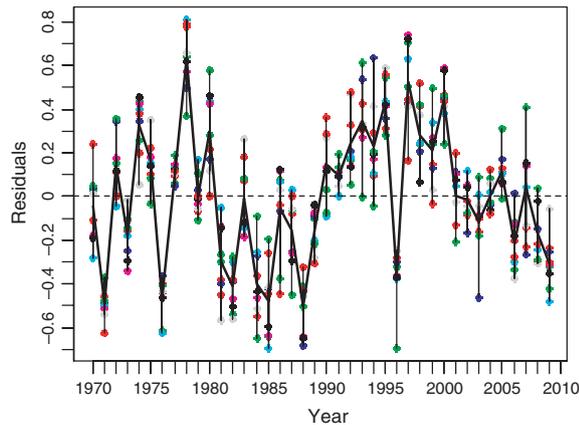
terman and Bradford, 1987; Cury and Roy, 1989; Ware and Thompson, 1991), although we recognize that using monthly averages masks higher frequency variability in wind speed.

Another possible cause for the optimal upwelling strength is the rapid advection off the continental shelf of phytoplankton and zooplankton during strong upwelling periods, causing these food sources to be unavailable to predators that do not stray from the continental shelf (Botsford *et al.*, 2003). Botsford *et al.* (2003, 2006) showed with a simple ecosystem model how the optimal upwelling strength, or similarly optimal wind speed, for shelf productivity of phytoplankton and zooplankton decreases as the shelf width decreases for a given time scale of biological production. Applying the same model to shelf conditions near Newport, OR, and using initial conditions taken from Ruzicka *et al.* (2011), we found that maximum phytoplankton and zooplankton production would occur at constant wind speeds of 4.5 and 2  $\text{m s}^{-1}$ , respectively. These values correspond to UWI of 66 and 13  $\text{m}^3 \text{s}^{-1} (100 \text{ m})^{-1}$ , respectively. Although not conclusive, this suggests that off-shelf transport during strong upwelling periods is more likely than turbulent mixing to be the cause for the apparent dome-shaped response seen in Figs 3, 6 and 7.

In most cases, the sign (positive or negative) of the slope between recruitment and the strongest predictor variable was consistent with our initial hypotheses. One exception was with the NPI during January–March (NPI.JFM), where recruitment decreased with increasing values of NPI. However, both the relationship provided by the multivariate GAM and the correlation between log recruits and NPI.JFM ( $\rho = 0.04$ ) were weak. Consistent with our results, Ryding (1998) and Logerwell *et al.* (2003) did not find NPI to be a significant predictor of coho marine survival of either Washington or Oregon hatchery coho, respectively.

Another finding contrary to our original hypothesis involved fall upwelling (UWI.SON), where we observed recruitment decreasing with increasing UWI (Fig. 7). However, by this time of year, the upwelling season has ended, so it is greater downwelling that is associated with increased recruitment. A lower UWI could indicate greater storm activity. Fall storms can intensify mixing in the upper ocean layer, bringing nutrients to the surface and increasing productivity. Fall phytoplankton blooms have been observed in a minority of years off the Oregon (Feinberg *et al.*, 2010), although it is not known if increased storm activity was a primary cause. Another explanation may be related to the directional changes and strength

**Figure 9.** Time series of log-recruitment residuals for the final six-three-variable GAMs (circles) and the ensemble mean (heavy line). Each color represents one of the six GAMs.



of the prevailing currents. When they became larger, juvenile coho tend to migrate northward after the prevailing summer current has first driven the newly arrived smolts southward (Percy, 1992). It may be that in the fall, a stronger northward current, implied by a lower UW1, means that coho expend less energy during their northward migration.

As mentioned previously, the forecasts from the GAMs tended in general to be biased high throughout the 1990s (including the year 2000), the period of lowest recruitment on record. This could be cause for concern should we enter another prolonged period of low recruitment. However, this bias occurred, at least in part, because throughout this period forecasts were being made of recruitment that was near, if not beyond, the lower limit of recruitment on record up to the time of the forecasts. In other words, the models were operating near, or outside, the boundaries of the known predictor–predictand space. Prior to being trained to these lowest recruitment values, the relationship between recruitment and PDO.MJJ-4 was essentially linear (see upper left and upper right panels in Fig. 2) and did not have the downward curve at higher values of the PDO index once all the data from 1990s were included (lower left panel, Fig. 2). Furthermore, given that outside of the known predictor–predictand space, the GAM extrapolates linearly from the ends of fitted spline, it is evident by comparing the panels in Fig. 2 how the GAM over-predicted the very low recruitment for many years during the 1990s.

However, a short calibration data set that is poorly represented at the tails of the distribution may not be the only cause of changes in forecast performance over

time. An examination of model residuals through time reveals that the predictions from all models fitted to the entire period of record still generally overestimate recruitment during 1990–2000 (Fig. 9). The time series of residuals also shows other periods of general over- and under-prediction lasting various years, the longest one being 1981–1989. Moreover, empirical autocorrelation functions (ACFs) of the residuals reveal that autocorrelation was positive among all models at lags of 1 and 2 yr, and in most cases, 3 yr as well. Although the empirical ACFs were not significantly different from white noise ( $\alpha = 0.05$ ), these analysis results suggest we are still missing some important environmentally driven variability in the models.

We selected a subset of models based on what we thought were reasonable selection criteria. However, it may be that through an iterative process with the management community, fisheries scientists, and oceanographers, the model selection procedure used here could be modified, resulting in a different set of forecast models. Still, with the six three-variable GAMs selected here (see highlighted three-variable models in Table 5), the ensemble mean forecasts performed very well compared with past methods of forecasting adult OCN river coho abundance.

It has long been recognized that stock-production variations of fisheries are strongly affected by climate regime shifts and ecosystem phase transitions (e.g., Walters, 1987; Francis and Hare, 1994; Duffy-Anderson *et al.*, 2005). Given this problem, it is not clear that the relationships we have identified for short-term forecasts will retain predictive power in the long term. Although experience tells us that past performance is no guarantee of future results, we are encouraged that all of the selected models showed reasonable hind-cast skill over a period of 40 yr through multiple climate regimes, and that they exhibited good forecast skill across a wide range of production conditions in the past 20 yr. Our proposed forecast method has been adopted by the Pacific Fisheries Management Council for use in 2011 and subsequent harvest management, so we will have the opportunity to see whether the potential of this new method is fulfilled.

## ACKNOWLEDGEMENTS

This work was supported by the NOAA Fisheries and the Environment (FATE) program (project #09-10). We thank Jim Ruzicka for his thoughtful input and Brian Burke, Robert Kope, Ed Casillas and three anonymous reviewers for their comments and suggestions on an earlier draft of this paper.

## APPENDIX A

List of URLs for data sources.

Multi-variate El Niño-Southern Oscillation Index (MEI): <http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/table.html>.

North Pacific Gyre Oscillation (NPGO) index: <http://www.o3d.org/npgo/data/NPGO.txt>.

North Pacific Index (NPI): <http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#npmon>.

Oceanic Niño Index (ONI): <ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/sstoi.indices>.

Pacific Decadal Oscillation (PDO) index: <http://jisao.washington.edu/pdo/PDO.latest>.

Sea level pressure (SLP): <http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.derived.surface.html>.

Date of spring transition (SPR): [http://www.cbr.washington.edu/data/trans\\_data.html](http://www.cbr.washington.edu/data/trans_data.html).

Sea surface height (SSH): <http://ilikai.soest.hawaii.edu/uhsdc/data1.html>.

Sea surface temperature (SST): <http://www.scc.oos.org>. <http://www.ndbc.noaa.gov/data/historical/stdmet/>. [http://opendap.co-ops.nos.noaa.gov/dods/IOOS/Water\\_Temperature.html](http://opendap.co-ops.nos.noaa.gov/dods/IOOS/Water_Temperature.html).

Upwelling winds index (UWI): <ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon>.

## APPENDIX B

Testing for significant correlation.

Both the OCN recruit time series and the time series of environmental variables showed strong to moderate autocorrelation (results not shown). When testing for significant cross-correlation between pairs of variables, autocorrelation has the effect of increasing the probability of erroneously rejecting the null hypothesis at a given level of significance  $\alpha$  under the assumption of serial independence. In other words, autocorrelation has the effect of reducing the number of degrees of freedom. To calculate the effective degrees of freedom under autocorrelation, we used the method of Pyper and Peterman (1998).

Moreover, when testing for significant correlation between recruits and a given environmental index, we are actually making multiple individual comparisons because we examined multiple time lags for each environmental index. This multiple testing is known as ‘multiplicity’ and has the effect of increasing the probability of erroneously rejecting at least one null hypothesis (e.g., Katz and Brown, 1991). Various methods have been developed to account for multiple comparisons (Miller, 1981), but a very simple one is to

make the following calculation for the significance level of an individual test  $\alpha$  necessary to achieve an overall level  $\alpha_0$  for all  $K$  comparisons:

$$\alpha = 1 - (1 - \alpha_0)^{1/K} \quad (B1)$$

Eqn (B1) assumes the  $K$  comparisons are independent. However, the lags of the monthly means are moderately to strongly correlated (particularly given we have calculated 3-month running means). This means the effective number of comparisons is actually smaller than  $K$ .

There have been investigations into the question of coping with multiplicity given autocorrelation in the individual time series and dependency among the individual tests (e.g., correlation between lags) (Katz and Brown, 1991; Olden and Neff, 2001). However, we still lack an analytical adjustment to account for multiplicity under arbitrary autocorrelation and lag-correlation structures. Therefore, we took the simple approach of Mueter *et al.* (2005), which was to apply a significance level of  $\alpha = 0.01$  in place of the more standard  $\alpha = 0.05$ , assuming that the effective number of tests ranged from  $K = 5$  to 10 (of 14) for strong to moderate correlation among lags. This meant that  $\alpha_0$  would be between approximately 0.05 and 0.1 for each environmental variable.

## REFERENCES

- Bakun, A. (1973) Coastal upwelling indices, west coast of North America, 1946–71. U.S. Department of Commerce, NOAA Technical Report NMFS–SSRF–671.
- Botsford, L.W., Lawrence, C.A., Dever, E.P., Hastings, A. and Largier, J. (2003) Wind strength and biological productivity in upwelling systems: an idealized study. *Fish. Oceanogr.* **12**:245–259.
- Botsford, L.W., Lawrence, C.A., Dever, E.P., Hastings, A. and Largier, J. (2006) Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems. *Deep-Sea Res. II* **53**:3116–3140.
- Brodeur, R.D., Daly, E.A., Schabetsberger, R.A. and Mier, K.L. (2007) Interannual and interdecadal variability in juvenile coho (*Oncorhynchus kisutch*) salmon diets in relationship to environmental changes in the northern California current. *Fish. Oceanogr.* **16**:395–408.
- Cole, J. (2000) Coastal sea surface temperature and coho salmon production off the north-west United States. *Fish. Oceanogr.* **9**:1–16.
- Curry, P. and Roy, C. (1989) Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* **46**:670–680.
- Daly, E.A., Brodeur, R.D. and Weitkamp, L.A. (2009) Ontogenetic shifts in diets of juvenile and subadult coho and chinook salmon in coastal marine waters: important for marine survival? *Trans. Am. Fish. Soc.* **138**:1420–1438.

- DelSole, T. and Shukla, J. (2009) Artificial skill due to predictor screening. *J. Clim.* **22**:331–345.
- Di Lorenzo, E., Schneider, N., Cobb, K.M. et al. (2008) North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys. Res. Lett.* **35**:L08607, doi:10.1029/2007GL032838.
- Di Lorenzo, E., Fiechter, J., Schneider, N. et al. (2009) Nutrient and salinity decadal variations in the central and eastern North Pacific. *Geophys. Res. Lett.* **36**:L14601, doi:10.1029/2009GL038261.
- Duffy-Anderson, J.T., Bailey, K., Ciannelli, L., Cury, P., Belgrano, A. and Stenseth, N.C. (2005) Phase transitions in marine fish recruitment processes. *Ecol. Complexity* **2**:205–218.
- Feinberg, L.R., Peterson, W.T. and Shaw, C.T. (2010) The timing and location of spawning for the Ephausiid *Thysanoessa spinifera* off the Oregon coast, USA. *Deep-Sea Res. II* **57**:572–583.
- Fisher, J. and Pearcy, W. (1988) Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of differing coastal upwelling. *Can. J. Fish. Aquat. Sci.* **45**:1036–1044.
- Francis, R.C. and Hare, S.R. (1994) Decadal scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. *Fish. Oceanogr.* **3**:279–291.
- Gargett, A. (1997) The optimal stability “window”: a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fish. Oceanogr.* **6**:109–117.
- Good, T.P., Waples, R.S. and Adams, P. (editors) (2005) Updated status of federally listed ESUs of West Coast salmon and steelhead. U. S. Department of Commerce, NOAA Tech. Memo. NMFS-NWFSC-66, 598 p.
- Greene, C.M., Jensen, D.W., Pess, G.R. and Steel, E.A. (2005) Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. *Trans. Am. Fish. Soc.* **134**:1562–1581.
- Hare, S.R., Mantua, N.J. and Francis, R.C. (1999) Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries* **24**:6–14.
- Holtby, L., Andersen, B. and Kadawaki, R. (1990) Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **47**:2181–2194.
- Huyer, A. and Smith, R.L. (1978) Seasonal differences in low-frequency current fluctuations over the Oregon continental shelf. *J. Geophys. Res.* **83**:5077–5089.
- Jacobs, S.E. and Nickelson, T.E. (1998) Use of stratified random sampling to estimate the abundance of Oregon coastal coho salmon. Oregon Department of Fish and Wildlife, Fish Research Project Final Report F-145-R-09. 29 p.
- Kalnay, E. and Coauthors. (1996) The NCEP/NCAR 40-year reanalysis project. *Bull. Am. Meteorol. Soc.* **77**:437–471.
- Katz, R.W. and Brown, B.G. (1991) The problem of multiplicity in research on teleconnections. *Int. J. Climatol.* **11**:505–513.
- Koslow, J., Hobday, A. and Boehlert, G. (2002) Climate variability and marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. *Fish. Oceanogr.* **11**:65–77.
- Kousky, V.E. and Higgins, R.W. (2007) An alert classification system for monitoring and assessing the ENSO cycle. *Weather Forecasting* **22**:353–371.
- Lawson, P. (1993) Cycles in ocean productivity, trends in habitat quality, and the restoration of salmon runs in Oregon. *Fisheries (Bethesda)* **18**:6–10.
- Lawson, P.W. (1997) Interannual variability in growth and survival of chinook and coho salmon. In: *Estuarine and Ocean Survival of Northeastern PACIFIC Salmon: Proceedings of the Workshop*. R.L. Emmett & M.H. Schiewe (eds) U.S. Department of Commerce, NOAA Tech. Memo: NMFS-NWFSC-29, 81–92.
- Lawson, P.W., Logerwell, E.A., Mantua, N.J., Francis, R.C. and Agostini, V.N. (2004) Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **61**:360–373.
- Lewis, M., Brown, E., Sounhein, B., Weeber, M., Suring, E. and Truemper, H. (2009) *Status of Oregon stocks of Coho Salmon, 2004 through 2008. Monitoring Program Report Number OPSW-ODFW-2009-3*, Salem, Oregon: Oregon Department of Fish and Wildlife. 51 p.
- Logerwell, E.A., Mantua, N., Lawson, P.W., Francis, R.C. and Agostini, V.N. (2003) Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. *Fish. Oceanogr.* **12**:554–568.
- Magnuson, J.J., Allendorf, F.W., Beschta, R.L. et al. (1996) *Upstream: Salmon and Society in the Pacific Northwest*. Washington, DC: National Academy Press.
- Mantua, N., Hare, S., Zhang, Y., Wallace, J. and Francis, R. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**:1069–1079.
- Miller, R.G., Jr. (1981) *Simultaneous Statistical Inference*, 2nd edn. New York: Springer-Verlag.
- Mueter, F.J., Pyper, B.J. and Peterman, R.M. (2005) Relationship between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. *Trans. Am. Fish. Soc.* **134**:105–119.
- Nickelson, T. (1986) Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. *Can. J. Fish. Aquat. Sci.* **43**:527–535.
- Olden, J.D. and Neff, B.D. (2001) Cross-correlation bias in lag analysis of aquatic time series. *Mar. Biol.* **138**:1063–1070.
- Pearcy, W.G. (1992) *Ocean Ecology of North Pacific Salmonids*. Seattle: Washington Sea Grant Program, University of Washington Press.
- Peterman, R.M. and Bradford, M.J. (1987) Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science* **235**:354–356.
- Peterson, W.T. and Schwing, F.B. (2003) A new climate regime in northeast Pacific ecosystems. *Geophys. Res. Lett.* **30**:1896, doi:10.1029/2003GL017528.
- Peterson, W.T., Hooff, R.C., Morgan, C.A., Hunter, K.L., Cassilas, E. and Ferguson, J.W. (2006) *Ocean Conditions and Salmon Survival in the Northern California Current*. Seattle: Northwest Fisheries Science Center.
- PFMC (Pacific Fishery Management Council) (2003a) *Pacific Coast Salmon Plan: Fishery Management Plan for Commercial and Recreational Salmon Fisheries of the Coasts of Washington, Oregon, and California as revised through Amendment 14*. Portland: Pacific Fishery Management Council.

- PFMC (Pacific Fishery Management Council) (2003b) *Preseason Report I: Stock Abundance Analysis for 2003 Ocean Salmon Fisheries (Document prepared for the Council and its advisory entities)*. Portland: Pacific Fishery Management Council.
- PFMC (Pacific Fishery Management Council) (2010) *Preseason Report I: Stock Abundance Analysis for 2010 Ocean Salmon Fisheries (Document prepared for the Council and its advisory entities)*. Portland: Pacific Fishery Management Council.
- Polovina, J., Mitchum, G. and Evans, C. (1995) Decadal and basin-scale variation in mixed-layer depth and the impact on biological production in the central and North Pacific, 1960–88. *Deep-Sea Res.* **42**:1701–1716.
- Pyper, B.J. and Peterman, R.M. (1998) Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**:2127–2140.
- Ruzicka, J.J., Wainwright, T.C. and Peterson, W.T. (2011) A simple plankton model for the Oregon upwelling ecosystem: sensitivity and validation against time-series ocean data. *Ecol. Modell.* **222**:1222–1235.
- Ryding, K.E. (1998) *Analyzing Adult Returns to Assess Ocean Effects and Salmon Survival Relationships*. M.S. thesis, Seattle: University of Washington.
- Ryding, K. and Skalski, J. (1999) Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **56**:2374–2384.
- Scarnecchia, D.L. (1981) Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. *Can. J. Fish. Aquat. Sci.* **38**:471–475.
- Scheuerell, M.D. and Williams, J.G. (2005) Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon. *Fish. Oceanogr.* **14**:448–457.
- Schwing, F.B., O'Farrell, M., Steger, J.M. and Baltz, K. (1996) Coastal upwelling indices west coast of North America 1946–95, NOAA Technical Memorandum, NOAA-TM-NMFS-SWFSC-231, 32 p.
- Strub, P.T., Allen, J.S., Huyer, A. and Smith, R.L. (1987) Seasonal cycles of currents, temperatures, winds, and sea level over the Northeast Pacific continental shelf: 35° N to 45° N. *J. Geophys. Res.* **92**:1507–1526.
- Tebaldi, C. and Knutti, R. (2007) The use of the multi-model ensemble in probabilistic climate projections. *Philos. Trans. R. Soc. A* **365**:2053–2075 doi:10.1098/rsta.2007.2076.
- Trenberth, K.E. and Hurrell, J.W. (1994) Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics* **9**:303–319.
- U.S. Federal Register (2008) Endangered and Threatened Species: Final Threatened Listing Determination, Final Protective Regulations, and Final Designation of Critical Habitat for the Oregon Coast Evolutionarily Significant Unit of Coho Salmon. Docket 08-552, U.S. Department of Commerce, NOAA, Federal Register 73 (28): 7816–7873.
- Walters, C.J. (1987) Nonstationarity of production relationships in exploited populations. *Can. J. Fish. Aquat. Sci.* **44**:s156–s165.
- Ware, D.M. and Thompson, R.E. (1991) Link between long-term variability in upwelling and fish production in the northeast Pacific Ocean. *Can. J. Fish. Aquat. Sci.* **48**:2296–2306.
- Weitkamp, L. and Neely, K. (2002) Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insights from marine coded-wire tag recoveries. *Can. J. Fish. Aquat. Sci.* **59**:1100–1115.
- Wolter, K. and Timlin, M.S. (1993) Monitoring ENSO in COADS with a seasonally adjusted principal component index. Proc. of the 17th Climate Diagnostics Workshop, Norman, OK, NOAA/NMC/CAC, NSSL, Oklahoma Clim. Survey, CIMMS and the School of Meteor., University of Oklahoma, 52–57.
- Wood, S.N. (2006) *Generalized Additive Models: An Introduction with R*. Boca Raton, FL: CRC/Chapman & Hall.
- Wright, S.G. (1968) Origin and migration of Washington's chinook and coho salmon. Wash. Dept. Fish. Inf. Booklet 1. 25 pp.