

Wintertime ocean conditions synchronize rockfish growth and seabird reproduction in the central California Current ecosystem

Bryan A. Black, Isaac D. Schroeder, William J. Sydeman, Steven J. Bograd, and Peter W. Lawson

Abstract: Chronologies developed from annual growth-increment widths of splitnose rockfish (*Sebastes pinniger*) and yelloweye rockfish (*Sebastes ruberrimus*) otoliths were compared with time series of lay date and fledgling success for the common murre (*Uria aalge*) and Cassin's auklet (*Ptychoramphus aleuticus*) in the north-central California Current. All time series were exactly dated and spanned 1972 through 1994. In a principal components analysis, the leading principal component (PC1_{bio}) accounted for 64% of the variance in the data set. By entering the upwelling index, the Northern Oscillation index, sea surface temperatures, and the multivariate ENSO (El Niño Southern Oscillation) index into principal components analysis, a time series of environmental variability PC1_{env} was developed for each month of the year. Over the interval 1972 through 1994, PC1_{bio} most strongly correlated with PC1_{env} for February and, to a lesser extent, January and March. Moreover, when each of the six biological time series was related to the 12 PC1_{env} through stepwise multiple regression, February was always the most significant ($p < 0.01$). The same was true if upwelling index was substituted for PC1_{env}. As upper-trophic predators, rockfish and seabirds independently corroborate that wintertime ocean conditions are critical for productivity in the California Current ecosystem.

Résumé : Nous avons comparé les chronologies obtenues à partir des largeurs des incréments de croissance annuelle sur les otolithes du sébaste canari (*Sebastes pinniger*) et du sébaste aux yeux jaunes (*Sebastes ruberrimus*) et les séries chronologiques des dates de ponte et du succès de l'envol chez le guillemot marmette (*Uria aalge*) et le starique de Cassin (*Ptychoramphus aleuticus*) dans le centre nord du courant de Californie. Toutes les séries chronologiques portent des dates précises et couvrent la période de 1972 à 1994. Dans une analyse des composantes principales, la première composante principale (PC1_{bio}) explique 64 % de la variance de l'ensemble de données. Nous avons produit une série chronologique de la variabilité de l'environnement PC1_{env} pour chaque mois de l'année en incluant l'indice de résurgence, l'indice d'oscillation boréale, les températures superficielles de la mer et l'indice multidimensionnel ENSO (oscillation australe d'El Niño) dans l'analyse des composantes principales. Dans l'intervalle de 1972 jusqu'à la fin de 1994, la PC1_{bio} est le plus fortement corrélée avec PC1_{env} en février et, à un degré moindre, en janvier et en mars. De plus, lorsque chacune des six séries chronologiques biologiques est mise en relation avec les 12 PC1_{env} par une régression multiple pas à pas, février est toujours le mois le plus significatif ($p < 0,01$). Il en est de même si on substitue l'indice de résurgence à PC1_{env}. En tant que prédateurs de haut niveau trophique, les sébastes et les oiseaux marins confirment de manière indépendante que les conditions de l'océan en hiver sont déterminantes pour la productivité de l'écosystème du courant de la Californie.

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Introduction

Climate variability is increasingly recognized as a major factor influencing structure, function, and productivity in the California Current ecosystem (CCE) of the Northeast Pacific (McGowan et al. 1998; Chavez et al. 2003). In the CCE, regional changes in upwelling, stratification, and temperature have been linked to productivity and reproductive success in a wide range of species. Among the most sensi-

tive to environmental variability include several upper-trophic-level species such as the Cassin's auklet (*Ptychoramphus aleuticus*; Sydeman et al. 2006), common murre (*Uria aalge*; Miller and Sydeman 2004), shortbelly rockfish (*Sebastes jordani*; Field et al. 2007), splitnose rockfish (*Sebastes diploproa*), and yelloweye rockfish (*Sebastes ruberrimus*; Black et al. 2008; Black 2009), as well as lower-trophic-level planktonic species including copepods (Roemich and McGowan 1995; Hooff and Peterson 2006) and

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krill (Dorman et al. 2005). Life history traits and growth patterns of these species typically respond at annual time scales and integrate or amplify ecosystem variability and, as such, represent potentially powerful, yet underutilized, indices of ecosystem response to climate forcing.

Establishing the effects of climate on growth requires observational time series of sufficient length to ensure adequate statistical power and reasonably capture the historical range of variability inherent to the system. To date, a number of time series of direct observations exist for several fisheries of the Northeast Pacific, including such variables as catch (Spencer and Collie 1997; Hare et al. 1999; Field and Ralston 2005), recruitment (Hollowed and Wooster 1992; Hollowed et al. 2001), and body size and fecundity (Harvey et al. 2006). These data sets provide valuable insight into long-term patterns of variability and their relationships with climate. However, repeated sampling is costly and the number of lengthy time series of direct measurements is consequently limited. Apart from direct observations, various proxies of environmental variability can be used, e.g., the scales or other hard parts of fishes preserved in varved sediments (Soutar and Isaacs 1974). Another increasingly applied approach is the analysis of growth-increment widths in otoliths or other bony structures using dendrochronology (tree-ring analysis) techniques (Black et al. 2005, 2008; Black 2009). To date, several exactly dated chronologies have been developed for rockfish in the Northeast Pacific that strongly relate to climate records, corroborate indices of productivity, and thus represent a novel means by which to summarize the influences of climate on growth (Black et al. 2005, 2008; Black 2009).

In this study, we incorporate several multidecadal time series from Pacific rockfish and seabirds, all of which are centered on the Farallon Islands off the central California coast. The data consist of egg-laying dates and reproductive success (chicks per pair) for Cassin's auklet and common murre, as well as otolith growth-increment chronologies for splitnose and yelloweye rockfish. Considering the wide range of life histories and mechanisms through which lower-trophic productivity has been integrated, these time series will likely be relevant to additional species of the CCE, especially shared food sources such as krill. In addition, these biological records may be compared with climatic records to establish not only those variables to which rockfish and seabirds are most sensitive, but also the times of year (i.e., seasons) in which these sensitivities are greatest. An increasing number of studies suggest that January, February, and March ocean conditions are critical for CCE productivity (Logerwell et al. 2003; Miller and Sydeman 2004; Schroeder et al. 2009), even though the upwelling processes traditionally associated with productivity are largely spring, summer, and autumn phenomena (Bograd et al. 2009). Thus, the objectives of this study are (i) to explore the interrelationships among rockfish and seabird time series in the CCE, (ii) to extract shared patterns of variability to generate multispecies indicators, and (iii) to relate time series and their derivatives to climate data, with particular emphasis on better establishing the importance of wintertime ocean variability to these diverse measures of biological function in the CCE.

Materials and methods

Biological time series

Six biological time series were used in this study: (i) lay date for Cassin's auklet, (ii) lay date for common murre, (iii) breeding success for Cassin's auklet, (iv) breeding success for common murre, (v) an otolith growth-increment chronology for splitnose rockfish, and (vi) an otolith growth-increment chronology for yelloweye rockfish. These six time series were selected because of their length, spatial overlap, temporal overlap, and the fact that all time series were exactly dated and contain measures of success or failure specific to each calendar year.

For both Cassin's auklet and common murre, phenology and breeding success data have been collected at the Farallon Islands (located approximately 30 miles west of San Francisco Bay, California, USA; 37.7°N and -123.0°W) by Point Reyes Bird Observatory under contract with the US Fish and Wildlife Service since 1972 (Ainley et al. 1995; Sydeman et al. 2001; Schroeder et al. 2009). During the breeding season (March–July), individual pairs of auklets and murre were selected and studied for dates of egg laying and overall annual reproductive output. Auklet pairs were observed every five days beginning on 2 March, whereas murre were studied every day from 16 April to ~1 July. Date of egg laying (reported as day of the year from 1 to 365) was defined as the date when an egg was first noted for each pair, and breeding success was defined as the proportion of pairs successfully rearing a chick to independence (for auklets), or to “jumping” stage (for murre). Murre offspring leave the breeding colony when development is incomplete (approximately half grown), so unlike the auklets, the breeding success of murre is defined as survival of the chicks to a departure stage, which is typically when they are 20–25 days old (Sydeman 1999). In the case of auklets, pairs may attempt to raise a second chick within a single year, though success is extremely rare. Notwithstanding these unusual occurrences, the parameter “breeding success” of these seabirds is binary, fledged or failed (0 or 1), as they lay only a single egg per reproductive season.

Cassin's auklets are planktivorous and feed on krill, whereas the diet of common murre is more varied and consists of krill, Pacific hake, market squid, juvenile rockfish, anchovy, and sardines (Sydeman et al. 1997, 2001; Mills et al. 2007). As for the rockfish, yelloweye consume juvenile rockfish, herring, sandlance, and flatfishes, as well as shrimps and crabs, whereas splitnose feed primarily on krill (Love et al. 2002). The yelloweye and splitnose rockfish chronologies were developed using annual growth-increment widths from otoliths obtained by commercial and sport fishing vessels and NOAA National Marine Fisheries Service surveys. Though exact locations for several samples are unknown, all otoliths were collected over the continental shelf between approximately 35°N and 39°N (Black et al. 2005, 2008). For details on otolith preparation and development of these splitnose and yelloweye rockfish chronologies, see Black et al. (2005, 2008). In summary, otoliths were embedded in resin, mounted on a lapidary saw, and thin-sectioned through the dorsal–ventral axis to 0.4 mm in thickness. Otolith thin sections were polished with 2000-grit sandpaper and 10 µm lapping film to reveal the annual increments, which were best viewed with reflected light in

splitnose rockfish and transmitted light in yelloweye rockfish. Within each species, samples were visually crossdated to ensure that all annual growth increments were assigned the correct calendar year. Universally applied in tree-ring studies, crossdating is the process of matching among all specimens in a sample set the synchronous growth patterns in increment width induced by climate. If an annual increment has been missed or falsely added, the synchronous growth pattern will be offset by a year relative to that in the other samples, and the point at which the offset begins indicates the location of the error. Without crossdating, errors can accumulate and diminish accuracy, especially in early portions of a chronology. A total of 48 otoliths were used to develop the splitnose rockfish master chronology and 27 were used to develop the yelloweye rockfish master chronology.

After visual crossdating, the dorsal half of the otolith was then photographed and the annual increment widths were measured continuously from the margin to as close to the focus as possible using the program ImagePro Plus (version 6.0, Media Cybernetics, Bethesda, Maryland). Crossdating was statistically verified with the Dendrochronology Program Library program COFECHA (Holmes 1983; Grissino-Mayer 2001; Black et al. 2005). Each otolith measurement time series was then fit with a negative exponential function and divided by the values predicted, thereby removing age-related growth declines and standardizing each time series to a mean of 1. Within each species, these detrended time series were averaged to form the master chronology in which each value represented sample-wide growth for a given calendar year. A value greater than 1 represented above-average growth, whereas a value below 1 represented below-average growth. All chronology development was conducted using the program ARSTAN (developed by Ed Cook and Paul Krusic, available at <http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html>). The quality of each chronology was quantified using the expressed population signal (EPS) statistic, which describes how well the sample means represents the mean of the theoretical population from which it was drawn. Though there is no significant threshold for this statistic, an EPS value of 0.85 or greater is considered adequate (Wigley et al. 1984).

Physical time series

Monthly averages of four environmental variables including sea surface temperatures (SST), upwelling (UW), the Northern Oscillation index (NOI), and the multivariate ENSO index (MEI) were related to the time series of rockfish growth and seabird reproductive success. Sea surface temperatures were obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICADS) and averaged between 36°N and 40°N and from 131°W to the coast, a geographic extent comparable with that of rockfish sampling. The coastal upwelling index (UI) represents the magnitude of the offshore component of Ekman transport (Bakun 1973; Schwing et al. 1996). Data from the upwelling station located at 39°N were used in this study. The NOI is the anomaly sea level pressure difference between the annual mean position of the North Pacific High and Darwin, Australia, and captures the strength of atmospheric circulation between the tropics and the North Pacific, particularly with

respect to the El Niño – Southern Oscillation (Schwing et al. 2002). NOI (1948–2007) and UW (1946–2007) records were obtained through the Pacific Fisheries Environmental Laboratories live-access server at <http://www.pfeg.noaa.gov/>. Finally, the MEI is the leading principal component of six marine and atmospheric variables in the tropical Pacific and was obtained (1950–2005) from the NOAA Earth Systems Research Laboratory (<http://www.cdc.noaa.gov/people/klaus.wolter/MEI/>). These four variables represent a combination of local (SST, UW) and regional (MEI, NOI) indices that have been shown to relate to the biology of the California Current ecosystem (Roemmich and McGowan 1995; Miller and Sydeman 2004; Dorman et al. 2005). All biological and environmental variables included the years 1972 through 1994, and the analysis in this study was consequently restricted to this common interval.

Detrending and normalization

The detrending procedure used to generate the rockfish growth-increment chronologies would have eliminated any long-term trends, if present. To ensure equal treatment of the data, long-term trends were removed from all biological and environmental time series over the common interval of 1972–1994. Each biological and environmental time series was fit with a linear regression, and where significant ($p < 0.05$), the observed values were divided by the predicted values. Cassin's auklet lay date was the only biological or environmental time series in which a regression was significant ($p < 0.05$). Finally, each environmental and biological time series was normalized to a mean of 0 and standard deviation of 1.

Relationships among biological and physical time series

Principal components analysis was used to develop a single environmental time series for each month of the year using the monthly resolved MEI, NOI, UW, and SST data. For each of the 12 months of the year, a 4×23 data matrix was constructed with one column for each of four environmental variables and one row for each year over the 1972–1994 common interval. Thus, each cell was the monthly mean of MEI, NOI, UW, or SST for a given calendar year. The leading principal component ($PC1_{env}$) was extracted from each of the 12 data matrices, capturing between 44.8% and 60.1% (mean = 52.1%) of the variance. In so doing, 48 environmental variables were distilled into 12.

A principal components analysis was performed that included all six biological time series over the common interval of 1972–1994. More specifically, a 6×23 data matrix was constructed with one column for each biological time series and one row for each calendar year spanned by the analysis. The leading principal component ($PC1_{bio}$) was used as an index of shared variability among the rockfish and seabird data sets. Next, the 12 monthly environmental principal components ($PC1_{env}$) were correlated with the six biological time series, as well as the leading principal component ($PC1_{bio}$) from the biological time series. To summarize relationships among the biological and environmental time series, a redundancy analysis (RDA) was performed that included the six biological time series and the 12 monthly $PC1_{env}$ as environmental variables (Legendre and Legendre 1998). RDA is a canonical form of principal com-

Table 1. Pairwise correlation coefficients (r) among bird and rockfish time series, as well as correlations (loadings) with the leading principal component ($PC1_{bio}$) extracted from the six time series, all over the common interval of 1972–1994.

	Span	Cassin's auklet lay date	Common murre success	Cassin's auklet success	Yelloweye rockfish	Splitnose rockfish	$PC1_{bio}$	First-order autocorrelation
Common murre lay date	1972–2006	0.94	-0.93	-0.64	-0.38	-0.71	-0.95	0.08
Cassin's auklet lay date	1972–2006	1.00	-0.90	-0.62	-0.41	-0.66	-0.93	0.05
Common murre success	1972–2006		1.00	0.67	0.46	0.66	0.95	-0.11
Cassin's auklet success	1972–2006			1.00	0.26	0.45	0.74	0.01
Yelloweye rockfish chronology	1948–2001				1.00	0.23	0.49	-0.52
Splitnose rockfish chronology	1948–1994					1.00	0.80	-0.12

Note: Cassin's auklet, *Ptychoramphus aleuticus*; common murre, *Uria aalge*; splitnose rockfish, *Sebastes diploproa*; yelloweye rockfish, *Sebastes ruberrimus*. Significant ($p < 0.05$) correlations are in bold, with the exception of $PC1_{bio}$, which is a function of the biological time series. Lay dates negatively correlate with the other time series, indicating that high fledgling success and early lay dates, both indicators of reproductive success, are associated with above-average rockfish growth. Also shown is the first-order autocorrelation for each time series.

ponents analysis in which axes were restricted to linear combinations of the environmental variables. Finally, stepwise multiple regressions ($p < 0.01$ to enter) were performed to better identify the months of the year during which environmental variability was most closely linked to rockfish growth and seabird reproduction. A separate regression was performed on each biological time series, including ($PC1_{bio}$), with 12 monthly $PC1_{env}$ from the current year plus five monthly $PC1_{env}$ from the previous year (August, September, October, November, and December lagged by one year) as predictors. The procedure was then repeated with upwelling, a variable more easily interpreted than $PC1_{env}$ and likely the most relevant of the original four environmental indices (UW, NOI, MEI, SST) considered in this study.

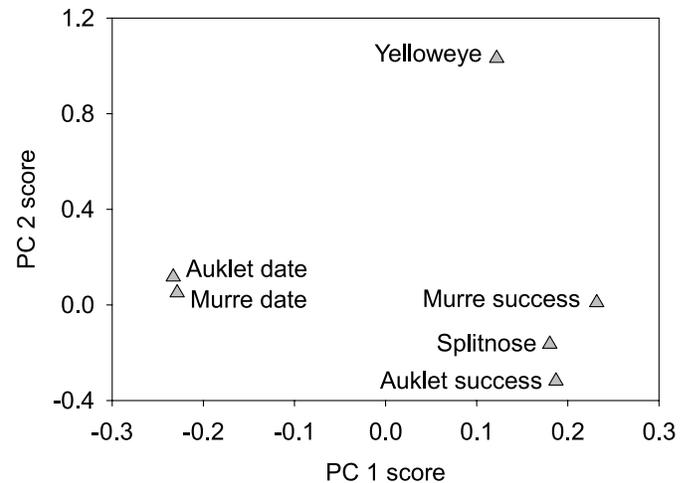
The stability of the regression between $PC1_{bio}$ and the 12 $PC1_{env}$ was assessed using a bootstrapping procedure. At each iteration ($n = 1000$) of the bootstrapping technique, a calibration data set equal to the number of years shared by both variables ($n = 23$) was randomly selected with replacement. Thus, some years in this shared time period were omitted, while other years were selected multiple times. Those years not selected were used as an independent verification data set. The reduction of error coefficient (RE), a measure of shared variance between the independent data and the values modeled from the calibration data set, was also calculated at each iteration (Fritts 1976). The maximum theoretical value of the RE statistic is +1, and a positive value indicates that the regression model has some degree of skill.

As a way to summarize the physical forcings on the biological variables, composite maps of wind and sea level pressure (SLP) were constructed from the five highest and lowest years of $PC1_{bio}$. The wind and SLP data used for the composite maps were from the National Centers for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR), with data starting in 1979 for the region spanning 33°N to 55°N and 140°W to 120°W.

Results

All biological time series exceeded 30 years in length and overlapped by a minimum of 23 with a common interval of 1972 through 1994 (Table 1), and the EPS for both rockfish chronologies exceeded 0.85 during that time period (data not shown). The yelloweye rockfish chronology contained sig-

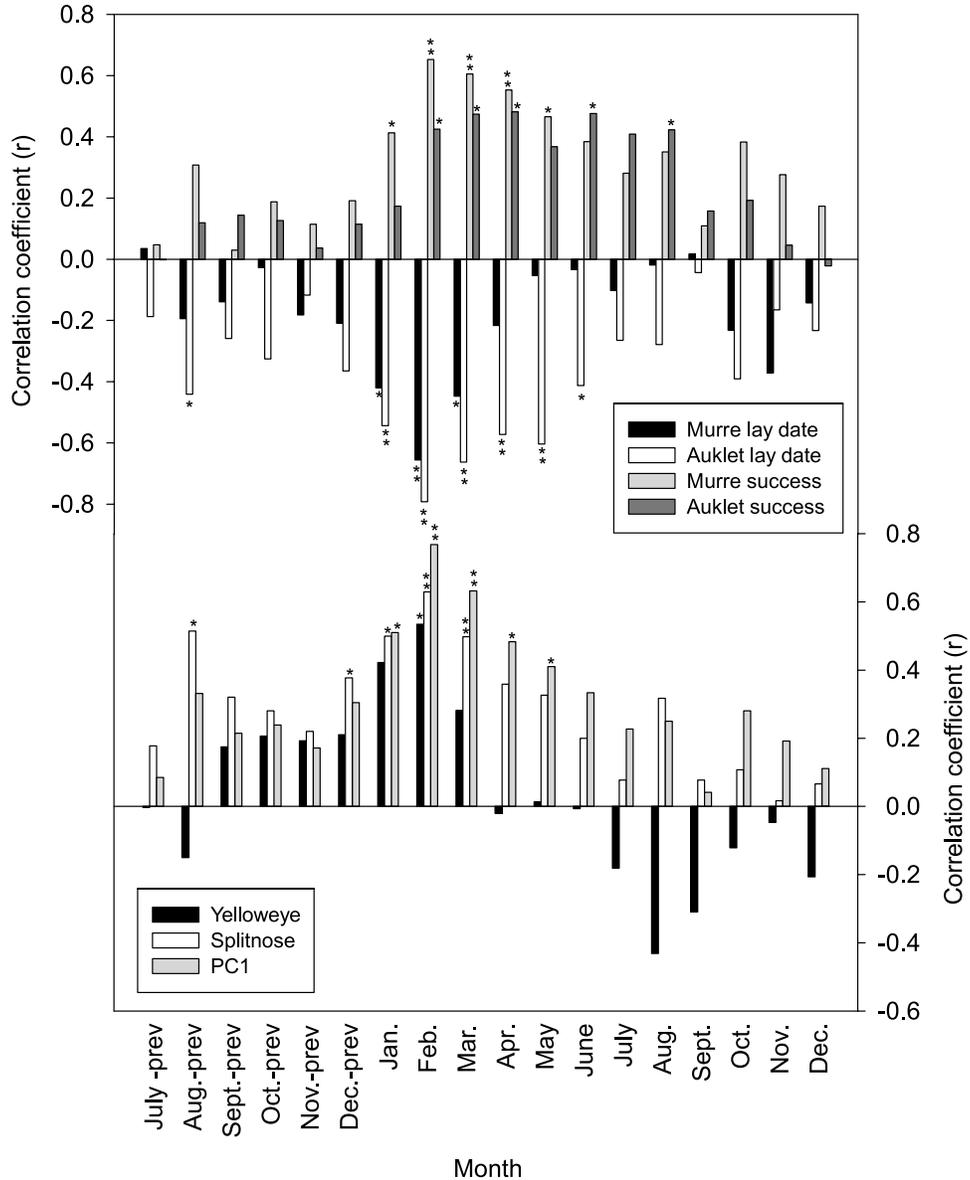
Fig. 1. Principal component scores of six biological time series centered on the Farallon Islands, central California: a yelloweye rockfish (*Sebastes ruberrimus*) otolith growth-increment chronology, a splitnose rockfish (*Sebastes diploproa*) otolith growth-increment chronology, mean lay date for common murre (*Uria aalge*) and Cassin's auklet (*Ptychoramphus aleuticus*), and fledgling success for common murre and Cassin's auklet. The common period shared by all time series is 1972 to 1994.



nificant ($p < 0.05$) autocorrelation, and effective sample size was adjusted according to the methods of Pyper and Peterman (1998) prior to correlation analyses. The majority of time series significantly ($p < 0.05$) correlated with one another, and in general, seabird lay date and the rockfish chronologies were positively related, yet negatively related to seabird reproductive success (Table 1). Thus, early lay date and high fledgling survival, both indicators of reproductive success, were positively associated with one another, as well as with rockfish otolith growth. All nonsignificant relationships involved the yelloweye rockfish chronology (Table 1).

The leading principal component of the six biological time series ($PC1_{bio}$) calculated across the common interval of 1972 to 1994 explained 69% of the variance in the data set (eigenvalue of 4.1) and significantly loaded against all six measurement time series (Table 1). $PC1_{bio}$ separated lay dates from reproductive success and the rockfish chronologies, negatively loading against the two lay date time series

Fig. 2. Correlations between a monthly resolved time series of climate and the time series of seabird reproduction and rockfish growth. The climate variable is the leading principal component from upwelling, sea surface temperature, the Northern Oscillation index, and the multivariate ENSO index ($PC1_{env}$) for each month of the current year (lag 0), as well as the prior year (prev) (lag -1) through July. The biological time series are as follows: a yelloweye rockfish (*Sebastes ruberrimus*) otolith growth-increment chronology, a splitnose rockfish (*Sebastes diploproa*) otolith growth-increment chronology, mean lay dates for common murre (*Uria aalge*) and Cassin's auklet (*Ptychoramphus aleuticus*), and fledgling success for common murre and Cassin's auklet. In addition, the leading principal component ($PC1_{bio}$) from these six biological time series is correlated with climate. *, $p > 0.05$; **, $p > 0.01$.

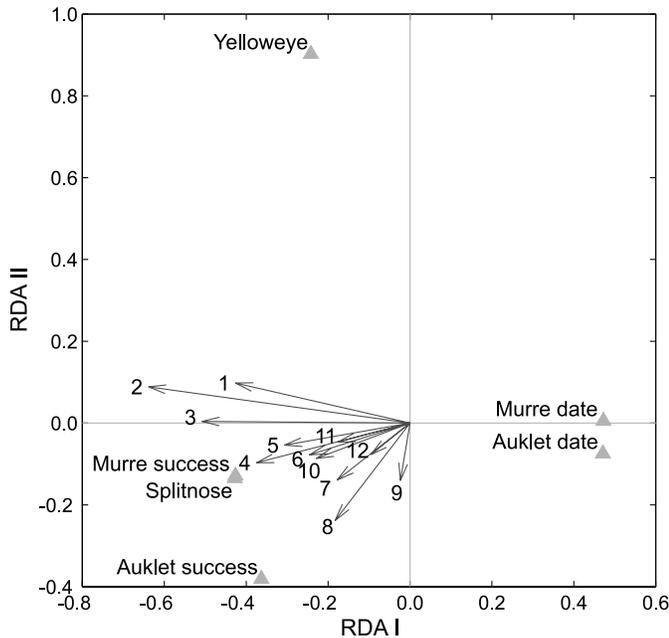


and positively loading against the other four time series (Table 1; Fig. 1). Overall, positive values of $PC1_{bio}$ indicated years of favorable seabird reproductive success (early lay dates and fledgling success) and vigorous rockfish otolith growth. The second principal component explained an additional 14% of the variance, with an eigenvalue of 0.86. This component significantly ($p < 0.05$) loaded only against the yelloweye chronology, separating it from the other five time series (Table 1; Fig. 1). Because of the low portion of variance captured and the fact that it was only related to one of the six time series, the second principal component was dropped from further analysis. Removing linear trend in the

seabird time series minimally affected the analysis, and $PC1_{bio}$ calculated prior to detrending related very strongly to that calculated after detrending ($R^2 = 0.997$). No linear trends were identified in the environmental data.

For each month of the year, the leading environmental principal component ($PC1_{env}$) positively loaded against UW and NOI and negatively loaded against SST and MEI such that high values of each $PC1_{env}$ reflected cool ocean conditions, while low values of each $PC1_{env}$ reflected warm ocean conditions. In summary, the correlations between the $PC1_{env}$ and the biological time series indicated that cool ocean conditions were associated with rapid rockfish otolith growth

Fig. 3. Redundancy analysis (RDA) of the six biological time series and 12 monthly PC_{env} . In this biplot, each triangle corresponds to a biological time series (common murre (*Uria aalge*) lay date, Cassin's auklet (*Ptychoramphus aleuticus*) lay date, common murre fledgling success, Cassin's auklet fledgling success, splitnose rockfish (*Sebastes diploproa*) otolith growth-increment chronology, and yelloweye rockfish (*Sebastes ruberrimus*) otolith growth-increment chronology), and each arrow represents one of the 12 monthly environmental variables (1 = January PC_{env} , . . . , 12 = December PC_{env}). February PC_{env} (arrow 2) is the most important of the environmental variables and is strongly correlated with axis I.



and seabird reproductive success in the form of early egg lay dates and increased fledgling survival (Fig. 2).

Correlations with environmental variables tended to be highest from January through April, especially for murre lay date, murre success, auklet lay date, and the splitnose rockfish chronology (Fig. 2). An exception was auklet success, which maintained nearly continuous correlations with $PC1_{env}$ from February through June and July (Fig. 2). Also anomalous, though not significant, were negative correlation between the yelloweye rockfish chronology and $PC1_{env}$ in late summer (Fig. 2). The leading principal component of the six biological time series ($PC1_{bio}$) captured the strongest climate-growth relationships of any of the six original time series in the study. $PC1_{bio}$ positively loaded against the rockfish chronologies and seabird fledgling success while negatively loading against seabird lay date such that positive values indicated years with favorable rockfish growth and seabird reproduction. Positive correlations between $PC1_{bio}$ and $PC1_{env}$ reflected that good years for rockfish and seabirds were associated with cool, upwelling-favorable ocean conditions (Table 1; Fig. 2).

In the RDA, RDA I accounted for 54% of the variance in the data set and separated seabird lay date from fledgling success and the rockfish chronologies, similar to the pattern observed in the PCA (Fig. 3). With respect to environmental variables, RDA I was most strongly correlated to the winter months, especially January ($r = -0.43$), February ($r = -0.64$),

and March ($r = -0.51$) PC_{env} (Fig. 3). RDA II accounted for only 7% of the variance in the data set and separated the yelloweye rockfish chronology from the other biological time series. This secondary axis was most strongly correlated with late summer and early autumn months, including July ($r = -0.14$), August ($r = -0.24$), and September ($r = -0.14$) PC_{env} . Overall, the RDA closely followed the PCA with a leading axis related to winter and a secondary axis related to summer. These axes accounted for only 10% less of the variance than did those in the PCA, indicating that the 12 PC_{env} explained a large portion of the variability in the biological data.

Multiple regression analysis confirmed that February was the most important month of the year for rockfish growth and seabird reproductive success. Relationships between biological time series and PC_{env} time series or UW were non-linear, and log transformation of PC_{env} and UW time series eliminated problems with autocorrelation in the regression residuals. For this reason, all PC_{env} and UW time series were log-transformed prior to regression analysis. For each regression, February was the most important month for all biological time series whether PC_{env} or UW were used as predictor variables (Table 2). Also, R^2 values were comparable for UW and PC_{env} , although summertime PC_{env} were also significant for auklet fledgling success and the splitnose chronology. Signs for each regression, which were positive for all but lay date, were consistent with all other analyses in that favorable rockfish growth and seabird reproduction were associated with cool, upwelling-favorable ocean conditions.

The relationship with upwelling was heavily influenced by the two extreme years of 1992 and 1983 (Fig. 4), yet even when these values were removed, the regression was still significant ($R^2 = 0.29$, $p = 0.01$). A bootstrapping analysis confirmed that the relationship between $PC1_{bio}$ and February upwelling was stable. Mean R^2 for the dependent data sets was 0.64 (± 0.01 95% confidence interval, CI), whereas mean R^2 for the independent data sets was somewhat lower, but still quite high at 0.58 (± 0.02 95% CI). Mean reduction of error (RE) was strongly positive at 0.74 (± 0.01 95% CI), indicating agreement between the independent data and the values modeled from the calibration data sets.

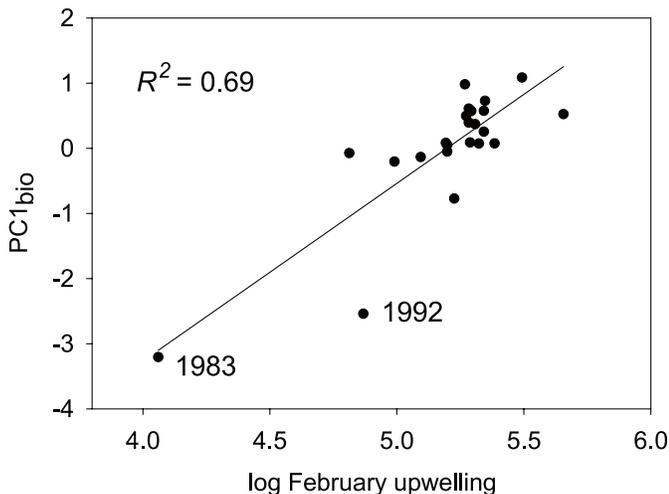
On a broader spatial scale, the timing and magnitude of coastal upwelling in the central California Current is impacted by the strength and position of the North Pacific High (NPH) sea level pressure (SLP) system. Composite maps of SLP and surface wind vectors are presented for the five years of highest $PC1_{bio}$ values (1985, 1982, 1989, 1988, 1979; Fig. 5a) and the five years of lowest $PC1_{bio}$ values (1983, 1992, 1986, 1990, 1993; Fig. 5b). In the five years with highest $PC1_{bio}$ values, the mean center of the NPH was at 35°N, 135°W and had a mean amplitude of ~1023 mbar. The 10 m wind vectors along the coast associated with this NPH pattern are directed towards the southeast (upwelling-favorable), with magnitudes exceeding 4 $m \cdot s^{-1}$. The SLP composite map (Fig. 5b) of the five years with lowest $PC1_{bio}$ has the center of the NPH (25°N, 130°W) farther south and weaker than the five years of highest $PC1_{bio}$. North of 36°N, the mean wind vectors along the coast are directed towards the north and northeast, i.e., downwelling-favorable. Also,

Table 2. Results for multiple stepwise regressions.

Time series	Month	Sign	R^2 (p)
PC_{env}			
Cassin's auklet lay date	February	–	0.71 ($p < 0.001$)
Common murre lay date	February	–	0.64 ($p < 0.001$)
Cassin's auklet success	February	+	0.24 ($p = 0.008$)
	July	+	0.20 ($p = 0.014$)
Common murre success	February	+	0.53 ($p < 0.001$)
Splitnose rockfish chronology	February	+	0.49 ($p < 0.001$)
	August	+	0.12 ($p = 0.003$)
Yelloweye rockfish chronology	February	+	0.28 ($p < 0.001$)
PC1 _{bio}	February	+	0.69 ($p < 0.001$)
Upwelling			
Cassin's auklet lay date	February	–	0.66 ($p < 0.001$)
Common murre lay date	February	–	0.66 ($p < 0.001$)
Cassin's auklet success	February	+	0.33 ($p = 0.004$)
Common murre success	February	+	0.57 ($p < 0.001$)
Splitnose rockfish chronology	February	+	0.43 ($p < 0.001$)
Yelloweye rockfish chronology	February	+	0.25 ($p = 0.009$)
PC1 _{bio}	February	+	0.69 ($p < 0.001$)

Note: Cassin's auklet, *Ptychoramphus aleuticus*; common murre, *Uria aalge*; splitnose rockfish, *Sebastes diploproa*; yelloweye rockfish, *Sebastes ruberrimus*. Each biological time series was regressed against 17 environmental time series, one environmental variable for each month of the year plus five (prior August through prior December) lagged from the previous year. The analysis was performed using PC_{env} as environmental variables and then repeated using upwelling. Months that were significant ($p > 0.01$) in the regression are shown, in addition to July PC_{env} for auklet success, which was very close to the 0.01 threshold. The sign of the relationship (positive or negative), R^2 , and p value are shown for each significant variable.

Fig. 4. Relationship between log-transformed February upwelling and PC1_{bio}. The extreme years of 1983 and 1992, which heavily influence the relationship, are shown.



the magnitudes of the wind vectors around the Farallones are small ($< 2 \text{ m}\cdot\text{s}^{-1}$).

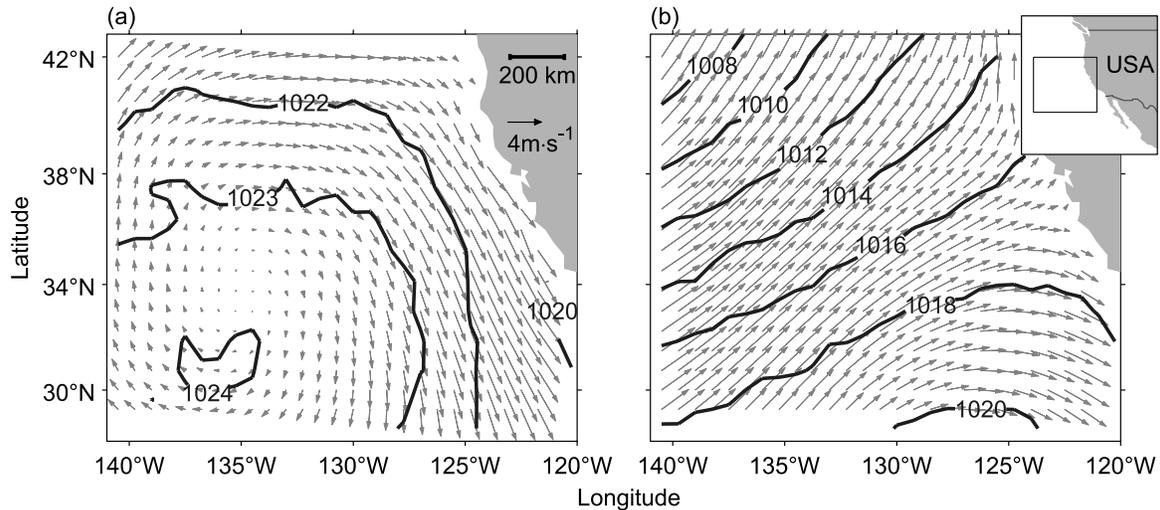
Discussion

Indices of rockfish growth and seabird reproductive success are exactly dated, share a uniquely long interval of more than 20 years, and experience a high degree of covariability. Interrelationships among these diverse time series almost certainly reflect the influence of climate on lower-

trophy productivity. For example, earlier research has identified strongly positive relationships between the rockfish chronologies and coastal upwelling, the principal driver of primary and secondary productivity in the CCE (Black et al. 2008; Black 2009). Such climate–growth relationships are consistent with unusually narrow growth-increment width in widow rockfish (*Sebastes entomelas*) and low levels of visceral fat in yellowtail rockfish (*Sebastes flavidus*) during the 1983 El Niño, an event characterized by abnormally warm water and below-average levels of upwelling in the CCE (Lenarz and Echeverria 1986; Woodbury 1999). Further supporting a link between fish growth and climate, Pacific salmon (*Oncorhynchus* spp.) catch tends to be higher during relatively cool, productive periods in the California Current, especially on decadal time scales (Hare and Francis 1995; Hare et al. 1999). As for seabirds, early lay date for common murre and Cassin's auklets has been linked to strong upwelling in the CCE (Schroeder et al. 2009). Moreover, Jones et al. (2008) found that Brandt's cormorant (*Phalacrocorax penicillatus*) lay date and fledgling success in the central CCE were significantly reduced in the 1998 El Niño, particularly in comparison with the much greater upwelling and productivity that occurred during the 1999 La Niña. Overall, the time series of rockfish otolith growth and seabird reproductive success used in this study appear to be linked through a shared sensitivity to climate variability, especially upwelling.

Upwelling and the productivity that it enables are generally regarded as spring and summertime phenomena, with greatest intensities between the months of May and July (Bograd et al. 2009). However, the synchrony shared be-

Fig. 5. Composite maps of February sea level pressure (SLP) and wind vectors for (a) mean of the five highest $PC1_{bio}$ years, corresponding to the best conditions for rockfish growth and seabird reproduction, and (b) mean of the five lowest $PC1_{bio}$ years, corresponding to the poorest conditions for rockfish growth and seabird reproduction. The SLP and wind vectors are from the North American Regional Reanalysis and start in 1979. For clarity, arrows are plotted at every degree.



tween rockfish growth and seabird reproductive success is a function of shared sensitivity to wintertime, especially February, ocean variability. Indeed, other studies have addressed the importance of ocean conditions early in the year, particularly with respect to the start of the productivity season as indexed by the spring transition. In the CCE, the spring transition has been related to a wide range of ecosystem dynamics, including upwelling (Schwing et al. 2006), zooplankton diversity (Hooff and Peterson 2006), and recruitment of salmonids (Logerwell et al. 2003) and crustaceans (Shanks and Roegner 2007). The definition of spring transition varies among studies and may involve upwelling, sea level, or some combination thereof (Logerwell et al. 2003; Kosro et al. 2006; Shanks and Roegner 2007). Yet when calculated across broad regions, all indicate that the spring transition is much later in the northern CCE than in the southern CCE. The spring transition occurs, on average, on 30 January at 36°N latitude in comparison with 24 April at 45°N latitude (Bograd et al. 2009), generally consistent with a mean date of 31 March for the Oregon coast according to Logerwell et al. (2003). Thus, for our study region, the spring transition date may occur in February, though it does not relate as strongly to the rockfish and seabird time series as measures of upwelling intensity. In comparison with a spring transition index defined as the date when the cumulative upwelling index reaches its minimum value (Bograd et al. 2009), relationships with $PC1_{bio}$ ($R^2 = 0.39$, $n = 23$ years, $p = 0.001$) are considerably weaker than that between $PC1_{bio}$ and February PC_{env} ($R^2 = 0.59$, $n = 23$ years, $p < 0.0001$) or the log-transformed February upwelling intensity ($R^2 = 0.69$).

These relationships suggest that a specific date may not be as important as the upwelling dynamics prior to and near the beginning of the spring transition, which is February for this study region. Variation in January and February upwelling intensity relates much more strongly to $PC1_{bio}$ than to spring transition date. In their analyses of the auklet and murre lay date time series, Schroeder et al. (2009) suggest

that anomalous wintertime upwelling preconditions the system, priming it for high levels of productivity early in the season. During the winter months prior to or near the spring transition, north winds are intermittent, though water column stratification is generally weak. Under these conditions, even relatively short-duration upwelling-favorable winds could provide pulses of nutrients to stimulate primary productivity (Schroeder et al. 2009). Consistent with this mechanism, Logerwell et al. (2003) also noted the importance of winter ocean climate in their analysis of coho salmon (*Oncorhynchus kisutch*) marine survival along the Oregon coast. Weak downwelling winds during the winter were associated with weak water column stratification in the spring, preconditioning the system for high levels of productivity (Logerwell et al. 2003).

For seabirds, the nutritional status of females is known to affect the timing of lay date (Perrins 1970; Jones et al. 2008). Along the British Columbia coast at Triangle Island, Sorensen et al. (2009) found that the prebreeding diet of Cassin's auklets with early lay dates was energetically superior to the prebreeding diet of those birds with later lay dates. Though lay date ranged from early April through mid-May, the prebreeding diet in February and March was critical not only for lay date phenology, but also for egg size. In the CCE, an increase in productivity in January, February, and March would be well timed to influence the condition of breeding females, the results of which would be realized later in the spring as eggs are laid and chicks are fledged in late March through early June (Schroeder et al. 2009). Mean lay date for Cassin's auklet was 14 April and that for common murre was 14 May, as calculated for the interval 1972 through 1994. With respect to rockfish, high levels of productivity in January, February, and March could have the effect of lengthening the growing season. Perhaps relatively low levels of upwelling later in the spring and summer are adequate for productivity, but favorable winter conditions allow growth during a period when it would not otherwise occur. The initiation of the productivity

season appears to be much more important than its conclusion, as evidenced by the general lack of climate correlations in the late summer and fall.

Wintertime ocean conditions may also be important farther north, considering that rockfish chronologies in the CCE relate to rockfish and Pacific geoduck chronologies along the British Columbia coast through shared sensitivities to climate in January, February, and March (Black et al. 2008; Black 2009). Also, the biological and physical indices described in this study may be relevant to other species in the CCE. For example, $PC1_{env}$ for February significantly relates to the Sacramento River index for salmon (1983–1994, $n = 12$ years, $R^2 = 0.32$, $p = 0.05$). The leading principal component from the rockfish and seabird time series provides a closer fit (1983–1994, $n = 12$ years, $R^2 = 0.46$, $p = 0.01$), suggesting that wintertime ocean conditions are important to salmon ecology and also that the $PC1_{bio}$ may serve as a more reliable ecosystem indicator than physical variables.

In summary, rockfish and seabird time series both provide a multiproxy, multidecadal, and annually resolved “view from the top” by integrating ecosystem productivity after it has cascaded up through lower trophic levels. The fact that the data set includes species with such diverse life histories, diets, and processes through which biological success is expressed (i.e., growth and reproduction) provides strong evidence as to the importance of wintertime ocean variability. From an applied perspective, these time series indicate significant bottom-up regulation and underscore the importance of climate to ecosystem function prior to the peak upwelling season. Also, the leading principal component from these rockfish and seabird time series could represent a new multi-species indicator of regional productivity with potential relevance to ecosystem-based management. Moreover, the relationship between February upwelling and $PC1_{bio}$ reflects strongly nonlinear responses between the physical environment and ecology of the CCE such that strong climatic extremes such as the 1983 El Niño exert a disproportionately large influence on the system. Thus, February upwelling, in particular, could have predictive value as an early indicator of productivity in the coming year, and on longer time scales, forecasts of February ocean conditions could be highly relevant for assessing the biological impacts of future climate change and variability. Future work will be necessary to determine whether similar relationships between wintertime ocean conditions and rockfish growth and seabird reproduction extend beyond the 23-year window used in this study. Yet the combination of diverse species used in this study suggests that wintertime ocean conditions prior to peak upwelling are an important component of CCE structure and function.

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