

Integrated Assessment of Wind Effects on Central California's Pelagic Ecosystem

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ABSTRACT

Ecosystem-based management requires integrated physical studies on biological functions. In this study, we hypothesized that seasonal variation in upwelling-favorable winds has differential influences on species of the central California Current pelagic ecosystem. To test this hypothesis, we developed multivariate indicators of upwelling and species' responses using wind and sea surface temperature (SST) data from buoys and growth and reproductive data for 11 species of fish and seabirds. From previous work, we predicted that winds and SST could be decomposed into winter and spring/summer 'modes' of variability, but only a single mode of "winter/spring" environmental variability was observed. We attribute this difference from expectations to the local and shorter-term measurements of winds and SST used in this study. Most

species responded to winds and SST variability similarly, but SST was a better predictor of most biological responses. Both SST and wind were better predictors than the traditional upwelling index. Notably, Pacific sardine (*Sardinops sajax*) was dissociated with the other biotic measurements and showed no relationships with coastal upwelling. The multivariate indicators developed here are particularly appropriate for integrated ecosystem assessments of climatic influences on marine life because they reflect both structure and processes (upwelling and timing/growth/productivity) known to determine functions in marine ecosystems.

Key words: seabirds; rockfish; salmon; sardine; upwelling; growth; breeding success; recruitment; temperature.

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INTRODUCTION

Ecologists have long sought to understand the physical and biological factors that drive demographic processes in animal populations (Andrewartha and Birch 1954; Lack 1954). Many of these issues remain as relevant today as they were 60 years ago, but with increased interest given the potential implications of anthropogenic change. Indeed, since the industrial revolution, various

anthropogenic pressures have modified global climatic and biotic systems, making robust predictions as to their future a societal imperative (Solomon and others 2007).

Marine ecosystems are not immune to changes in climate (Burrows and others 2011) or other human pressures including fishing, contamination, and CO₂ build-up (acidification), among others (Jackson and others 2001; Halpern and others 2008; Doney and others 2012). Over the past few decades, ecosystem-based approaches have been proposed to better incorporate physical and human factors into management (May and others 1979; Botsford and others 1997; Pikitch and others 2004; Levin and others 2009). Yet, to date, the scientific framework for their design and implementation is still developing. Amongst the most critical needs is information concerning the effects of environmental variability on marine life across species and within and between trophic levels (Cury and others 2008). Multi-species studies of physical–biological interactions are infrequent but relevant for populating ocean ecosystem models, especially those considering the nexus of fishing and climate impacts (Moloney and others 2011).

Eastern boundary current ecosystems (EBCE) of the oceans are among the most studied and productive marine regions in the world. Represented by the California (California–Oregon, USA), Humboldt (Peru–Chile), Canary (Iberian Peninsula–Morocco), and Benguela (Namibia–South Africa) systems, EBCE cover about 1% of the ocean's surface, yet contribute upwards of about 20% of global fisheries catch (Mann 2000). In these systems, equatorward winds coupled with the Coriolis force transport surface waters offshore, lifting cold, nutrient-rich water from below the thermocline into the photic zone. These nutrients fuel robust phytoplankton blooms (Chavez and Messié 2009) that in turn support high levels of mid and upper trophic level productivity, including some of the most commercially and societally valuable fisheries in the world (Pauly and Christensen 1995). Global warming is hypothesized to increase the warm-season pressure gradient between the land and sea that drives upwelling favorable winds (Bakun 1990; Bakun and others 2010), but this hypothesis is still equivocal (Narayan and others 2010). Nonetheless, it provides a plausible mechanism concerning how upwelling, a key oceanographic and biologically relevant process in EBCE worldwide, could be impacted by anthropogenic global warming.

For EBCEs with long-term field programs, one approach to integrated assessment is retrospective investigation of multi-species assemblages and their

responses to environmental variability over time. The California Current Ecosystem (CCE) is perhaps the best studied EBCE, in which numerous multi-decadal physical and biological data sets have been developed (Pena and Bograd 2007). Moreover, estimates of upwelling are systematically calculated from large-scale atmospheric pressure fields, and the traditional Upwelling Index (UI, Bakun 1973) has been widely used to evaluate CCE biological responses to environmental variability at multiple temporal scales (for example, Abraham and Sydeman 2004; Black and others 2011; Iles and others 2012). However, at many locations along this coastline, winds are constrained and modified by the marine atmospheric boundary layer and local topography (Winant and others 1988; Strom and Tjernstrom 2004), resulting in stronger or weaker alongshore winds and substantial spatial variability in upwelling-related processes (Checkley and Barth 2009). Although providing an excellent system-wide perspective, the coarse-resolution UI does not resolve these features (Pickett and Schwing 2006) and therefore may not be representative of local wind stress over much of the continental shelf where upwelling affects the ecosystem. In the central sector of the CCE, from about Point Sur (36°N) to Cape Mendocino (40°N), California, upwelling occurs through most of the year (Bograd and others 2009). Here, the amplitude of upwelling is greatest, and has apparently increased over the last three decades (García-Reyes and Largier 2010; Black and others 2011). Recent research shows that the effects of upwelling on upper trophic level species are indirect, operating mainly through variation in pelagic food webs and predator–prey interactions (Abraham and Sydeman 2004; Wells and others 2008; Field and others 2010; Thompson and others 2012; Wells and others 2012).

Previously, we demonstrated (Black and others 2011; Thompson and others 2012) that the monthly UI could be decomposed into distinct winter and spring/summer “modes” that have differential effects on marine top predators, including pelagic and demersal fishes (salmonids and rockfish), seabirds, and marine mammals. Despite the fact that upwelling is clearly strongest from May through June in the central-northern region of the CCE (Schwing and others 1996), many of the predator response variables were most sensitive to upwelling in January–March (Schroeder and others 2009; Black and others 2010). García-Reyes and Largier (2012) showed that upwelling intensity calculated from local winds is comparable to that estimated by the UI during the core of the upwelling season (April–June). How-

ever, for the winter months, the UI showed net downwelling whereas the local winds showed no net upwelling or downwelling. Given the seasonal differences between local measured winds and the estimated winds used to calculate the UI, there is a need to confirm previous findings (Black and others 2011) of (i) the winter and spring/summer modes of variability, and (ii) the responses of the pelagic community to upwelling. To more broadly generalize our results, we evaluate a suite of upwelling proxies including buoy-based coastal winds and sea surface temperature (SST) (García-Reyes and Largier 2010, 2012) against an expanded group of 15 fish and seabird response variables (Black and others 2008; Sydeman and others 2001; Sydeman and others 2009). We test the hypothesis that upwelling estimated from buoy-based data has distinct seasonal modes of variability that differentially relate to predator time series. Multivariate indicators of upwelling and upper-trophic “productivity” are generated to summarize the climate–biology relationships identified.

MATERIALS AND METHODS

Upwelling: Winds and SST

We quantified local upwelling using two variables: (1) an estimate of offshore Ekman transport (U_w) calculated from buoy winds and (2) SST as an integrated estimate of ocean conditions that reflects the shoaling and mixing of deep water in response to upwelling winds, alongshore and cross-shore transport, and air-sea heat fluxes (Dever and Lentz 1994) as well as variability in water column characteristics that could impact the upwelling process (Jacox and Edwards 2011). Hourly wind data, from 1988 to 2010, were obtained from 12 NOAA buoys located from 34°N to 47°N along the continental shelf of the U.S. west coast (Figure 1), available at <http://www.ndbc.noaa.gov> (García-Reyes and Largier 2010, 2012). Missing data ranged from 4% at buoy 46025 to 26% at buoy 46041, with an average of 15% in all buoys. Gaps were 77 days long on average, with the longest gaps ranging from 4 months at buoy 46025 to 1.8 years at buoy 46011. Data were highly correlated ($r > 0.9$ for wind and > 0.75 for SST, except for buoy 46025), so neighboring buoys could be used to fill the gaps via linear regressions. Wind stress was calculated from wind speed following Large and Pond (1981), and the alongshore component was calculated using the orientation of the principal axis of the wind, which largely follows the coastal orientation (details in García-Reyes and Largier 2010). We

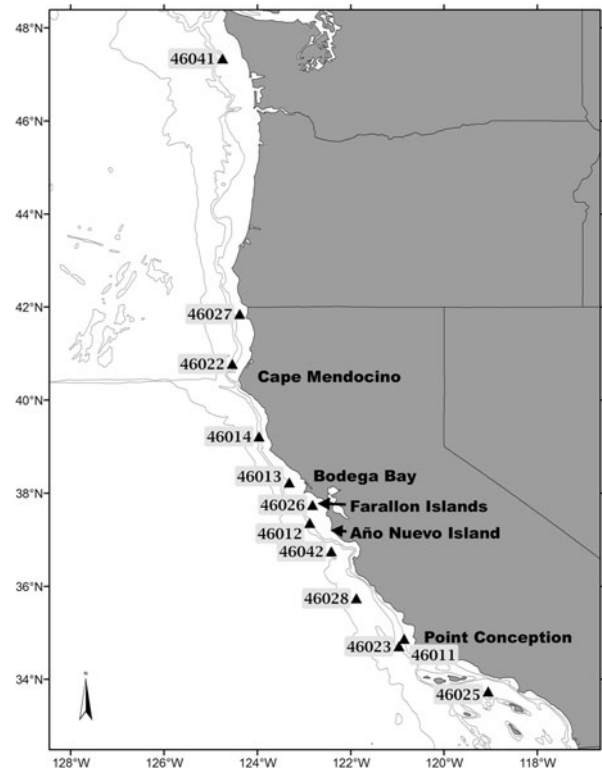


Figure 1. Location of NDBC/NOAA buoys (triangles) along the US west coast.

compared these variables to the UI provided by NOAA (Schwing and others 1996). The UI quantifies the offshore Ekman transport caused by alongshore wind stress, but is calculated from cross-shore gradients in sea level pressure. Although UI data is provided at 3° intervals along the Northeast Pacific coast, the scale of the cross-shore sea level pressure used in its calculation is 6°. Here, we considered data (<http://www.pfeg.noaa.gov/products/las.html>) from 33°N to 48°N across the 1988 to 2010 interval shared by the buoy data.

Biological Variables

We selected 15 upper trophic level biological variables (also referred to as “indicators”) for this analysis based on overlapping geographic extent, availability of long-term data, and species diversity (Table 1). Egg-laying date (phenology) and reproductive success (offspring fledged per pair) were obtained from the literature for six seabird species nesting on Southeast Farallon Island, California (SEFI; 37.7°N 123.0°W) and Año Nuevo Island, California (ANI; 37.1°N 122.3°W) (Sydeman and others 2001; Thayer and Sydeman 2007; Schroeder and others 2009; Thayer 2009). Species included were common murre (*Uria aalge*), pigeon guillemot

Table 1. Biological Indicators Information

Indicator	Label	Location	Years	References
Common murre lay date	MuLD	SEFI, 37°42'N	1972–2006	Sydeman and others (2001), Thayer and Sydeman (2007),
Cassin's auklet lay date	AuLD	SEFI, 37°42'N	1972–2006	Schroeder and others (2009), Thayer (2009)
Common murre reproductive success	MuRS	SEFI, 37°42'N	1972–2007	
Cassin's auklet reproductive success	AuRS	SEFI, 37°42'N	1972–2007	
Pigeon guillemot reproductive success	PGRS	SEFI, 37°42'N	1971–2007	
Rhinoceros auklet reproductive success	RARS	SEFI, 37°42'N	1986–2007	
Pelagic cormorant reproductive success	PCRS	SEFI, 37°42'N	1971–2007	
Brandt's cormorant reproductive success	BCRS	SEFI, 37°42'N	1971–2007	
Rhinoceros auklet reproductive success	AARS	ANI, 37°06'N	1995–2008	Hill and others (2010)
Pacific sardine recruitment	SrRe	Southern California	1981–2008	Black and others (2005), Black and others (2011)
Splitnose rockfish otolith chronology	SRGC	California coast 35°N–40°N	1948–2006	
Yelloweye rockfish otolith chronology	YRGC	California continental shelf, 36°N–40°N	1950–2003	
Aurora rockfish otolith chronology	ARGC	Oregon coast 42°N–46°N	1980–2004	Thompson and Hanna (2010)
Chinook salmon otolith chronology	SaGC	Smith river, California 42°N	1978–2001	Wells and others (2007)
Brandt's cormorant survival	BCSv	SEFI, 37°42'N	1974–1998	Nur and Sydeman (1999)

“Location” is the area of sampling and “years” the years sampled. SEFI Southeast Farallon Island, ANI Año Nuevo Island.

(*Cepphus columba*), Cassin's auklet (*Ptychoramphus aleuticus*), rhinoceros auklet (*Cerorhinca monocerata*), pelagic cormorant (*Phalacrocorax pelagicus*), and Brandt's cormorant (*P. penicillatus*). A sample of focal nests was selected for monitoring on both islands, beginning on 2 March each year. The sample size of nests varied by species, from a low of $n = 30$ –100 for auklets to $n = 150$ –250 for murre. Each nest site was marked and mapped, and the nest contents were assessed every 3–5 days. In addition, we collated Brandt's cormorant adult survival estimated during the spring time initiation of breeding (Nur and Sydeman 1999). Brandt's cormorants were marked (banded) when about 30 days of age. Upon return to the colony 2–3 years later, bands were read from a distance of 10–30 m using a telescope. We also used three Pacific rockfish (*Sebastes* spp.) chronologies that represent sample-wide anomalies in annual otolith growth-increment widths following the removal of age-related growth declines. Chronologies were generated using standard dendrochronological techniques as described by Black and others (2008, 2011). The first two chronologies were for splitnose (*S. diploproa*) and yelloweye rockfish (*S. ruberrimus*) from individuals collected between approximately 35°N to 40°N (Black and others 2005, 2011). An aurora rockfish (*S. aurora*) otolith growth-increment chronology from the Oregon coast (42°N to 46.2°N) was also obtained from the literature (see Thompson and Hanna 2010 for details). In addition, we used a northern California Chinook salmon (*Oncorhynchus tshawytscha*) chronology (~42°N; Wells and others 2007) that had been derived from growth-increment widths in scales, as calculated by Black and others (2011). Pacific sardine (*Sardinops sagax*) recruitment (stock biomass for sardines age 1+) based on a stock assessment model for the entire west coast (Hill and others 2010) was added as a final biological indicator.

Statistical Analysis

To investigate variability in upwelling with respect to season, we computed the monthly mean, standard deviation, and coefficient of variation for each physical variable (U_w , SST, and UI). Subsequently, we conducted a Principal Component Analysis (PCA) (Jolliffe 2002) to explore shared patterns of variability among these time series, which were extracted and used as multivariate indices of the CCE (Frederiksen and others 2007; Hemery and others 2008; Koslow and others 2011). Given that upwelling varies among locations, among season, and among years (García-Reyes and Largier 2012;

Thompson and others 2012), we arranged each physical data variable (U_w , SST, and UI) into a three-dimensional matrix consisting of 12 locations \times 12 months \times 23 years; resulting components were labeled as PC_{U_w} , PC_{SST} , and PC_{UI} . Each column was normalized (zero mean and variance equal to 1 standard deviation) before calculating the PCA. Next we ran a PCA that combined U_w and SST data by arranging their data arrays into a single matrix with dimensions: 24 locations (12 U_w locations + 12 SST locations) \times 12 months \times 23 years. Resulting PCs, labeled as PC_{env} , captured the dominant and sub-dominant seasonal “modes” or patterns in upwelling and their interannual variability. PCs (scores) from the three physical variables (PC_{U_w} , PC_{SST} , and PC_{UI}) were compared to one another as well as to PC_{env} using Spearman ranked correlations. PCs with Eigenvalues less than 1 and explaining less than 10% of the variability in the data set were dropped from further analysis (Jolliffe 2002).

The 15 biological indicators included in the study were cross-correlated with one another to generally assess the extent to which they shared common patterns. Subsequently, we conducted a PCA (resulting components labeled as PC_{bio}) using the nine longest (1982–2006) biological indicators (Table 2, Figure 2). Biological indicators excluded from the PCA were correlated against the PC_{bio} components as a measure of their agreement with dominant patterns in the longer datasets (Table 2). Those that were significant at the $P < 0.05$ level were retained. To summarize physical–biological interactions, the scores of the environmental PCs

(PC_{U_w} , PC_{SST} , PC_{UI} , and PC_{env}), the biological indices, and biological PCs (PC_{bio}) were compared using Spearman correlations (Table 3).

Finally, we compared the environmental and biological PCs with climate indices known to impact upwelling and biological productivity in the CCE: The Northern Oscillation Index (NOI), which is the difference in sea level pressure anomaly between the North Pacific High and Darwin, Australia (Schwing and others 2002); the Multivariate El Niño–Southern Oscillation (ENSO) Index, a comprehensive index of tropical atmospheric and oceanic conditions (Wolter and Timlin 1993); the Pacific Decadal Oscillation (PDO) index, which describes the main mode of SST variability in the North Pacific (Mantua and Hare 2002; Chavez and Messié 2009); and the North Pacific Gyre Oscillation (NPGO) index, which tracks low frequency variability in sea surface height over the North Pacific (Di Lorenzo and others 2008).

RESULTS

Monthly Variation in Winds and SST

The intensity and variability of local upwelling (U_w) were uneven over the course of the year. Winter months (December–February) were characterized by high variability and low intensity, spring months (April–June) were characterized by high intensity and moderate variability, and late summer and autumn months (July–October) were characterized by moderate intensity and low variability (Figure 3A, B). March and November appeared to be transitional months among these

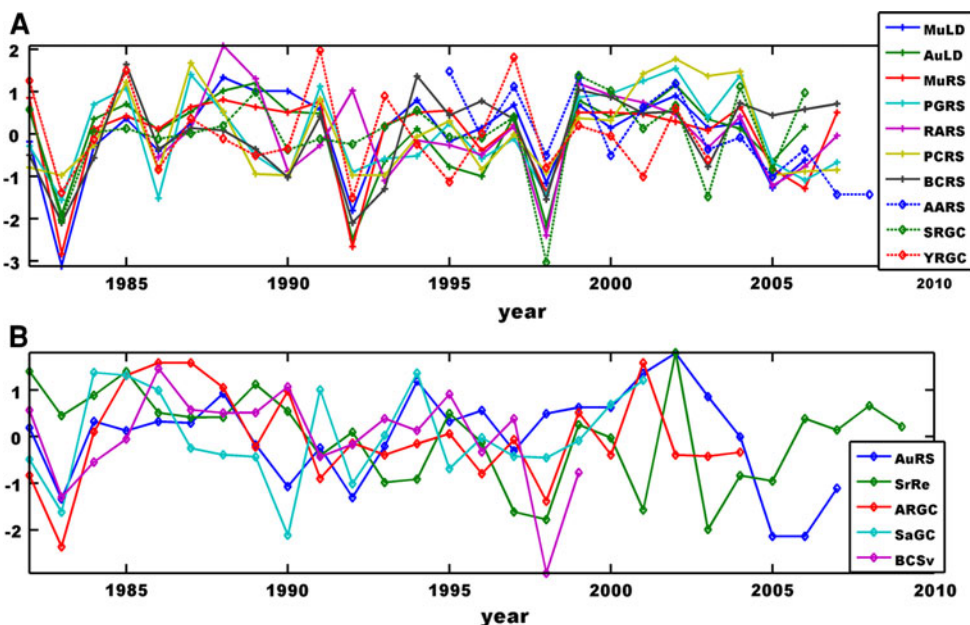


Figure 2. Normalized time series of biological indicators. **A** Indicators with PC_{bio1} loadings greater than 0.3 or significant correlations greater than 0.5 with PC_{bio1} (Table 2). **B** Other indicators.

Table 2. Relation of Biological Indicators with Biological PCs

Biological indicators included in PC _{bio} (loadings)	PC _{bio1} 56%	PC _{bio2} 16%	Biological indicators excluded (correlations)	PC _{bio1} 56%	PC _{bio2} 16%
Common murre lay date	0.39	0.04	SEFI rhinoceros auklet reproductive success	0.67	
Cassin's auklet lay date	0.39	0.21	ANI rhinoceros auklet reproductive success	0.78	
Common murre reproductive success	0.40	0.03	Yelloweye rockfish otolith chronology	0.54	
Cassin's auklet reproductive success	0.29	-0.38	Aurora rockfish otolith chronology	0.46	
Pigeon guillemot reproductive success	0.37	-0.23	Chinook salmon otolith chronology	0.48	
Pelagic cormorant reproductive success	0.33	-0.41	Brandt's cormorant survival		0.48
Brandt's cormorant reproductive success	0.34	0.07			
Pacific sardine recruitment	0.09	0.61			
Splitnose rockfish otolith chronology	0.31	0.46			

First 3 columns show the biological indicators included in the PCA and their loadings for each component. The remaining columns show the biological indicators not included in the PCA and their correlation, if significant ($P < 0.05$), with the first and second PC_{bio}.

Table 3. Ranked Correlations of Biological Indicators and PC_{bio1} with PC_{env1}, PC_{SST1}, PC_{Uw1}, and PC_{UI2} Scores

	PC _{env1} 21%	PC _{SST1} 32%	PC _{Uw1} 13%	PC _{UI2} 13%
Common murre lay date	0.74	0.67	0.70	0.50
Cassin's auklet lay date	0.85	0.81	0.60	0.59
Common murre reproductive success	0.60	0.60		
Cassin's auklet reproductive success	0.57	0.57	0.46	
Pigeon guillemot reproductive success	0.66	0.66		
SEFI rhinoceros auklet reproductive success	0.56	0.52		
Pelagic cormorant reproductive success	0.60	0.57	0.49	0.49
Brandt's cormorant reproductive success	0.47	0.49		
ANI rhinoceros auklet reproductive success				
Pacific sardine recruitment				
Splitnose rockfish otolith chronology	0.47			
Yelloweye rockfish otolith chronology				
Aurora rockfish otolith chronology				
Chinook salmon otolith chronology				
Brandt's cormorant survival				
PC _{bio1}	0.85	0.82	0.63	0.56

Only significant ($P < 0.05$) correlations are shown.

three broad groupings. Seasonal patterns were largely consistent across latitudes, though the highest levels of variance occurred early in the winter at southern latitudes (Figure 3A). Summer months were clearly warmer than winter months, however, seasonal patterns were much less apparent in SST variance (Figure 3C, D). There was also a sharp latitudinal gradient at approximately 38°N above which SST variability was considerably

higher than in the southern portion of the study region (Figure 3C).

Seasonal Modes of Variability

The leading principal component for upwelling from buoy winds (PC_{Uw1}) explained 13% of the variability in the data set and was significantly correlated ($r = 0.63$, $P < 0.01$) with the leading

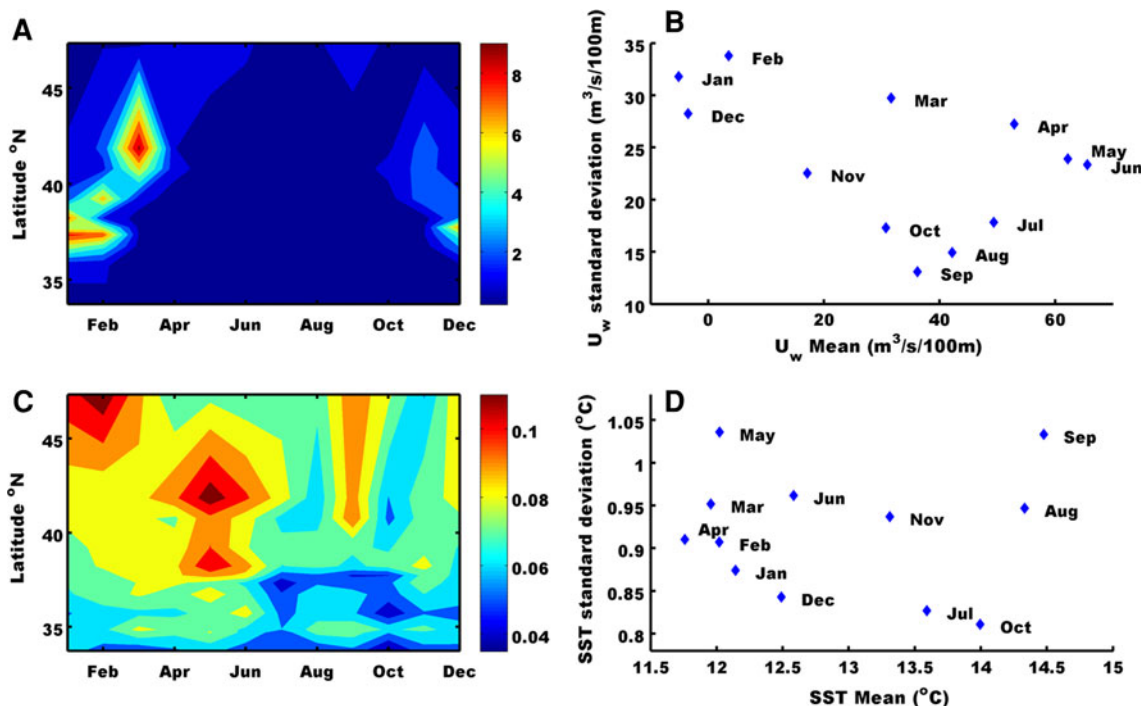


Figure 3. Hovmöller diagram of the coefficient of variation of **A** upwelling winds and **C** SST. Distribution of monthly means and standard deviations for **B** upwelling winds and **D** SST.

principal component of SST (PC_{SST1}), which explained 32% of the variability in the data. Both leading PCs had similar loadings over space and across seasons with peak values from January to June south of $40^{\circ}N$ and from March to May north of $40^{\circ}N$ (Figure 4A, B). Subordinate principal components captured slightly less variability for upwelling winds (11 and 10% for second and third PCs, respectively) and SST (18% and 7% for second and third PCs, respectively) (Figure 4F), however, their loadings were highly localized in space and season (data not shown). Thus, these components were interpreted as fine-scale climate patterns resulting from high frequency variability and topographic influences on winds rather than coherent, broad scale patterns characteristics of the north-central CCE. Therefore, only PC_{Uw1} and PC_{SST1} , which have strong coast-wide loadings, were retained for further analysis.

The leading PC of the UI (PC_{UI1}) explained 18% of the variance in the data, whereas the second component (PC_{UI2}) explained an additional 13%. PC_{UI1} represented a summer-focused mode of variability (data not shown) described in detail by Black and others (2011), and was not significantly ($P > 0.05$) correlated to the leading or subordinate components of PC_{Uw} and PC_{SST} . This indicates that variability near shore (where buoys are located) during summer differs from that of larger-scale UI

winds (García-Reyes and Largier 2012). By contrast, PC_{UI2} correlated well with PC_{Uw1} ($r = 0.84$, $P < 0.001$) and PC_{SST1} ($r = 0.70$, $P < 0.001$), and all three had very similar loading patterns (Figure 4C). Thus, components PC_{Uw1} , PC_{SST1} , and PC_{UI2} reflected a coherent, coast-wide climate pattern specific to the winter and spring months (about January–June). These three components were retained for the rest of the analysis given that they captured the nearshore, winter and spring signals of interest.

PC_{env} : A Multivariate Indicator of Upwelling

The leading PC_{env} (PC_{env1}) explained 21% of the variability in the data (Figure 4F) and was strongly correlated to PC_{SST1} ($r = 0.99$, $P < 0.001$), PC_{Uw1} ($r = 0.71$, $P < 0.001$), and PC_{UI2} ($r = 0.75$, $P < 0.001$) (Figure 4D, E, G). The strongest loadings between U_w and PC_{env1} occurred in April and May with peak values south of $40^{\circ}N$. There were also some negative loadings with U_w in the early fall at these southern latitudes. Loadings with SST followed similar patterns, though peak values were more broadly distributed from February through May and inverse loadings during the fall were strong and centered farther north (Figure 4D, E). Loadings for U_w and SST were opposite in sign

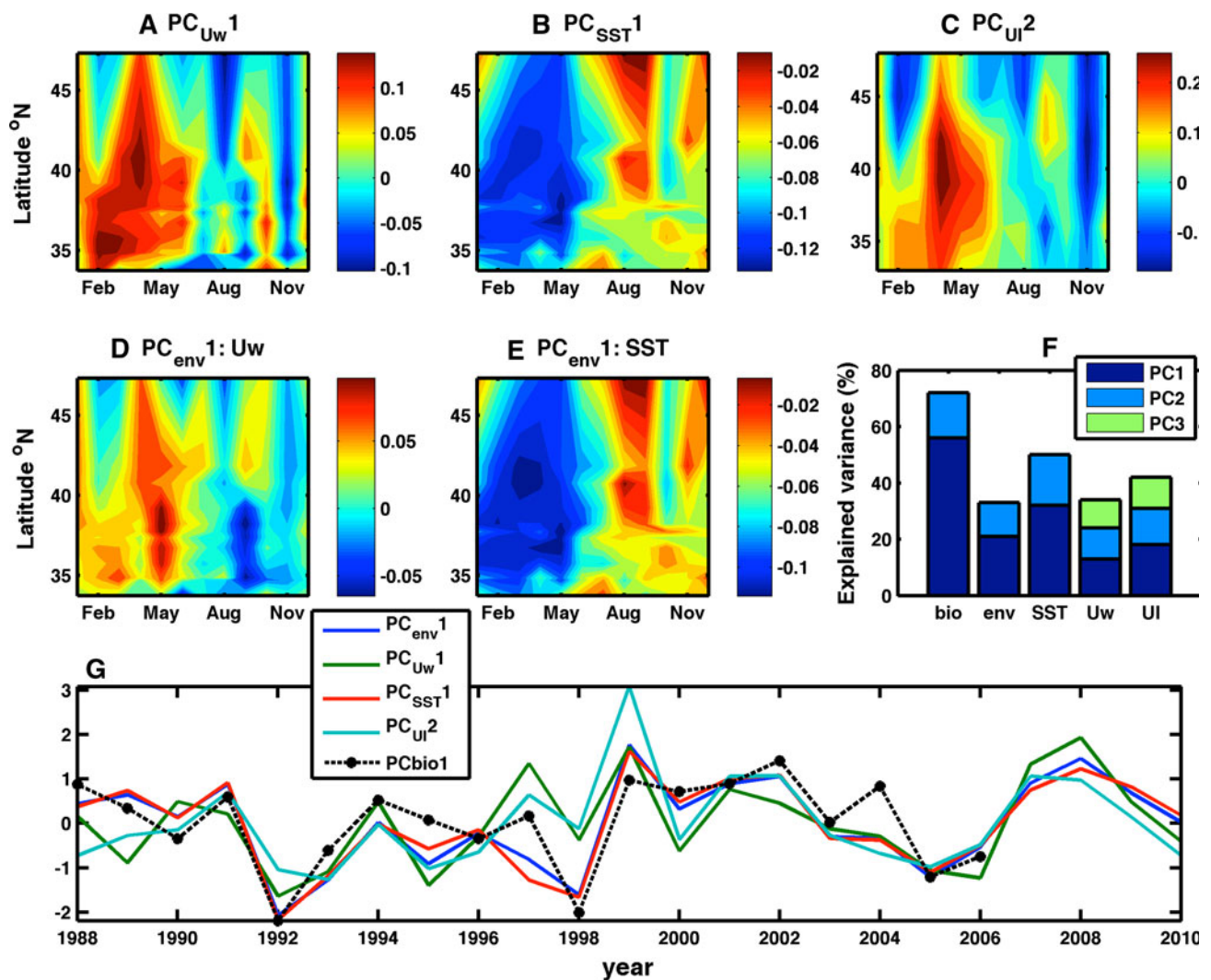


Figure 4. Principal component analysis of environmental variables from 1988 to 2010. Loadings of **A** PC_{Uw1} , **B** PC_{SST1} , **C** PC_{UI2} , **D** U_w against PC_{env1} , **E** SST against PC_{env1} . **F** PCs with explained variance greater than 10%. **G** Normalized scores for PC_{env1} , PC_{Uw1} , PC_{SST1} , PC_{UI2} , and PC_{bio1} (here shown for the period 1988–2006).

given that colder temperatures correspond to upwelling-favorable winds. The second PC_{env} accounted for 12% of the variability and mostly represented one large anomaly in late 1997 focused in the southern part of the region, possibly related to the early onset of that year's El Niño event. Thus, this component, similarly to PC_{SST2} , was not considered further in the analysis.

Biological Time Series

Among the biological time series, a subset of variables strongly correlated among one another including the splitnose rockfish chronology, Cassin's auklet and common murre phenology, and reproductive success for pigeon guillemot, pelagic cormorant, common murre and SEFI rhinoceros

auklet (Figure 5). For clarity, the signs for phenological measurements (timing of egg-laying in auklets and murre) were reversed so that all correlations were positive. Pigeon guillemot reproductive success significantly correlated with the most biological variables whereas Pacific sardine recruitment significantly correlated only with Cassin's auklet timing of breeding.

Nine biological time series shared a common interval from 1982 to 2006 and were included in the PCA: the splitnose rockfish otolith chronology, Pacific sardine recruitment, Cassin's auklet and common murre phenology, and reproductive success for pigeon guillemot, pelagic cormorant, common murre, Brandt's cormorant, and Cassin's auklet. The leading PC_{bio} (PC_{bio1}) explained 56% of

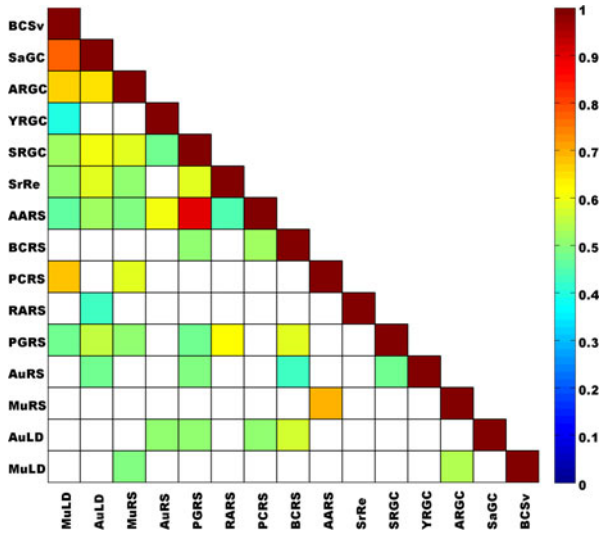


Figure 5. Rank correlations between biological indicators. Only significant ($P < 0.05$) and absolute values are shown.

the variability whereas the second PC_{bio} (PC_{bio2}) explained an additional 16%. Subordinate components explained less than 10% of the variability in the data set with Eigenvalues less than 1 (data not shown) and therefore were discarded from further analysis. In an ordination plot between PC_{bio1} and PC_{bio2} , most biological time series grouped together, though Pacific sardine recruitment was a

conspicuous outlier (Figure 6). Overall, PC_{bio1} showed consistently high loadings for all biological indicators included in the PCA except Pacific sardine recruitment. It also significantly ($P < 0.05$) correlated with five of the six biological time series not included in the PCA; Brandt’s cormorant survival was the only exception. With respect to PC_{bio2} , Pacific sardine recruitment had the highest loadings (0.61). PC_{bio2} also captured some of the variability in pelagic cormorant reproductive success, Cassin’s auklet reproductive success, the splitnose rockfish chronology, and to a lesser extent, Cassin’s auklet phenology and pigeon guillemot reproductive success (Table 2). Note that although some of the loadings for PC_{bio2} were higher than those for PC_{bio1} , PC_{bio2} explained much less variability in the data set. Among the biological indicators not included in the PCA, PC_{bio2} was significantly ($P < 0.05$) correlated only with Brandt’s cormorant survival (Table 2).

Biophysical Interactions

Biological time series were consistently correlated to PC_{SST1} ($r = -0.82$, $P < 0.001$), PC_{Uw1} ($r = -0.63$, $P < 0.005$), and PC_{UI2} ($r = -0.56$, $P < 0.05$), though the strongest significant correlations were generally with PC_{env1} ($r = -0.85$, $P < 0.001$) (Table 3). However, the close coupling

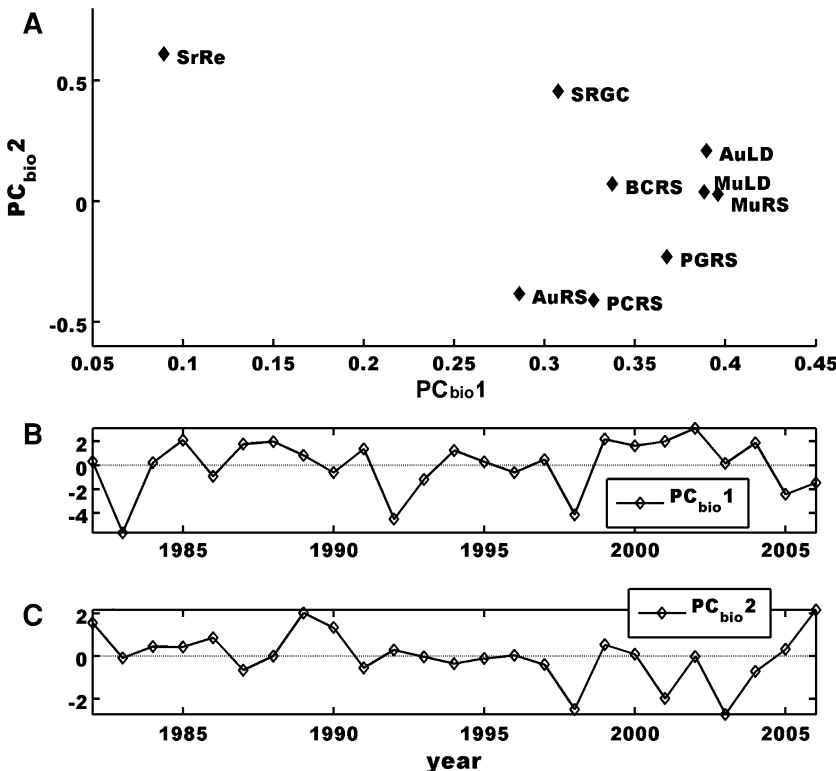


Figure 6. PCA of biological indicators time series (1982–2006). **A** PC_{bio1} versus PC_{bio2} loadings. Scores of **B** PC_{bio1} and **C** PC_{bio2} .

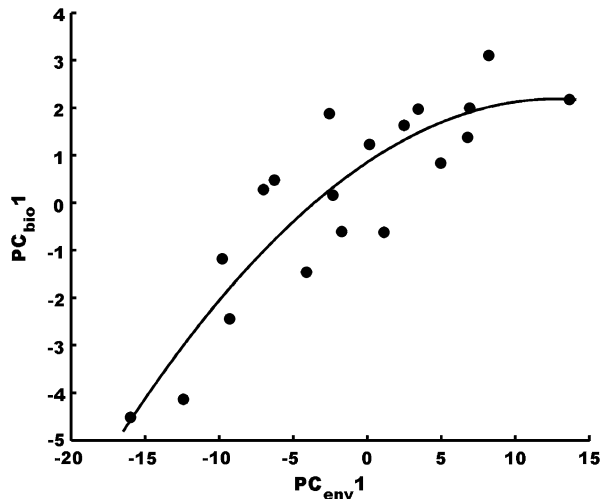


Figure 7. Bivariate plot of PC_{env1} versus PC_{bio1} scores (not normalized). *Line* shows the quadratic fit: $PC_{bio1} = -0.01 \times PC_{env1}^2 + 0.21 \times PC_{env1} + 0.85$, with $r^2 = 0.79$ and $P = 0.03$.

between biology and physics was best captured by a non-linear relationship between PC_{bio1} and PC_{env1} , (Figure 7) with a correlation $r^2 = 0.79$ ($P < 0.001$). Notably, several biological time series, including rockfish and salmon chronologies, did not correlate with any indicators of the physical environment (Table 3). Additionally, PC_{bio2} did not correlate significantly with any component of PC_{SST} , PC_{Uw} and PC_{UI} , or PC_{env} .

DISCUSSION

In this study we build upon earlier work of Black and others (2011) and Thompson and others (2012) to test the hypothesis that a key atmospheric driver (wind) and the oceanic conditions and response (SST) to upwelling have distinct seasonal modes of variability, and that these “modes” differentially relate to pelagic marine life in the central-northern California Current ecosystem. To date, this phenomenon has been examined only with broad-scale climate variables including the relatively coarse 3° upwelling intensity index, which decomposed into orthogonal winter and summer patterns. By contrast, finer-scale buoy-based upwelling (wind-driven Ekman transport) and SST could be described by a single mode of variability centered on the winter and spring (January through May) (Figure 4D, E). Thus, the dominant modes of environmental variability identified here (PC_{env1} , PC_{Uw1} , and PC_{SST1}) have different seasonal signatures than the dominant summer mode or even the subordinate winter mode derived from the 1946–2008 UI analysis

(Black and others 2011). This discrepancy could be due to the shorter time span covered by the present analysis. For example, variability at multi-decadal scales is a critical component of the summer mode described by Black and others (2011), but these lower-frequency processes would have been greatly reduced or eliminated in the 23-year reanalysis considered here. Moreover, the leading principal component generated from the 1988 to 2010 wind data (PC_{Uw1}) was much more consistent with PC_{UI1} calculated from data over this same interval than the summer or winter mode that resulted from the longer 1946 through 2008 interval of Black and others (2011) and Thompson and others (2012).

In addition to the time period of analysis, differences between seasonal modes of Black and others (2011) may also be the result of the coarse scale of the geostrophic wind field used to calculate UI. Such a spatial resolution does not resolve the impact of small-scale topographic features on the local atmospheric conditions (Capet and others 2004; Pickett and Schwing 2006). The dominant modes in the local variables (U_w and SST) do not reflect warm-season climate, and differences between UI and U_w are largest in the summer (July through September; García-Reyes and Largier 2012), suggesting that coherent coast-wide patterns are lacking during this time of year. Further differences between UI and U_w may reside in the use of a constant drag coefficient to calculate UI (Schwing and others 1996), different from the wind-speed-dependent drag coefficient used to calculate U_w in this study (Large and Pond 1981). Moreover, the calculation of UI has changed over time with the use of a more accurate drag coefficient and incorporation of higher-resolution models (see http://www.pfeg.noaa.gov/products/pfel/modeled/indices/upwelling/NA/how_computed.html), all of which could affect the ability to resolve seasonality in the data.

Based on this and previous analyses, we conclude that winter and spring variability in upwelling, described by PC_{env1} , is the dominant seasonal mode of variability in the local coastal environment. This mode is distinct from the period of peak upwelling in May/June (García-Reyes and Largier 2012) and appears to be linked to broad-scale atmospheric drivers. Black and others (2011) found an association between their UI “winter mode” and sea level pressure as indexed by the NOI (Schwing and others 2002). We found that the correlation between PC_{env1} and the January–April averages of NOI ($r = 0.8$, $P < 0.001$) is also quite strong. The clockwise rotation of an anomalously strong North

Pacific High would favor northerly winds along the central California Coast, possibly explaining its link to upwelling and SST. The state of the tropical Pacific is also important, as indicated by a strong correlation ($r = 0.7$, $P < 0.001$) between PC_{env1} and February–June averages of the Multivariate ENSO Index (MEI). Indeed, anomalies in PC_{env1} such as those in 1992 and 1998 track well-known El Niño events.

Most of the biological indices correlate with one another, PC_{bio1} , and PC_{env1} . Among the most synchronous are seabird phenology, murre reproductive success, and the splitnose rockfish growth chronology, all in agreement with the findings of Black and others (2011), as well as pigeon guillemot and Brandt's cormorant reproductive success. These variables were sampled in the same region (SEFI, Table 1), south of the Point Arena upwelling cell in a retention area that favors biological productivity (Vander Woude and others 2006). Moreover, Thompson and others (2012) showed these variables were all affected by winter upwelling indirectly through zooplankton, which could also help explain the covariance observed in this group. In contrast, variability in cormorant survival and sardine recruitment differs from the other biological series and is represented only by PC_{bio2} .

Although our biological variables were derived on an annual basis, the covariance between them represented by the PCA is related to the season over which measurements were made. For example, seabird reproductive success was derived from monitoring starting in March and ending in August each year whereas cormorant survival was studied from one breeding season to the next, reflecting environmental conditions in summer, fall, and the subsequent winter (Nur and Sydeman 1999). Rockfish otolith growth also represents an annual measurement and may integrate environmental conditions over all seasons, but could be particularly sensitive to growing season length. Therefore, many of these variables represent biological processes that occur at different times of the year than those represented by PC_{env1} (winter/spring). Moreover, there are some potential spatial disconnects in our data set, particularly with respect to Pacific sardine recruitment, which principally occurs off southern California (Smith and Moser 2003). Therefore, the lack of a fit of sardine recruitment with PC_{env1} may be due in part to the offshore curl of the wind stress rather than to coastal upwelling (Rykaczewski and Checkley 2008).

Another set of biological variables, including ANI rhinoceros auklet reproductive success and the salmon, yelloweye rockfish, and aurora rockfish

growth-increment chronologies covary with one other and PC_{bio1} , but have no association with PC_{env1} or PC_{bio2} . The fish in this group were largely sampled north of Point Arena, a region where environmental conditions are not dominated by year-round coastal upwelling (García-Reyes and Largier 2012). In contrast with those variables sampled at SEFI, the ANI rhinoceros auklets were sampled in a coastal area just north of the Monterey Bay upwelling cell (Rosenfeld and others 1994). The differences in upwelling conditions, and therefore nutrients and primary productivity, and between these locations may affect these species and also explain these intermediate levels of covariance with PC_{env1} . Another explanation for the variation in relationships between species and PC_{env1} is diet. The species most closely tied to PC_{env1} are mainly planktivorous (Cassin's auklet, splitnose rockfish) or at least planktivorous during the period leading up to the time when the measurement was made. For example, common murres are largely planktivorous in the pre-egg-laying period (Sydeman and others 1997) which may affect their timing of breeding. Chinook salmon may also be largely planktivorous during their initial period at sea (Wells and others 2012). Nonetheless, we consider it highly likely that the planktivorous species, represented by Cassin's auklet which shows the earliest annual breeding dates of all seabirds studied on the Farallones, show the strongest relationships to winter/spring environmental variation due to their lower trophic level. The auklets and splitnose rockfish are mostly dependent on the euphausiid crustaceans *Euphausia pacifica* and *Thysanoessa spinifera*, respectively (Love and others 2002; Abraham and Sydeman 2006).

Indeed, auklet phenology may be an indicator (sensu Rice and Rochet 2005) of the seasonal environmental conditions important to pelagic ecosystem productivity, as seen from its high correlation with PC_{env1} (Table 3). The use of auklet timing as an ecosystem indicator will be considered in greater detail elsewhere, but its high association with PC_{env1} and the other biological attributes examined in this paper provides initial support for its strength and use as an early-warning indicator of the conditions affecting a suite of other predators in the region.

Winds, SST, or PC_{env1} ?

For the nine biological variables in the primary group comprising PC_{bio1} , it is instructive to consider which environmental variable shows the greatest explanatory power. PC_{env1} has, in general,

a better correlation to the biological indicators and to PC_{bio1} than the other environmental PCs (Table 3), in particular PC_{Uw1} and PC_{U12} . Splitnose rockfish growth is not correlated with PC_{SST1} , presumably because this species is demersal, whereas PC_{SST1} reflects surface conditions. Murre phenology is more strongly correlated with PC_{Uw1} than PC_{SST1} . However, the remaining seven variables are more strongly associated with PC_{SST1} than PC_{Uw1} , and PC_{env1} is slightly more significant than PC_{SST1} . Therefore, combining the atmospheric driver and SST provides more explanatory power than considering the atmosphere or the ocean separately. However, if only ocean conditions are available, SST, not surprisingly, is likely to yield better relationships with biological components of the pelagic ecosystem than atmospheric measurements alone. This is most likely because SST integrate aspects of the pelagic habitats (including upwelling) which are more important to organisms than surface winds alone. In addition, PC_{env1} shows a better correlation with PC_{bio1} than other climate indices in the region commonly related to ecosystem variability: NOI, ENSO, PDO, and NPGO. PC_{bio1} has significant correlations ($P < 0.05$) with February-June averages of these indices: highest with NOI ($r = 0.78$), and lower with ENSO ($r = -0.64$), PDO ($r = -0.60$), and NPGO ($r = 0.60$). PC_{bio2} , however, does not show significant correlations with any of these climate indices.

Importance of Winter Winds and Upwelling

Why is winter and spring (January through May) upwelling so important to the pelagic ecosystem? This question is crucial to address because upwelling is greatest later in the year (May and June), leading to assumptions that spring/summer upwelling is key to ecosystem functions, such as productivity. Schroeder and others (2009) hypothesized that winter upwelling “pre-conditions” the pelagic ecosystem, seeding the region with nutrients early in the year, which facilitates vigorous biological productivity. Mechanistically, it is possible that even weak winds in winter could lead to weak stratification at that time, but this idea needs to be tested (Jacox and Edwards 2011). Alternatively, winter upwelling may facilitate an early transition to cold water conditions that may be important for setting the stage for the upcoming growing season. Mechanistically, this hypothesis, which is not mutually exclusive from that of Schroeder and others, suggests that winter upwelling may lengthen the growing season, leading to

enhanced productivity. A number of authors have suggested that the timing of the spring transition is important to pelagic ecosystem productivity (Logerwell and others 2003; Holt and Mantua 2009), however, our findings suggest that oceanographic conditions leading up to this transition may be more instructive than defining a specific transition date. A third possibility is that winter upwelling simply provides the lead time needed for robust plankton and forage fish populations to develop, to the betterment of fish and seabirds. Whatever the mechanism, it is clear that winter/spring upwelling is critical to the pelagic ecosystem of this region and we suspect that winter upwelling may also be important for other regions of the EBCs.

CONCLUSION

We demonstrated that local winter and spring winds and ocean conditions have a coherent influence on top marine predators in the central California Current Ecosystem (CCE). This non-linear relationship is best summarized by the correlation between the multivariate indicators PC_{bio1} and PC_{env1} , and shows bottom-up control of the pelagic ecosystem in the region, in agreement with Wells and others (2008) and Thompson and others (2012). This study is significant as U_w and SST (and PC_{env1}) confirm the climate–ecosystem interactions previously found using the UI, though with modification. Black and others (2011) and Thompson and others (2012) related pelagic ecosystem variability to regional winter upwelling, and we found that conditions in winter and spring (about January through May) were the most influential. These results are not substantially different, and probably reflect the larger suite of biological responses, the local-scale physical variables, and shorter timeframe used in this study. We also conclude that PC_{bio1} and PC_{env1} are appropriate indicators for integrated assessments of upwelling influences on pelagic life in the central California Current. These multivariate indicators may be useful for management, as they consolidate processes into a limited number of more easily examined univariate measurements.

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