Chinook salmon (*Oncorhynchus tshawytscha*) — seabird covariation off central California and possible forecasting applications

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Abstract: We evaluated covariation between Chinook salmon (*Oncorhynchus tshawytscha*) abundance and seabird breeding success in central California, USA, and compared potential forecasts to predictive models based on jack (2-year-old male) returns in the previous year. Stepwise regression models based on seabird breeding success in the previous year were comparable to or stronger than jack-based models. Including seabird breeding success in the current year improved the strength of the relationships. Combined approaches that included seabird and jack data further improved the models in some cases. The relationships based on seabird breeding success remained relatively strong over both shorter (1990–2004) and longer (1976–2004) time periods. Regression models based on multivariate seabird or combined seabird–jack indices were not as strong as stepwise regression models. Our results indicate that there is significant covariation in the responses of salmon and seabirds to variability in ocean conditions and that seabird data may offer an alternate way of forecasting salmon abundance in central California.

Résumé : Nous évaluons la covariation entre l'abondance des saumons chinook (*Oncorhynchus tshawytscha*) et le succès de la reproduction des oiseaux marins en Californie centrale. É.-U., et nous comparons les prédictions potentielles ainsi générées à celles des modèles prédictifs basés sur les retours des madeleineaux (mâles de 2 ans) de l'année précédente. Les modèles de régression pas à pas basés sur le succès de la reproduction des oiseaux marins durant l'année précédente sont aussi ou plus puissants que les modèles basés sur les madeleineaux. L'inclusion du succès de la reproduction des oiseaux marins de l'année courante augmente la force des relations. Dans certains cas, l'inclusion conjointe des données sur les oiseaux de mer et les madeleineaux améliore encore plus les modèles. Les relations basées sur le succès de la reproduction des oiseaux marins demeurent relativement fortes tant sur des périodes de temps plus courtes (1990–2004) que plus longues (1976–2004). Les modèles de régression basés sur des indices multidimensionnels relatifs aux oiseaux de mer ou conjointement aux oiseaux de mer et aux madeleineaux n'ont pas autant de puissance que les modèles de régression pas à pas. Nos résultats indiquent qu'il existe une covariation significative dans les réactions des saumons et des oiseaux marins à la variabilité des conditions océaniques et que les données sur les oiseaux marins peuvent servir d'outil de rechange pour prédire l'abondance des saumons en Calfornie centrale.

[Traduit par la Rédaction]

Introduction

The influences of ocean conditions and prey abundance on salmon populations are difficult to assess. Many researchers have focused on this issue and have demonstrated links between ocean conditions and salmon abundance and various life history and demographic characteristics. Studies of the effects of large-scale variation in ocean conditions have found that salmon catch and growth rates in the California Current System (CCS) are lower during El Niño – Southern Oscillation (ENSO) events and warm "regimes" that are characterized by lower ocean productivity (Mantua et al. 1997; Botsford and Lawrence 2002; Wells et al. 2006). Regional ocean conditions such as strong upwelling, low sea surface temperature, strong wind mixing, weak stratification

of the water column, and low coastal sea level are indicative of productive ocean conditions and have a positive effect on salmon survival (Cole 2000; Koslow et al. 2002; Scheuerell and Williams 2005). Additionally, Peterson and Schwing (2003) show that the relative abundance of "cold-water" copepods has a positive influence on salmon survival.

Similar relationships have been found between seabird breeding parameters and variations in ocean conditions and prey availability. Ainley et al. (1995) demonstrated that breeding success is linked to large-scale climate indices. Many studies have documented short-term reductions in breeding success or complete breeding failure during severe warm-water events (Hodder and Graybill 1985; Wilson 1991; Sydeman et al. 2006) and longer-term declines in breeding success during warm "regimes" (Sydeman et al. 2001). On

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regional scales, seabirds exhibit earlier breeding and increased breeding success in years of stronger upwelling, lower sea surface temperature, and greater prey availability (Gaston and Smith 2001; Abraham and Sydeman 2004; Roth et al. 2005). These findings suggest that salmon and seabirds respond similarly to variation in ocean conditions.

One of the proposed mechanisms for the responses of both salmon and seabirds to temporal environmental variation is a "bottom-up" (nutrient-driven) effect of ocean productivity on prey availability (Sydeman et al. 2001; Koslow et al. 2002; Logerwell et al. 2003). There is considerable overlap in the diets of salmon and seabirds, and they may be responding similarly to fluctuations in a common prey base. Chinook salmon (*Oncorhynchus tshawytscha*) forage on a wide variety of marine invertebrates and fish, including euphausiids, copepods, crab larvae, squid, northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea pallasii*), and rockfish (*Sebastes* spp.) in northern and central California (Merkel 1957; Hunt et al. 1999). In addition, Central Valley Chinook salmon enter and exit San Francisco Bay and may have considerable spatial overlap with seabirds breeding just offshore on Southeast Farallon Island (37°42′N, 123°00′W) and foraging in the surrounding area.

Seabirds breeding on the island include Cassin's auklets (*Ptychoramphus aleuticus*), common murres (*Uria aalge*), Brandt's cormorants (*Phalacrocorax penicillatus*), pelagic cormorants (*Phalacrocorax pelagicus*), and pigeon guillemots (*Cepphus columba*). These seabirds also forage on a wide variety of marine invertebrates and fish. Cassin's auklets are planktivores that primarily forage on euphausiids (Ainley et al. 1996*a*; Sydeman et al. 1997, 2001). Common murres forage on a variety of prey, including euphausiids, rockfish, market squid (*Loligo opalescens*), northern anchovy, Pacific whiting (*Merluccius productus*), and shiner surfperch (*Cymatogaster aggregata*; Ainley et al. 1996*b*; Sydeman et al. 1997, 2001). Brandt's cormorants are piscivores that forage on rockfish, flatfish (Bothidae and Pleuronectidae), plainfin midshipman (*Porichthys notatus*), and northern anchovy, whereas pelagic cormorants and pigeon guillemots forage on rockfish and sculpins (Cottidae; Ainley et al. 1990; Sydeman et al. 1997, 2001).

Based on the similarities outlined above, we propose that these seabirds and Chinook salmon are "trophic equivalents" and that seabirds can be used as indicators of the marine foraging conditions experienced by salmon during the ocean phase of their life cycle. To test this hypothesis, we evaluate covariation between Chinook salmon abundance and seabird breeding success in central California over two time scales, 1990–2004 and 1976–2004. Specifically, we evaluate the relationships between salmon abundance and seabird breeding success in the previous year, seabird breeding success averaged over 2- to 4-year periods (corresponding to the ocean phase of a typical salmon cohort), and multivariate indices (derived using principal components analysis) of seabird breeding success over multiple time scales. We compare models based on covariation with predictive models based on jack (2-year-old male) returns in the previous year. We repeat these procedures with jack returns in the previous year included in the models to evaluate the effectiveness of combined seabird–jack models in forecasting salmon abundance.

Materials and methods

Salmon data

We used estimates of the Central Valley index (CVI) and fall escapement in our analyses. The CVI is a measure of overall abundance that includes the ocean harvest south of Point Arena and total escapement (fish that "escape" the fishery and return to spawn) into the Central Valley. The Pacific Fishery Management Council (PFMC) currently uses linear regression to predict the CVI from the number of jack returns in the previous year (PFMC 2006). We also used fall escapement as a measure of abundance to assess whether relationships were stronger (or weaker) when we focused on only one of the salmon runs (groups of fish that undergo spawning migrations at the same time) in a given year. We chose the fall run because it currently makes up approximately 90% of the total escapement into the Central Valley (PFMC 2006). Ocean harvest for the fall run could not be partitioned out from overall harvest and was not included in the models.

Seabird data

We used estimates of Cassin's auklet, common murre, Brandt's cormorant, pelagic cormorant, and pigeon guillemot breeding success on Southeast Farallon Island in our analyses. We calculated mean breeding success (chicks per pair) for each species in each year based on data collected at individual nest sites (see Ainley and Boekelheide (1990) for a detailed description of collection methodology). We created additional variables for each seabird species that were comprised of running averages of breeding success for the current year (year x) and up to three previous years (years x and $x - 1$; years x, $x - 1$, and $x - 2$; years x, $x - 1$, $x - 2$, and $x - 3$). We used these running means as indices of ocean conditions over multiple time scales during the ocean phase of the Chinook salmon life cycle.

Statistical analyses

We evaluated the relationships between salmon abundance and seabird breeding success over two time periods. First, we assessed the relationships between the CVI and seabird breeding success for 1990–2004. We chose this time period because it corresponds to the time period used by the PFMC to forecast salmon abundance. Second, we repeated the analyses for 1976–2004 to evaluate the relationships over a longer time period and a greater range of environmental conditions. We used the same methods to evaluate relationships between fall escapement and seabird breeding success. Fall escapement numbers for 1976–2004 were log-transformed to normalize the data. We considered relationships significant at $p < 0.05$, though we focused primarily on coefficient of determination (r^2) values to evaluate covariation in regression models. We conducted all analyses in Stata 8.0 (Stata Corporation 2003).

We tested all time series data for positive autocorrelation using Durbin–Watson statistics at $p < 0.05$ (Kutner et al. 2005). The test statistic is compared with lower (d_l) and upper (d_u) bounds. Values less than d_l indicate that the data are serially correlated, values greater than d_u indicate that the data are independent, and values in between d_l and d_u indicate that the results are inconclusive. There was no evidence of autocorrelation in the seabird data for any species from 1990–

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2004 (d ranged from 1.59 to 2.26 compared with d_u = 1.36) or for most species from 1976–2004 (d ranged from 2.17 to 2.35 compared with d_u = 1.48). There may be slight autocorrelation in the Cassin's auklet data from 1976–2004 (d = 1.47 compared with d_u = 1.48), though the test was inconclusive. There was no evidence of autocorrelation in the CVI for either time period (1990–2004, d = 2.01 compared with d_u = 1.36; 1976–2004, d = 1.67 compared with d_u = 1.48). There may be slight autocorrelation in fall escapement numbers from 1990–2004 (d = 1.31 compared with d_u = 1.36). There was clear evidence of autocorrelation in fall escapement numbers from 1976–2004 (d = 0.83 compared with d_l = 1.34). Autocorrelation may have increased the chance of making type I errors when we assessed relationships between fall escapement and seabird breeding success. We accepted this possibility because our primary interests were in assessing covariation between salmon abundance and seabird breeding success and evaluating potential forecasting applications (i.e., we were not testing the hypothesis that seabird breeding success directly influences salmon abundance and we were not overly concerned with p values). Furthermore, autocorrelation may be present, in part, because the species are responding to longer-term changes in ocean conditions. We, therefore, did not want to remove effects that might be evidence that the two taxa are responding similarly to those changes.

We used linear regression to evaluate covariation between salmon abundance (CVI or fall escapement) and the number of jack returns in the previous year and seabird breeding success over multiple and varying time scales (Legendre and Legendre 1998). Initially, we conducted preliminary analyses to assess univariate relationships between each seabird species and salmon abundance. We evaluated both linear and quadratic terms at $p < 0.01$ because of the large number of comparisons. Common murre breeding success was excluded from further analyses because there were no significant univariate relationships with salmon abundance. We used forward stepwise regression to determine which of the remaining seabird species were related to salmon numbers. We included Cassin's auklet, Brandt's cormorant, pelagic cormorant, and pigeon guillemot breeding success as independent variables in each stepwise regression. We conducted a stepwise regression using breeding success in the previous year (year x – 1). We focused on the previous year to evaluate the possibility that data collected one year in advance of the salmon returns – fishing season could be used for forecasting. We conducted separate stepwise regressions for seabird breeding success in the current year (year x) and averaged over 2 (years x and x – 1), 3 (years x, x – 1, and x – 2), and 4 (years x, x – 1, x – 2, and x – 3) years to examine the strength of the relationships over multiple time scales during the ocean phase of a typical salmon year class (i.e., potential cohort). We repeated the stepwise regressions with jack returns in the previous year included as an independent variable to assess whether combined seabird–jack approaches could strengthen predictive relationships.

We used principal components analysis to assess whether multivariate seabird indices provided stronger relationships to salmon abundance than stepwise regression analyses (Legendre and Legendre 1998). As above, we developed indices for seabird breeding success in the previous year, in the current year, and averaged over 2, 3, and 4 years. We retained principal components with eigenvalues > 1. We used linear regression to assess covariation between salmon abundance and the retained seabird principal components. We repeated this procedure with jack returns in the previous year to assess whether combined seabird–jack multivariate indices were stronger than those based on seabird data alone.

We chose the best models from the analyses described above based on adjusted r^2 values that allowed us to compare models with varying numbers of observations and variables (Kutner et al. 2005). The method tends to favor models with more variables than other model-selection procedures (e.g., Akaike's information criterion). We accepted this possibility because we were interested in the forecasting capability of the models (i.e., we did not want to penalize them too heavily for including a second or third variable). We used a cross-validation procedure to assess the ability of those models to predict salmon numbers (Kleinbaum et al. 1988). We excluded each year in turn from each of the analyses, estimated regression equations using the remaining data, and predicted the values for the excluded years. We used linear regression to compare predicted and actual values for each model. We used the resulting r^2 value (cross-validation r^2) to assess how well the model would perform when applied to new data. We also calculated the average percent deviation between predicted and actual values.

Results

The predictive relationship between the CVI and jack returns in the previous year was strong for 1990–2004 (adjusted r^2 = 0.61) and weak for 1976–2004 (adjusted r^2 = 0.16; Table 1). The best seabird model based on data from the previous year included Cassin's auklet breeding success for both time periods. The seabird model was comparable to the jack model for 1990–2004 (adjusted r^2 = 0.60) and was an improvement over the jack model for 1976–2004 (adjusted r^2 = 0.33), though it is noteworthy that the predictive value was lower over the longer time period for both jacks and seabirds. Combining the seabird and jack data did not improve the relationships for 1990–2004. The combined model was a substantial improvement over other models for 1976–2004, explaining an additional 44% of the variation in the CVI compared with the jack model. This model included jack returns and Cassin's auklet, Brandt's cormorant, and pigeon guillemot breeding success.

Fall escapement was weakly related to fall jack returns in the previous year for 1990–2004 (adjusted r^2 = 0.26), and the relationship was not significant for 1976–2004 (adjusted r^2 = 0.07; Table 1). The best seabird models were much better and included Cassin's auklet breeding success for both time periods. These models explained 25%–30% more variation in fall escapement than the jack models and were significant over both shorter and longer time periods. Combining the seabird and jack data did not improve the relationships for either time period.

The best models for predicting the CVI based on multiyear averages of seabird data included a 2-year average (years x and x – 1) of Brandt's cormorant breeding success

Table 1. Comparisons of models relating salmon abundance to the number of jacks returning to spawn, seabird breeding success, and combinations of jack and seabird data in the previous year.

	Central Valley index		Fall escapement	
	1990–2004	1976–2004	1990–2004	1976–2004
Jack models				
Jacks	+	+	+	
Model results				
Adjusted r^2	0.61	0.16	0.26	0.07
p value	<0.001	<0.05	<0.05	>0.05
Seabird models				
CAAU	+	+	+	+
BRAC				
PIGU				
PECO				
Model results				
Adjusted r^2	0.60	0.33	0.56	0.32
p value	<0.001	<0.001	<0.001	<0.001
Combined models				
Jacks	+	+		
CAAU		+	+	+
BRAC		+		
PIGU		–		
PECO				
Model results				
Adjusted r^2	0.61	0.60	0.56	0.32
p value	<0.001	<0.001	<0.001	<0.001

Note: Variables included in all of the models were lagged by 1 year. Jack models were based on simple linear regressions. Seabird and combined models were based on stepwise regressions. Significant variables are denoted with a plus or minus depending on the sign of the regression coefficient. CAAU, Cassin's auklet; BRAC, Brandt's cormorant; PIGU, pigeon guillemot; PECO, pelagic cormorant.

for 1990–2004 (adjusted r^2 = 0.60) and 2-year averages of Cassin's auklet and Brandt's cormorant breeding success for 1976–2004 (adjusted r^2 = 0.64; Table 2). These seabird models were comparable to the jack model for 1990–2004 (adjusted r^2 = 0.61) and an improvement over the jack model for 1976–2004 (adjusted r^2 = 0.16). The best combined models strengthened the relationships for both time periods, explaining an additional 19% and 54% of the variation in the CVI compared with the jack models.

The best seabird model for predicting fall escapement was one including a 2-year average of Cassin's auklet breeding success for 1990–2004 (adjusted r^2 = 0.78; Table 3). Three-year averages of Cassin's auklet and Brandt's cormorant breeding success were important in predicting fall escapement for 1976–2004 (adjusted r^2 = 0.66). The seabird models explained an additional 52% and 59% of the variation in fall escapement compared with the jack models and were better than the combined models for both time periods.

The best models for predicting salmon numbers based on multivariate seabird indices were generally not as strong as the comparable stepwise regression models. For indices based on data from the previous year, only the combined index for predicting the CVI from 1990–2004 had a higher adjusted r^2 value (adjusted r^2 = 0.72; Table 4) than the comparable stepwise regression model (adjusted r^2 = 0.61). The models for predicting the CVI and fall escapement based on multiyear

averages of seabird breeding success had lower adjusted r^2 values than the comparable stepwise regression models for both the seabird and combined indices (Tables 5 and 6).

The seabird–jack index based on multiyear averages of seabird breeding success had the least shrinkage (i.e., the lowest drop in the r^2 value) when its ability to predict the CVI for 1990–2004 was tested (Table 7). The combined model based on multiyear averages had the lowest average percent deviation between predicted and actual values for that time period (Fig. 1). For 1976–2004, the seabird index based on multiyear averages of seabird breeding success had the least shrinkage, whereas the best combined seabird–jack model based on multiyear averages had the lowest average percent deviation between predicted and actual values. The best seabird models for predicting fall escapement based on multiyear averages had the least shrinkage and the lowest average percent deviation between predicted and actual values for 1990–2004. For 1976–2004, the seabird model and seabird index based on multiyear averages had the least shrinkage and the seabird model had the lowest average percent deviation between predicted and actual values.

Discussion

Our results indicate that there is covariation in the responses of seabirds and Chinook salmon to variability in

Table 2. Comparisons of models relating the Central Valley index to seabird breeding success and a combination of seabird breeding success and the number of jacks returning to spawn in the previous year.

	Current year (year x)		Two-year average (years x and $x-1$)		Three-year average (years x, $x-1$, and $x-2$)		Four-year average (years x, $x-1$, $x-2$, and $x-3$)	
	1990–2004	1976–2004	1990–2004	1976–2004	1990–2004	1976–2004	1990–2004	1976–2004
Seabird models								
CAAU	+	+		+	+			
BRAC			+	+		+	+	+
PIGU								
PECO								
Model results								
Adjusted r^2	0.26	0.28	**0.60**	**0.64**	0.51	0.53	0.37	0.53
p value	<0.05	<0.01	**<0.001**	**<0.001**	<0.01	<0.001	<0.01	<0.001
Combined models								
Jacks	+	+	+	+	+	+	+	+
CAAU		+		+				
BRAC			+	+	+	+		+
PIGU								
PECO								
Model results								
Adjusted r^2	0.61	0.38	**0.80**	**0.70**	0.70	0.67	0.61	0.58
p value	<0.001	0.001	**<0.001**	**<0.001**	<0.001	<0.001	<0.001	<0.001

Note: Values in bold indicate models with the highest adjusted r^2 values for each time period. Stepwise regression models were based on breeding success in the current year and averages of the current year and up to three previous years. All regression coefficients were positive.

Table 3. Comparisons of models relating fall escapement to seabird breeding success and a combination of seabird breeding success and the number of fall jacks returning to spawn in the previous year.

	Current year (year x)		Two-year average (years x and $x-1$)		Three-year average (years x, $x-1$, and $x-2$)		Four-year average (years x, $x-1$, $x-2$, and $x-3$)	
	1990–2004	1976–2004	1990–2004	1976–2004	1990–2004	1976–2004	1990–2004	1976–2004
Seabird models								
CAAU	+	+	+	+	+	+	+	+
BRAC						+		+
PIGU								
PECO								
Model results								
Adjusted r^2	0.57	0.49	**0.78**	0.63	0.71	**0.66**	0.64	0.58
p value	<0.001	<0.001	**<0.001**	<0.001	<0.001	**<0.001**	<0.001	<0.001
Combined models								
Jacks								
CAAU	+	+	+	+	+	+	+	+
BRAC						+		+
PIGU								
PECO								
Model results								
Adjusted r^2	0.57	0.49	**0.78**	0.63	0.71	**0.66**	0.64	0.58
p value	<0.001	<0.001	**<0.001**	<0.001	<0.001	**<0.001**	<0.001	<0.001

Note: Values in bold indicate models with the highest adjusted r^2 values for each time period. Stepwise regression models were based on breeding success in the current year and averages of the current year and up to three previous years. All regression coefficients were positive.

ocean conditions and that seabird data may be useful in a forecasting context. Others have discussed the use of seabirds as indicators of forage fish abundance and zooplankton availability (Monaghan et al. 1989; Cairns 1992; Abraham and Sydeman 2006). However, most previous studies have focused on "nowcasting" of fish abundance rather than the predictive capabilities of the relationships. Velarde et al. (2004) provide an exception to this, with a focus on predictive models of Pacific sardine (*Sardinops caeruleus*) catch in Baja California that incorporate seabird diet and breeding

Table 4. Comparisons of models relating salmon abundance to seabird indices (principal components) and combined seabird–jack indices using data from the previous year.

	Central Valley index		Fall escapement	
	1990–2004	1976–2004	1990–2004	1976–2004
Seabird models[a]				
Factor 1	+	+	+	+
Model results				
Adjusted r^2	0.27	0.23	0.42	0.15
p value	<0.05	<0.01	<0.01	<0.05
Combined models[b]				
Factor 1	+	+	+	+
Factor 2	+	NA	NS	NA
Model results				
Adjusted r^2	0.72	0.27	0.48	0.17
p value	<0.001	<0.01	<0.01	<0.05

Note: Factors were derived from principal components analyses. NA, the second factor was not retained for the regression analyses shown above (eigenvalue < 1); NS, the factor was not significant and was subsequently dropped from the regression analyses. All regression coefficients were positive.
[a]Principal components analysis included data on CAAU, BRAC, PIGU, and PECO.
[b]Principal components analysis included seabird breeding success for all species listed above and jacks in the previous year.

Table 5. Comparisons of models relating the Central Valley index to seabird indices (principal components) and combined seabird–jack indices.

	Current year (year x)		Two-year average (years x and $x - 1$)		Three-year average (years x, $x - 1$, and $x - 2$)		Four-year average (years x, $x - 1$, $x - 2$, and $x - 3$)	
	1990–2004	1976–2004	1990–2004	1976–2004	1990–2004	1976–2004	1990–2004	1976–2004
Seabird models[a]								
Factor 1	+	+	+	+	+	+	+	+
Model results								
Adjusted r^2	0.34	0.22	**0.49**	**0.46**	0.38	0.31	0.24	0.24
p value	<0.01	<0.01	**<0.01**	**<0.001**	<0.01	<0.001	<0.05	<0.01
Combined models[b]								
Factor 1	+	+	+	+	+	+	+	+
Factor 2	NA	+	NA	NA	NA	+	+	NA
Model results								
Adjusted r^2	0.46	0.39	**0.63**	0.50	0.50	**0.56**	0.58	0.28
p value	<0.01	<0.001	**<0.001**	<0.001	<0.01	**<0.001**	<0.01	<0.01

Note: Values in bold indicate models with the highest adjusted r^2 values for each time period. Factors were derived from principal components analyses. NA, the second factor was not retained for regression analyses. All regression coefficients were positive.
[a]Based on seabird breeding success in the current year and averages of the current year and up to three previous years.
[b]Based on jacks in the previous year and seabird breeding success in the current year and averages of the current year and up to three previous years.

parameters. Velarde et al.'s (2004) effort is based, in part, on the direct consumption of sardines by the seabirds. Our effort is unique in that our models are based on an apparent similarity in the responses of specific seabirds and Chinook salmon that is presumably due to the similarity in their diets. Indeed, the one species that consumes juvenile Chinook salmon, common murre, was dropped from our modeling effort early on. The covariation we found offers support for the idea that seabirds and salmon are "trophic equivalents" and are both being influenced by "bottom-up" (nutrient-driven) processes. In the California Current System, ecosystem productivity is influenced by two main factors: (*i*) the strength of the California Current that brings nutrient-rich waters into the region from the north and (*ii*) seasonal upwelling that brings nutrients to the surface (Chelton et al. 1982; Schwing

et al. 2000). If the seabirds in this study directly influenced Chinook salmon in a "top-down" fashion, we would have found negative correlations. Although we cannot rule out the possibility that other top predators are affecting both seabirds and salmon, we suggest that a "bottom-up" mechanism is most compelling.

We found significant relationships between salmon abundance and seabird breeding success in the previous year and seabird breeding success averaged over multiple years. Models including averages of the current (year *x*) and 1 (year *x* – 1) or 2 (years *x* – 1 and *x* – 2) previous years were stronger than those based only on the previous year. Though we were not able to analyze the data by salmon year class (cohort), our results suggest that ocean conditions in the later phases of the salmon life cycle at sea are important.

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Table 6. Comparisons of models relating fall escapement to seabird indices (principal components) and combined seabird–jack indices.

	Current year (year x)		Two-year average (years x and $x-1$)		Three-year average (years x, $x-1$, and $x-2$)		Four-year average (years x, $x-1$, $x-2$, and $x-3$)	
	1990–2004	1976–2004	1990–2004	1976–2004	1990–2004	1976–2004	1990–2004	1976–2004
Seabird models[a]								
Factor 1	+	+	+	+	+	+	+	+
Model results								
Adjusted r^2	0.52	0.40	**0.73**	**0.54**	0.70	0.48	0.54	0.35
p value	0.001	<0.001	**<0.001**	**<0.001**	<0.001	<0.001	0.001	<0.001
Combined models[b]								
Factor 1	+	+	+	+	+	+	+	+
Factor 2	NA	NS	NS	NA	NS	+	NS	+
Model results								
Adjusted r^2	0.59	0.42	**0.76**	0.56	0.73	**0.61**	0.60	0.46
p value	<0.001	<0.001	**<0.001**	<0.001	<0.001	**<0.001**	<0.001	<0.001

Note: Values in bold indicate models with the highest adjusted r^2 values for each time period. Factors were derived from principal components analyses. NA, the second factor was not retained for regression analyses; NS, the second factor was not significant and was subsequently dropped from the regression analyses. All regression coefficients were positive.

[a]Based on seabird breeding success in the current year and averages of the current year and up to three previous years.

[b]Based on jacks in the previous year and seabird breeding success in the current year and averages of the current year and up to three previous years.

Our results are consistent with studies that have documented influences of ocean conditions in both the year of ocean entry and the year of return on coho salmon (*Oncorhynchus kisutch*) growth and survival in the northern California Current System (Botsford and Lawrence 2002; Koslow et al. 2002; Wells et al. 2006). Relationships between Chinook salmon and ocean conditions are generally more complex as a result of wide variation in age-at-return, but ocean conditions in the year of return appear to be important (Botsford and Lawrence 2002; Wells et al. 2006). Scheuerell and Williams (2005) developed predictive models of Snake River Chinook salmon survival, finding that including upwelling in the year of return substantially improved the predictive capability of their models. There is, however, a trade-off between the quality of the prediction and data availability in our models. Seabird data from the current year are not available before the start of the fishing season and would, therefore, be difficult to include in management decisions.

Patterns across time scales

The strength of the relationships between salmon abundance and both seabird breeding success and jack returns was generally weaker over the longer time period, 1976–2004. This result is not surprising given the greater range of marine conditions that salmon and seabirds are likely to experience in longer versus shorter time periods and the associated difficulty in capturing that variation (Sydeman et al. 2001; Chavez et al. 2003). However, relationships between salmon abundance and seabird breeding success and combined seabird–jack data remained relatively strong in comparison to models based only on jacks, which were poor for the longer time series. These results are encouraging because relationships between salmon survival and physical indices of ocean conditions have tended to break down over time. For instance, Lawson (1997) found that an established relationship between coho salmon survival and upwelling was not significant during a later period of weaker upwelling. Miller and Sydeman (2004) noted a similar breakdown be-

tween upwelling and rockfish productivity. Consequently, researchers have included multiple physical variables in their analyses in order to better capture the variation in the ocean environment (Koslow et al. 2002; Logerwell et al. 2003). Our results suggest that including seabird data in fisheries models may offer an additional method for capturing the important biological and physical variation driving fish population dynamics.

Univariate versus multivariate approaches

The models based on individual variables (stepwise regressions) were generally stronger than those based on multivariate indices (principal components). We developed the multivariate indices to evaluate the possibility that a single seabird index or a single combined seabird–jack index could be developed that would simplify analytical considerations and interpretations. However, the seabirds included in the indices have different sensitivities to variation in ocean conditions because of differences in reproductive strategies and trophic ecology (Ainley et al. 1995; Sydeman et al. 2001), and combining them into a single index appears to obscure some of the covariation evident in single-species analyses. The fact that not all species were included in stepwise regression models supports this interpretation.

Interestingly, Cassin's auklet breeding success was included in most of the stepwise regression models. Cassin's auklets may be especially good indicators of ocean conditions for salmon because they feed extensively on euphausiids off central California (Ainley et al. 1996*a*; Abraham and Sydeman 2004, 2006). Euphausiids probably represent the lowest trophic level directly exploited by seabirds and salmon and may be one of the most responsive prey items to changes in ocean characteristics. Brandt's cormorant breeding success was also included in many of the stepwise regression models based on multiyear averages of seabird breeding success. Brandt's cormorants feed on a wide variety of fish species in neritic habitats (Sydeman et al. 1997) and may be good indicators of average ocean conditions over longer time periods be-

Table 7. Comparisons of the predictive capability of the best models from each analysis, including r^2 values from the original models, cross-validation r^2 values, shrinkage, and the average percent deviation between predicted and actual values.

|	$r^{2\ a}$	Cross-validation $r^{2\ b}$	Shrinkage[c]	Average percent deviation ± SD
Central Valley index (1990–2004)				
Previous year				
Jack model	0.64	0.54	0.10	5±25
Seabird model	0.62	0.48	0.14	7±39
Combined model	NA	NA	NA	NA
Seabird index	0.32	0.17	0.15	14±58
Seabird–jack index	0.76	0.59	0.17	5±30
Multiyear averages				
Seabird model	0.63	0.49	0.14	5±40
Combined model	0.83	0.73	0.10	1±22
Seabird index	0.53	0.42	0.11	9±38
Seabird–jack index	0.65	0.56	0.09	6±31
Central Valley index (1976–2004)				
Previous year				
Jack model	0.19	0.09	0.10	12±40
Seabird model	0.36	0.27	0.09	9±37
Combined model	0.66	0.50	0.16	5±34
Seabird index	0.26	0.17	0.09	11±43
Seabird–jack index	0.29	0.21	0.08	10±42
Multiyear averages				
Seabird model	0.66	0.58	0.08	4±25
Combined model	0.73	0.63	0.10	2±24
Seabird index	0.48	0.42	0.06	7±30
Seabird–jack index	0.59	0.51	0.08	5±26
Fall escapement (1990–2004)				
Previous year				
Jack model	0.31	0.18	0.13	29±59
Seabird model	0.59	0.46	0.13	17±77
Combined model	NA	NA	NA	NA
Seabird index	0.46	0.30	0.16	33±118
Seabird–jack index	0.51	0.38	0.13	26±98
Multiyear averages				
Seabird model	0.80	0.72	0.08	2±45
Combined model	NA	NA	NA	NA
Seabird index	0.75	0.65	0.10	11±63
Seabird–jack index	0.78	0.68	0.10	6±48
Fall escapement (1976–2004)				
Previous year				
Jack model	0.10	0.02	0.08	16±56
Seabird model	0.34	0.25	0.09	10±52
Combined model	NA	NA	NA	NA
Seabird index	0.18	0.07	0.11	14±64
Seabird–jack index	0.20	0.10	0.10	14±62
Multiyear averages				
Seabird model	0.68	0.61	0.07	5±33
Combined model	NA	NA	NA	NA
Seabird index	0.56	0.49	0.07	7±40
Seabird–jack index	0.64	0.53	0.11	8±44

Note: The best models from simple and stepwise regressions for each estimate of salmon abundance and each time period were tested using leave-one-out cross-validation. SD, standard deviation; NA, either jack returns in the previous year or seabird breeding success did not enter the combined stepwise regression models.
[a]Note that these are original r^2 values and do not match adjusted r^2 values shown in other tables.
[b]Cross-validation r^2 values reflect the relationships between predicted and actual salmon abundances.
[c]Difference between the r^2 values of the original models and the cross-validation r^2 values that reflects the drop in the amount of variation explained by the models when they were tested.

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Fig. 1. Comparisons of actual and predicted salmon numbers for (*a*) the Central Valley index from 1990–2004, (*b*) the Central Valley index from 1976–2004, (*c*) fall escapement from 1990–2004, and (d) fall escapement from 1976–2004. The solid line represents actual abundance estimates in all graphs, the dotted line represents predicted abundances based on jacks in the previous year in all graphs, and the broken line represents predicted abundances based on combined seabird–jack models in (*a*) and (*b*) and predicted abundances based on seabird models in (*c*) and (*d*).
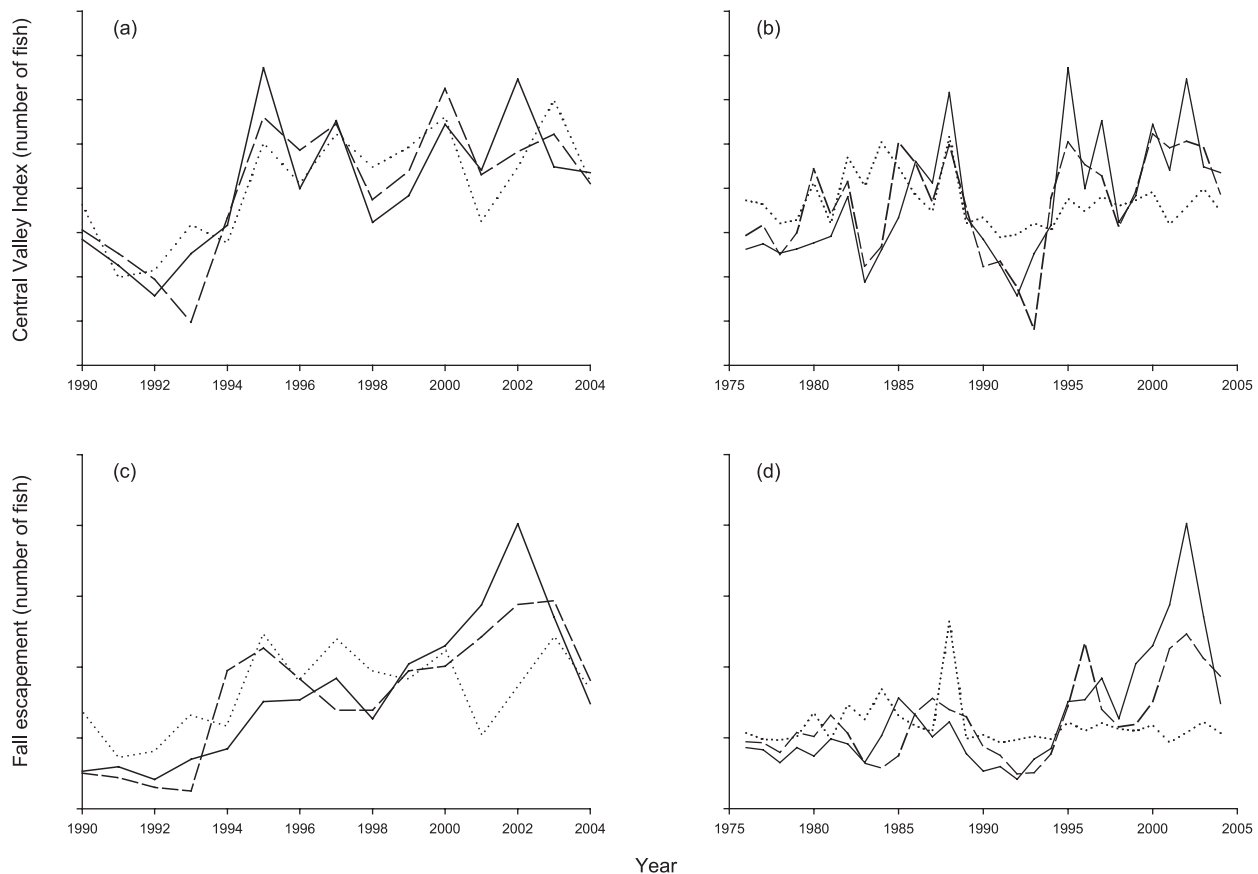
cause of their reliance on fish populations that exhibit complex age structures and, therefore, respond more slowly than zooplankton to ocean changes. Spatial distribution of foraging seabirds also may explain some of our results. Brandt's cormorants forage over the continental shelf, whereas Cassin's auklets forage primarily over outer continental shelf and slope waters (Ainley et al. 1996*a*; Sydeman et al. 1997; Yen et al. 2004). Relationships between Brandt's cormorants and salmon at longer time lags may reflect greater use of nearshore waters by both cormorants and younger salmon, though little is known about age-specific use of marine habitats by salmon.

Potential applications

Botsford et al. (1997) argued that an ecosystem approach to fisheries management is important to improving forecasts of fish abundance and maintaining sustainable fisheries. In addition, they stressed the importance of including both biological and physical parameters in predictive models. Seabird breeding success on the Farallon Islands is related to both biological and physical factors (Ainley et al. 1995; Abraham and Sydeman 2004) and integrates variation in the marine environment from egg laying (March) through chick rearing (August) each year. Our results indicate that this integrative parameter can be used to monitor marine ecological conditions important to other upper-trophic-level organisms such

as predatory fishes and may have a role in ecological forecasting. Seabird breeding success is relatively inexpensive to measure and has been calibrated against ocean conditions and prey abundance in some locations. Including seabird data in fisheries models may, therefore, enhance understanding of the factors affecting fish populations and may be valuable in a management context in regions where data on commercially important fish species and seabirds is available.

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