

Spatio-temporal dynamics of ocean conditions and forage taxa reveal regional structuring of seabird–prey relationships

JARROD A. SANTORA,^{1,2,5} ISAAC D. SCHROEDER,³ JOHN C. FIELD,⁴ BRIAN K. WELLS,⁴ AND WILLIAM J. SYDEMAN¹

¹Farallon Institute for Advanced Ecosystem Research, 101 H Street, Suite Q, Petaluma, California 94952 USA

²Center for Stock Assessment Research, University of California, 110 Shaffer Road, Santa Cruz, California 95060 USA

³Environmental Research Division, NOAA Southwest Fisheries Science Center, 1352 Lighthouse Avenue, Pacific Grove, California 93950 USA

⁴Fisheries Ecology Division, NOAA Southwest Fisheries Science Center, 110 Shaffer Road, Santa Cruz, California 95060 USA

Abstract. Studies of predator–prey demographic responses and the physical drivers of such relationships are rare, yet essential for predicting future changes in the structure and dynamics of marine ecosystems. Here, we hypothesize that predator–prey relationships vary spatially in association with underlying physical ocean conditions, leading to observable changes in demographic rates, such as reproduction. To test this hypothesis, we quantified spatio-temporal variability in hydrographic conditions, krill, and forage fish to model predator (seabird) demographic responses over 18 years (1990–2007). We used principal component analysis and spatial correlation maps to assess coherence among ocean conditions, krill, and forage fish, and generalized additive models to quantify interannual variability in seabird breeding success relative to prey abundance. The first principal component of four hydrographic measurements yielded an index that partitioned “warm/weak upwelling” and “cool/strong upwelling” years. Partitioning of krill and forage fish time series among shelf and oceanic regions yielded spatially explicit indicators of prey availability. Krill abundance within the oceanic region was remarkably consistent between years, whereas krill over the shelf showed marked interannual fluctuations in relation to ocean conditions. Anchovy abundance varied on the shelf, and was greater in years of strong stratification, weak upwelling and warmer temperatures. Spatio-temporal variability of juvenile forage fish co-varied strongly with each other and with krill, but was weakly correlated with hydrographic conditions. Demographic responses between seabirds and prey availability revealed spatially variable associations indicative of the dynamic nature of “predator–habitat” relationships. Quantification of spatially explicit demographic responses, and their variability through time, demonstrate the possibility of delineating specific critical areas where the implementation of protective measures could maintain functions and productivity of central place foraging predators.

Key words: anchovy; demographic response; ecosystem oceanography; forage fish; krill; management; preyscape; seabird reproduction; seascape; upwelling.

INTRODUCTION

Understanding predator–prey relationships is a cornerstone of modern ecosystem approaches to fisheries management (Cury et al. 2008, 2011, Link 2010, Hunsicker et al. 2011). Predator–prey relationships are classified as both functional and numerical responses (Holling 1973, Abrams 2000). Numerical responses are assessed by integrating information on prey availability with predator demographic statistics, such as production and/or aggregation statistics (Cairns 1987, Piatt et al. 2007, Cury et al. 2011, Hunsicker et al. 2011). While aggregative responses are important, recent efforts have focused on derivation of appropriately scaled demographic responses to establish thresholds and bench-

marks for fisheries management (Cury et al. 2011, Smith et al. 2011). This is a difficult undertaking because of spatial heterogeneity of prey populations, as well as heterogeneity in habitat use by predators. It has been well documented that many forage species in marine ecosystems (e.g., krill and forage fish) are unevenly distributed and are likely to exhibit dense aggregations (Hunt et al. 1998, Santora et al. 2011a, b). This heterogeneity may be due to intrinsic factors of prey populations (e.g., diel vertical migration and feeding behavior) or responses of these populations to physical oceanographic processes (e.g., the formation of upwelling fronts) that drive variation in horizontal and/or vertical water column structure underlying prey aggregations (Haury et al. 1978). Furthermore, based on the availability of prey, marine predators may exhibit complex prey-switching, highlighting the need to consider multiple prey and their habitat associations for assessing demographic and aggregative responses (Abra-

Manuscript received 19 August 2013; revised 20 February 2014; accepted 24 February 2014. Corresponding Editor: S. S. Heppell.

⁵ E-mail: jsantora@ucsc.edu

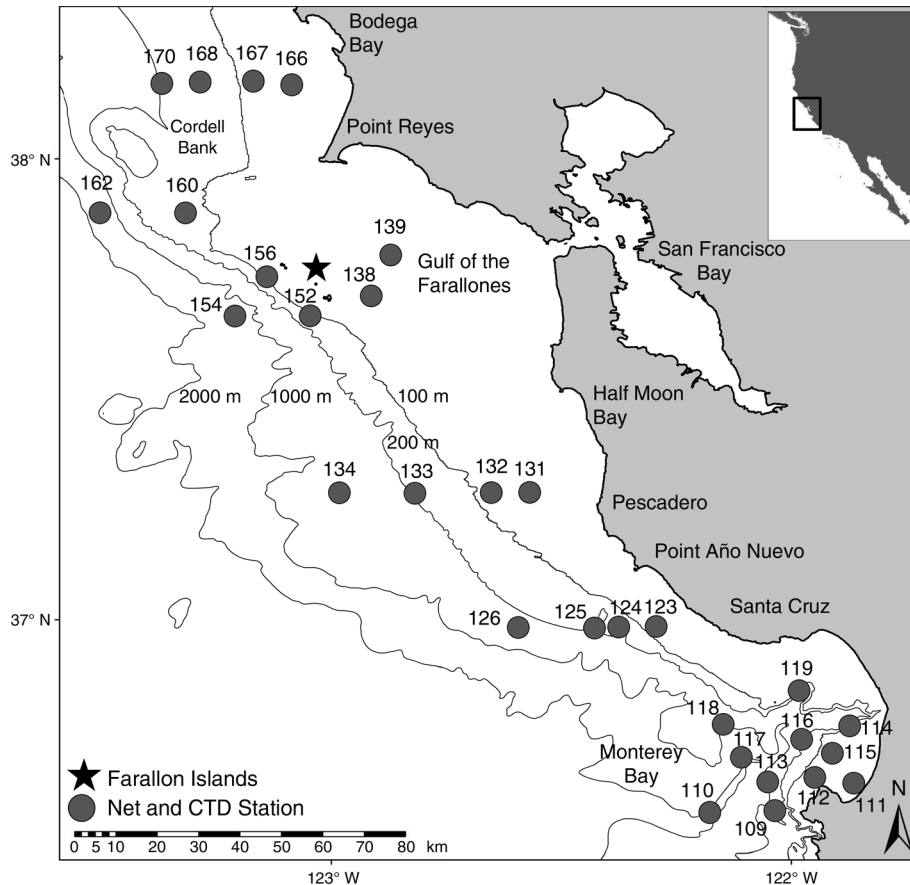


FIG. 1. Survey area sampled by the NMFS “Rockfish Recruitment and Ecosystem Assessment Survey” off central California during May and June, 1990–2010. Only those stations sampled every year are shown; numbers indicate station identification. The star indicates the location of the Farallon Islands where seabird reproductive success was estimated during 1990–2007.

ham and Sydeman 2006, Cury et al. 2011). As such, it is critical to establish the linkage between physical environmental variability and spatio-temporal aspects of predator–prey relationships in order to derive appropriate functional relationships (Hunsicker et al. 2011).

Mesoscale variability (10–1000 km) of ocean physics together with the variance of abundance of micronekton and top predators has been described in a number of well-studied, seasonally productive mid- to high-latitude marine ecosystems (Fauchald et al. 2000, Hunt et al. 2008, Santora et al. 2012a). Due to their variability, temperate eastern boundary upwelling ecosystems such as the Humboldt, Canary, Benguela, and California current systems are ideal for investigation of regional structuring of predator–prey interactions (Cury et al. 2008). In the California Current ecosystem, large-scale advection patterns, and spatial and temporal variation in coastal upwelling drive variability in mesoscale structuring of hydrographic conditions (Chelton 1982, Checkley and Barth 2009, Santora et al. 2012a). In the Gulf of the Farallones/Monterey Bay region of central-northern California (hereafter GoF/MB), regional

oceanographic variability is related to the horizontal and vertical dimensions of seasonal upwelling and thermal/density stratification (Steger et al. 2000, Collins et al. 2003). Santora et al. (2012a) demonstrated that mesoscale distribution of predators and prey (forage fish, krill, and squid) in this system may be used to delineate ecologically important areas that support a diverse predator assemblage. Distinct forage assemblages and top predators conform to oceanographic conditions within shelf, oceanic, and Monterey Bay regions (Fig. 1). Santora et al. (2012a) described the spatial climatologies of micronekton and top predator distributions of these assemblages, but did not examine their long-term spatio-temporal dynamics relative to oceanographic conditions. The objective of this contribution is to meld spatial and temporal information on ocean conditions and prey availability, a perspective essential for the development of spatially explicit predator–prey demographic responses.

Seabirds, marine mammals, and large fish are predators of micronekton within the GoF/MB region. Among these taxa, long-term demographic data on annual breeding success is only available for seabirds.

Evidence from breeding populations of seabirds on the Farallon Islands (Fig. 1) indicates fluctuations in reproductive success related to ocean conditions and prey availability (Ainley et al. 1995, Abraham and Sydeman 2004, Field et al. 2010, Sydeman et al. 2013). In general, years of high seabird reproductive success correspond to cooler ocean conditions and associated increased prey abundance. Reproductive failure coincides with warm, poor upwelling years such as those experienced during El Niño events (Ainley et al. 1995, Sydeman et al. 2013). While various relationships between climate–ocean conditions and Farallon seabird breeding success have been established, no study has yet investigated spatial structuring of predator–prey interactions.

Because life history attributes and behaviors vary (e.g., morphology, foraging habitat preference, diving ability), seabird species have differential sensitivities to variation in prey availability (Ainley et al. 1995, Furness and Tasker 2000, Velarde et al. 2013). Therefore, our overall goal is to understand spatially explicit ocean–prey and seabird–prey relationships from the perspective of variation in life histories. Based on our previous descriptions of ecologically important areas and “hot spots” of prey abundance (Santora et al. 2011a, b, 2012a, b), we hypothesize that predator–prey interactions and demographic responses vary spatially and are related to the seabird’s foraging ecology. To test this hypothesis, we quantify the spatio-temporal variability of ocean conditions, krill, and forage fish over 21 years (1990–2010) and model seabird demographic responses to prey abundance over 18 years (1990–2007). The quantification of spatio-temporal associations among ocean conditions, forage species, and seabird reproduction is vital to the ecosystem approach to management, especially in relation to marine spatial planning and fisheries (Cury et al. 2008, Edwards et al. 2010).

METHODS

Hydrographic conditions

The National Marine Fisheries Service “Rockfish-Recruitment and Ecosystem Assessment Survey” (RREAS) samples GoF/MB stations (Fig. 1) multiple times during May and June each year (Sakuma et al. 2006, Field et al. 2010, Ralston et al. 2013). During the RREAS, conductivity–temperature–depth (CTD) casts were used to characterize spatial and temporal variation in ocean conditions. At each station, CTD casts were made using a SeaBird Electronics SEACAT 19plus to a depth of 500 m, or 10 m from the bottom. We analyzed CTD casts that coincided with consistently sampled micronekton sampling locations (Fig. 1). A total of 1697 CTD and net stations were analyzed. For each cast, we estimated the mean sea temperature and salinity over 20–40 m; this depth was chosen to match the target depth of net hauls (Santora et al. 2012a, Ralston et al. 2013). Furthermore, to characterize the vertical hydrographic conditions, we estimated stratification strength

using the Brunt-Väisälä frequency (BVF) integrated to 100 m (Talley et al. 2011). We also determined the depth of the $\sigma_\theta = 26.1$ isopycnal as an indicator of upwelling and nutricline depth (Collins et al. 2003). We derived the mean of each physical variable within shelf, oceanic, and Monterey Bay habitats (Fig. 1) to illustrate interannual and spatial variability of physical ocean conditions.

Micronekton sampling

Micronekton samples were collected at night using a modified Cobb midwater trawl with a 9.5-mm cod-end liner; Sakuma et al. (2006) and Ralston et al. (2013) review net sampling procedures. Time series of average krill and forage fish abundance based on log-transformed catch-per-unit-effort were estimated for each sampling station (CPUE [Bjorkstedt et al. 2010]). Typically, 15-minute tows were made at each station with a headrope depth of 30 m. However, a 10 m depth was used in shallow waters, and shorter-duration tows (e.g., 5 minutes) were made in areas with dense jellyfish aggregations (e.g., nearshore GoF stations); data were extrapolated to the standard 15-minute tow duration (<5% of total tows). Due to their importance in the diets of upper-trophic-level predators, we quantified the spatio-temporal variability of krill (*Euphausia pacifica* and *Thysanoessa spinifera*), northern anchovy (*Engraulis mordax*), juvenile rockfish (*Sebastes* spp.), and juvenile sanddab (*Citharichthys* spp.) per habitat region.

Seabird reproduction

Seabird breeding success (number of chicks per pair) was recorded at Southeast Farallon Island (SEFI) located in the center of the RREAS (~50 km from San Francisco); details of this variable are provided by Ainley et al. (1995), Sydeman et al. (2001), and Cury et al. (2011; see Appendix). Data from 1990–2007 are available for analysis. We investigated the breeding success of Common Murre (*Uria aalge*), Cassin’s Auklet (*Ptychoramphus aleuticus*), Rhinoceros Auklet (*Cerorhinca monocerata*), Pigeon Guillemot (*Cepphus columba*), Brandt’s Cormorant (*Phalacrocorax penicillatus*), and Pelagic Cormorant (*Phalacrocorax pelagicus*). All of these seabirds are pursuit-diving species that select a variety of micronekton, including krill, and forage fish species such as juvenile rockfish, juvenile sanddab, and anchovy as prey for offspring provisioning (Ainley and Boekelheide 1990, Ainley et al. 1996a, b, Sydeman et al. 1997, 2001, Robinette et al. 2007; see Plate 1). Seabird breeding performance may be related to winter environmental conditions that occurred months before the initiation of breeding (e.g., egg lay date [Ainley and Boekelheide 1990, Schroeder et al. 2009]), but breeding success, measured as the number of young raised to fledging age, is largely a function of the parents ability to provision offspring during the chick-rearing phase (Sydeman et al. 2001). The age of chicks at fledging varied from ~25 d in murrelets to >60 d in Rhinoceros Auklets (Ainley and Boekelheide 1990, Thayer and

Sydeman 2007). Aside from the murre, offspring are independent of their parents once fledging occurs, so the number of independent offspring is averaged to calculate annual breeding success on a per breeding pair basis. As such, to model breeding success, we focus on prey abundance during the months of May–June when these seabirds are central-place foragers, departing from and returning to SEFI to provision young. Provisioning offspring lasts through July, but unfortunately no prey data are available for that latter time period. Depending on species, the maximum foraging ambit varied from ~20 to 100 km (Mills et al. 2007). While poorly known, it is believed that Pigeon Guillemot and Pelagic Cormorant are neritic foragers that rarely search for prey beyond 10 km from the colony. In contrast, Common Murre and Brandt's Cormorant routinely travel >30 km in search of prey (Ainley and Boekelheide 1990). Common Murre, Cassin's Auklet, and Rhinoceros Auklet lay a single egg per nesting attempt, whereas Pigeon Guillemot, Brandt's Cormorant, and Pelagic Cormorant lay more than one egg per nesting attempt (Sydeman et al. 2001). We used these fundamental differences in foraging behavior and reproductive effort to investigate how spatial variation in numerical responses varies according to seabird life-history attributes.

Analysis

A priori, based on previous studies of this data set and other published accounts of the California Current system, we thought that a multivariate synthesis of physical ocean conditions would partition the variance into “warm/weak upwelling” and “cool/strong upwelling” years off central-northern California (e.g., Peterson and Schwing 2003, Mackas et al. 2007, Sydeman et al. 2014). However, this is an oversimplification of marine ecosystem state, as spatio-temporal variations in environmental conditions impact ecosystem functions (Bakun 2010). To take spatial variability into account, micronekton sampling stations were categorized according to the three ecological regions identified by Santora et al. (2012a), with 9 stations in the “shelf region,” 10 in the “oceanic region” and 11 within the “Monterey Bay” region (Fig. 1; $n = 30$). At each station, interannual time series of the four hydrographic variables (temperature, salinity, depth of the 26.1 isopycnal, stratification) were constructed by averaging all of the CTD casts taken at that station.

Our first objective was to quantify the temporal variability in hydrographic conditions and krill and forage fish abundance within each region across 21 years, 1990–2010. For each region we estimated the average of subsurface (mean 20–40 m) temperature, salinity, stratification, and depth of the 26.1 isopycnal and then applied Principal Component Analysis (PCA) to index the *seascape*. We also conducted PCA to develop multivariate time series of ocean conditions to investigate spatially explicit correlations with mean

catches of krill and forage fish to resolve the *preyscape* (i.e., spatial availability of seabird prey). Second, we examined demographic responses between the *preyscape* and the breeding success of seabirds. To address this objective, we developed spatially explicit correlation maps between the time series of seabird breeding success (Southeast Farallon Island) and station-specific time series of krill and forage fish abundance. Pearson correlation coefficients were interpolated (bilinear) spatially to visualize coherence among stations. Our third objective was to examine the demographic response between seabird reproductive success and regional abundance estimates of krill and forage fish. As numerical responses are generally nonlinear and exhibit a variety of functional forms (Holling 1973, Hunsicker et al. 2011), we used non-parametric generalized additive models (GAM) (Cury et al. 2011). The mgcv package was used to analyze GAMs (Wood 2006) in the statistical program R (R Development Core Team 2014). We tested the demographic response between seabird breeding success and regional (e.g., shelf, oceanic) abundance of forage species using a univariate GAM: *Seabird Breeding Success* = $s(\text{Forage}_{i,x})$, where $\text{Forage}_{i,x}$ is the annual spatial mean abundance of forage species i in habitat x , and $s()$ is a smoothing function (regression spline). For each seabird species, the effect of $\text{Forage}_{i,x}$ was plotted to visually inspect the functional form (e.g., linear, hyperbolic, sigmoidal/step); calculated adjusted r^2 and percentage deviance explained were used to evaluate model performance. We examined the relationships of seabird reproduction with prey abundance in shelf and oceanic habitats only because Monterey Bay sampling stations were too far to provide indices of prey abundance being used by seabirds breeding at Southeast Farallon Island (Ainley and Boekelheide 1990).

RESULTS

Hydrographic conditions

Spatio-temporal variability of ocean conditions were highly synchronized among oceanic, shelf, and Monterey Bay regions (Figs. 2 and 3; Appendix: Fig. A1). Temperature is higher, salinity lower, and depth of the 26.1 isopycnal deeper in the oceanic region compared to shelf and Monterey Bay regions (Fig. 2a–c). Stratification strength tended to exhibit greater interannual variability (e.g., 1993 and 2006) on the shelf than in the oceanic and Monterey Bay regions (Fig. 2c, d). As expected, there were clear “warm/weak upwelling” and “cool/strong upwelling” years corresponding to several strong El Niño (e.g., 1992–1993; 1997–1998) and La Niña (1999) events, as well as years of poor upwelling (e.g., 2005–2006; Figs. 2 and 3). The coherent physical variability across the three regions justifies spatial averaging of the four hydrographic time series and calculation of a comprehensive PCA of environmental conditions (Fig. 3). PCA yielded a first principal

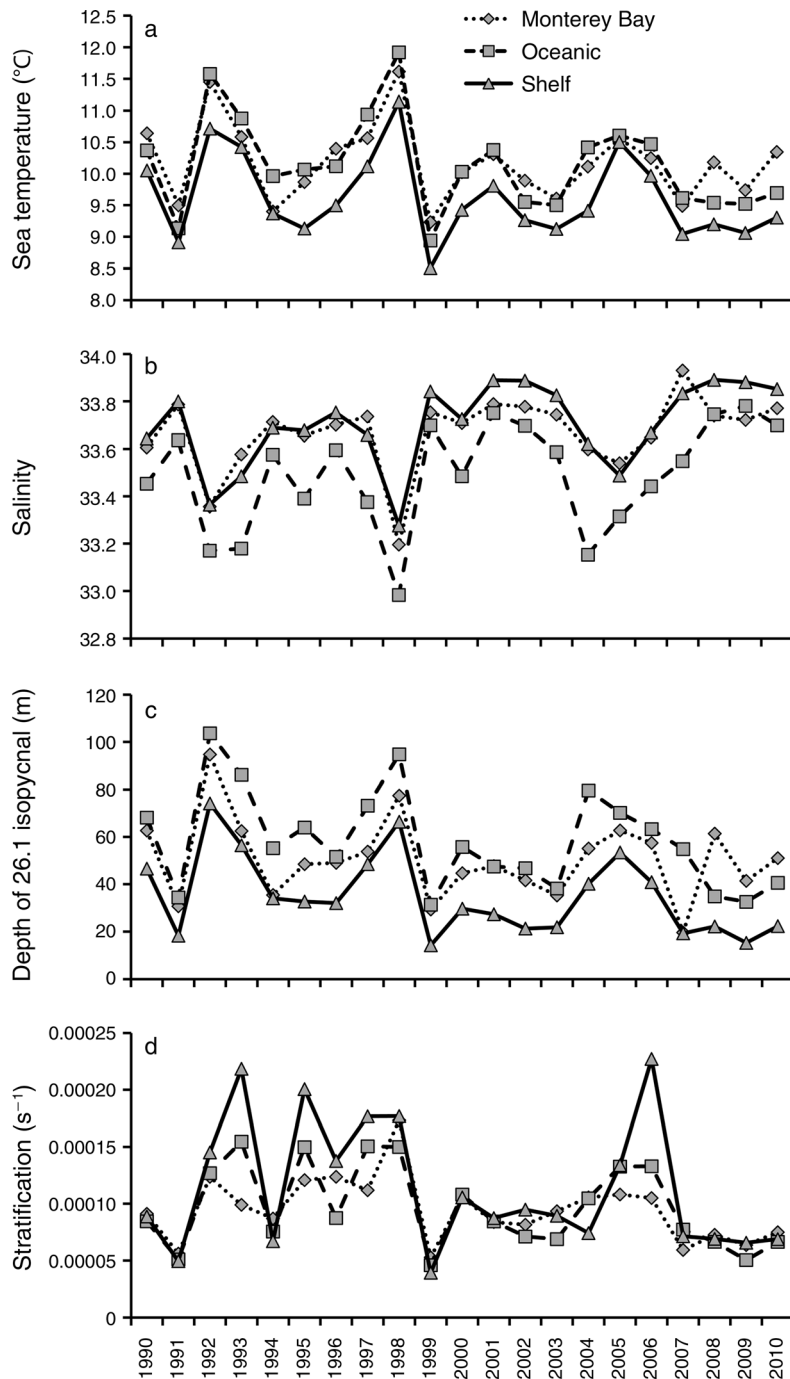


FIG. 2. Interannual variability of the spatial mean of (a) temperature at 22–40 m, (b) salinity (measured using the practical salinity system) at 22–40 m, (c) depth of the 26.1 isopycnal, (d) stratification within shelf, oceanic, and Monterey Bay regions.

component, “Physics PC1,” which captured 87% of variance and resolved interannual variability in hydrographic state, the *seascape* (Table 1, Fig. 3). Subsurface temperature was cooler, salinity was higher, stratification strength decreased, and the 26.1 isopycnal depth shallower during years characterized as negative by Physics PC1 (Fig. 3). Moreover, Physics PC1 indicates

that ocean conditions were different before and after the 1997–1998 El Niño. Sea temperature and stratification were comparatively higher during the 1990s than in later years, which were characterized by a prolonged period of mostly cooler temperatures, higher salinities, a shallow 26.1 depth, and decreased stratification (Figs. 2 and 3). For subsequent space–time comparisons

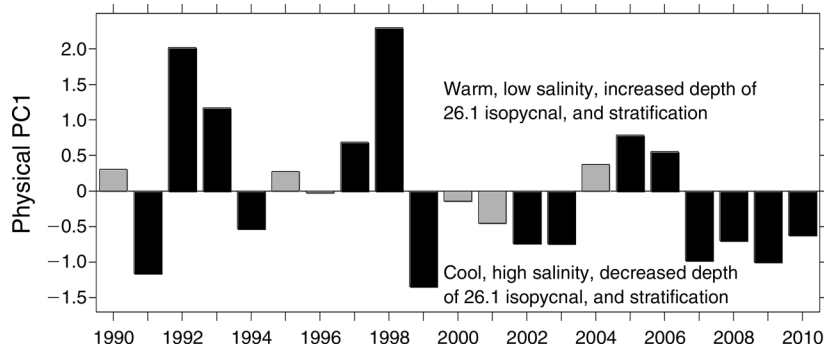


FIG. 3. PCA results illustrating Physics PC1 (87% variance) for the spatial mean of temperature, salinity, depth of the 26.1 isopycnal, and stratification for the entire seascape during May/June 1990–2010. Positive values represent poor coastal upwelling conditions; warm temperature, low salinity, deep isopycnal, and increased stratifications. Negative values represent good coastal upwelling conditions; cool temperature, high salinity, shallow isopycnal, and decreased stratification. To classify PC loadings, values less than +0.5 and greater than –0.5 are shaded gray (gray bars). This shows that the majority of years in the time series load high relative to warm/cool years.

among ocean conditions, krill, forage fish, and seabird reproduction, a separate PCA analysis of station-specific time series of Physics PC1 was developed for each sampling station (Fig. 1).

Spatio-temporal variability of krill and forage fish

Partitioning prey catches according to the three regions revealed distinct spatio-temporal differences (Fig. 4a). Over the 1990–2010 study period, krill catches were relatively stable in the oceanic and, to a lesser extent, the Monterey Bay region. However, krill catch variability on the shelf was extreme, with decreased krill CPUE in 1992, 1998, and 2005. Anchovy catches displayed periodic pulses during the 1990s, with greatest catches from Monterey Bay and secondarily shelf regions. This was followed by an extended period of elevated abundance in all three regions during 2004–2007, and a major decline starting in 2008 (Fig. 4b). Interannual abundance fluctuations of pelagic juvenile stages of rockfish and sanddabs in the three regions were similar over the 21-year period (Fig. 4c, d), with marked peaks attributed to the survival of larvae during optimal environmental conditions (Ralston and Howard 1995, Ralston et al. 2013).

Relationships between krill and forage fish and hydrographic conditions

To describe the structure of the seascape and prey-scape time series of Physics PC1, krill and forage fish were compared spatially. The resulting spatio-temporal correlation maps reveal the bio-physical structure underlying potential trophic interactions among micro-nekton taxa and the seabirds. Significant negative correlations between Physics PC1 and micro-nekton taxa indicate increased abundance during strong/cool upwelling years. Krill were negatively associated with Physics PC1 at seven stations primarily located on or adjacent to the shelf between Pt. Reyes and Santa Cruz

(Fig. 5a). Juvenile rockfish had generally weak negative associations with Physics PC1; at only one station within the GoF was the relationship significant (Fig. 5b). Juvenile sanddab also had generally weak negative relationships with Physics PC1, but five northern stations showed significance (Fig. 5c). In contrast, anchovy were positively associated with Physics PC1, indicating higher catches during warmer and weaker upwelling years, with significant positive correlations at two stations off Pescadero and one within Monterey Bay (Fig. 5d).

Correlation maps between krill, juvenile rockfish, and sanddab abundance revealed positive covariance in abundance within the shelf habitat (Fig. 5e, f, h; Appendix: Table A1). On the other hand, krill and anchovy were negatively associated on the shelf (Fig. 5g), indicating that their populations occur out of phase. Catches of juvenile rockfish and sanddabs also negatively associated with anchovy (Fig. 5i, j).

Spatial maps of predator–prey associations

Spatio-temporal correlations between seabird breeding success and krill and forage fish abundance revealed finer-scale predator–prey associations. Common Murre was positively correlated with krill in all regions, with strongest relationships in the shelf region (Fig. 6a). They also had positive relationships with juvenile rockfish on the shelf and in oceanic regions, and with juvenile

TABLE 1. PCA results for the loadings of temperature, salinity, stratification and depth of 26.1 isopycnal.

Variable	PC1 (88%, 3.25)	PC2 (8%, 0.29)
Temperature at 20–40 m	0.96	0.1
Salinity at 20–40 m	–0.95	–0.11
Stratification	0.87	–0.49
Depth of 26.1 isopycnal	0.97	0.24

Note: Values in parentheses indicate, first, the percentage of total variance and second, eigenvalue.

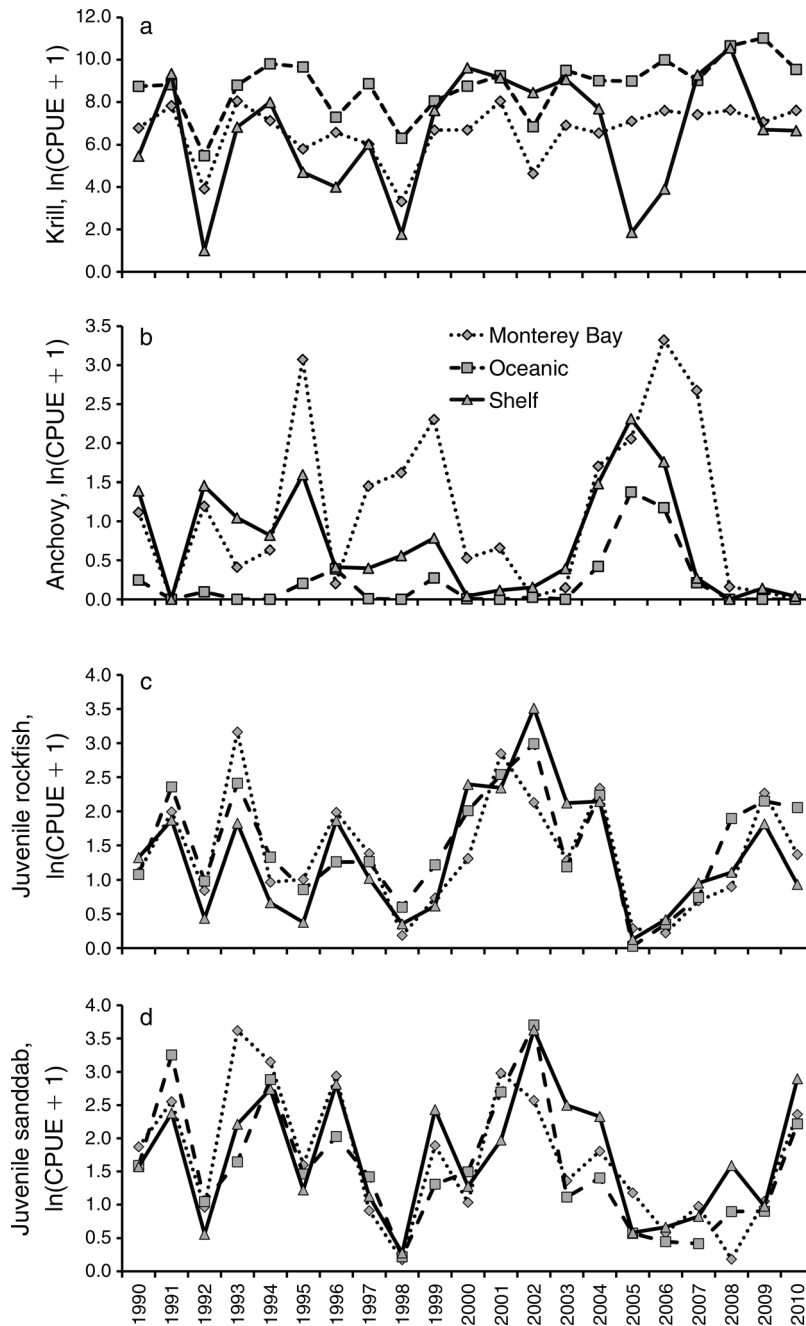


FIG. 4. Interannual variability of the spatial mean of (a) krill, (b) anchovy, (c) juvenile rockfish, and (d) juvenile sanddab within shelf, oceanic, and Monterey Bay regions.

sanddab across all regions (Fig. 6b, c). Cassin's Auklet was positively correlated with krill within the shelf region, particularly at two stations off Pescadero (Figs. 1 and 6d). Cassin's Auklets had strong positive relationships with juvenile rockfish and sanddab within all three regions, but these were strongest at stations closest to the Farallon breeding colony and off the San Mateo coast (Fig. 6e, f). Rhinoceros Auklet had a significant positive correlation with krill at one shelf station

adjacent to the breeding colony, and juvenile rockfish and sanddab in the oceanic region (Fig. 6g-i). Pigeon Guillemot had positive correlations with krill in the shelf region as well as juvenile rockfish at a number of stations within each region and with sanddab in shelf and oceanic regions (Fig. 6j-l). Brandt's Cormorant was positively correlated with krill in shelf and oceanic regions, but surprisingly, showed no relationships with juvenile rockfish or sanddab (Fig. 6m-o). Pelagic

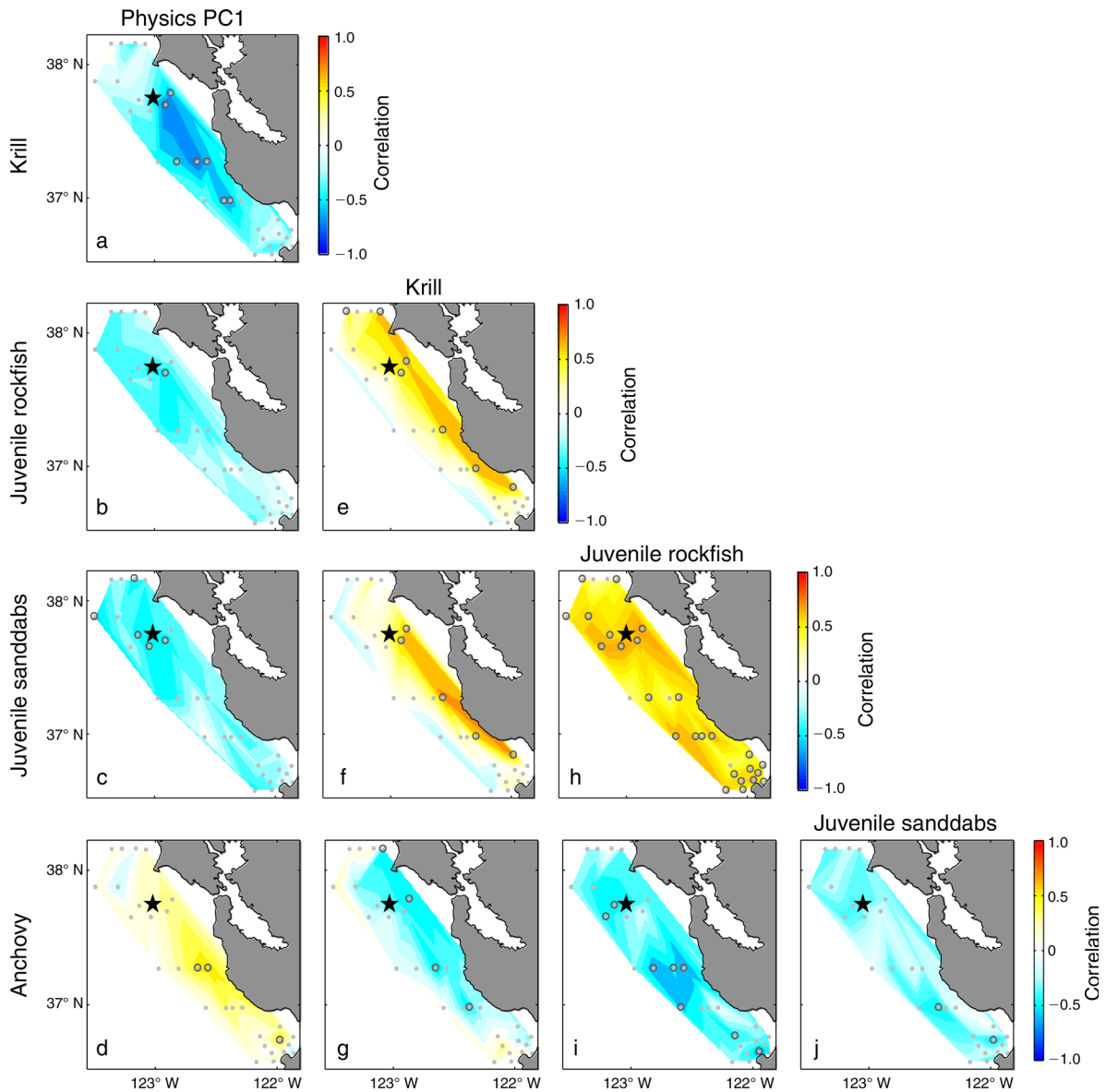


FIG. 5. Spatio-temporal association among Physics PC1, krill, juvenile rockfish, juvenile sanddab, and anchovy. Significant station correlations ($P < 0.05$) are indexed with larger circles. Note that time series are compared at each sampling station ($n = 30$). Black star indicates the location of the Farallon Islands.

Cormorant had a positive association with krill in the shelf region, with juvenile rockfish in all regions and with sanddab in shelf and oceanic regions (Fig. 6p–r). All seabird species had negative relationships with anchovy in all regions (not shown).

Demographic models of seabirds and forage species

The demographic response between seabird breeding success and station-specific forage abundance reveals marked differences among seabirds (Table 2, Fig. 7; Appendix: Figs. A2–A8). Fig. 7 presents the best forage model for each seabird species, based on the highest r^2 and percentage deviance explained for $Forage_{i,x}$.

Because these seabird species all exhibit broad diet breadths and complex prey switching based on availability, the likelihood of one prey species being singly important is unlikely. These relationships also reflect correlations, so may not be causal. Nonetheless, the best relationship for Common Murre was with krill shelf abundance, which revealed a classic hyperbolic numerical response highlighting a threshold level in krill abundance below which murre breeding success declines (Fig. 7a). The oceanic abundance of juvenile rockfish provided the best model for Cassin’s Auklet, and the relationship was close to linear (Fig. 7b). The best model for Rhinoceros Auklet was krill shelf

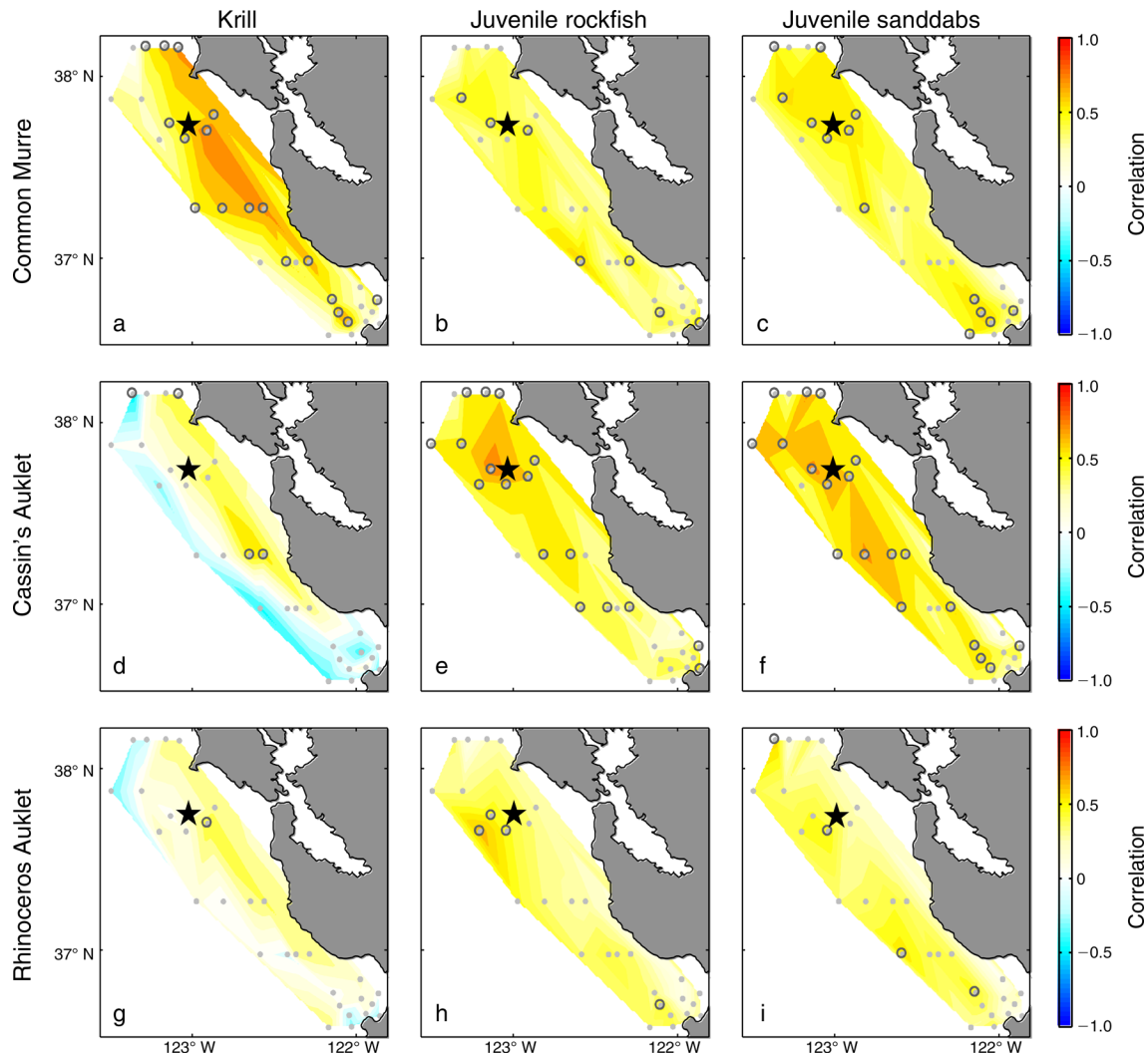


FIG. 6. Spatio-temporal correlation maps between seabird reproductive success with krill, rockfish, and sanddab: (a) Common Murre, (b) Cassin's Auklet, (c) Rhinoceros Auklet, (d) Pigeon Guillemot, (e) Brandt's Cormorant, and (f) Pelagic Cormorant. Significant station correlations ($P < 0.05$) are indexed with larger circles. Note that time series are compared at each sampling station ($n = 30$) to breeding success of seabirds on Southeast Farallon Island (black star).

abundance (Fig. 7c), while that for Pigeon Guillemot was juvenile sanddab shelf abundance (Fig. 7d). For the model fit between Rhinoceros Auklet and krill (Fig. 7c), there was a high breeding success point when krill abundance on the shelf was low. This indicates that Rhinoceros Auklets did well in that particular year because other suitable prey was probably available (e.g., anchovy). The only significant model for Brandt's Cormorant contained krill oceanic abundance with an apparent hyperbolic response (Fig. 7e). The best model for Pelagic Cormorant was juvenile rockfish in the shelf region; this exhibited a threshold response (sigmoidal/step) at higher concentrations of juvenile rockfish (Fig. 7f). Because anchovy abundance is positively correlated with weak/warm upwelling years, all seabird-

anchovy models yielded negative relationships (Appendix: Fig. A8).

DISCUSSION

We found evidence that spatio-temporal variability in hydrographic conditions shapes the regional distribution and abundance of krill and forage fish, which in turn, underlie the numerical responses of seabird breeding success to prey availability. There are four main points: (1) time series of hydrographic conditions broadly reflect warm/weak and cool/strong upwelling years and are consistent across habitats, (2) krill, juvenile rockfish, and sanddabs are more abundant and spatially available to seabirds within shelf and oceanic regions during cool/strong upwelling years, (3) anchovy are more abundant in coastal areas during warmer years, when other forage

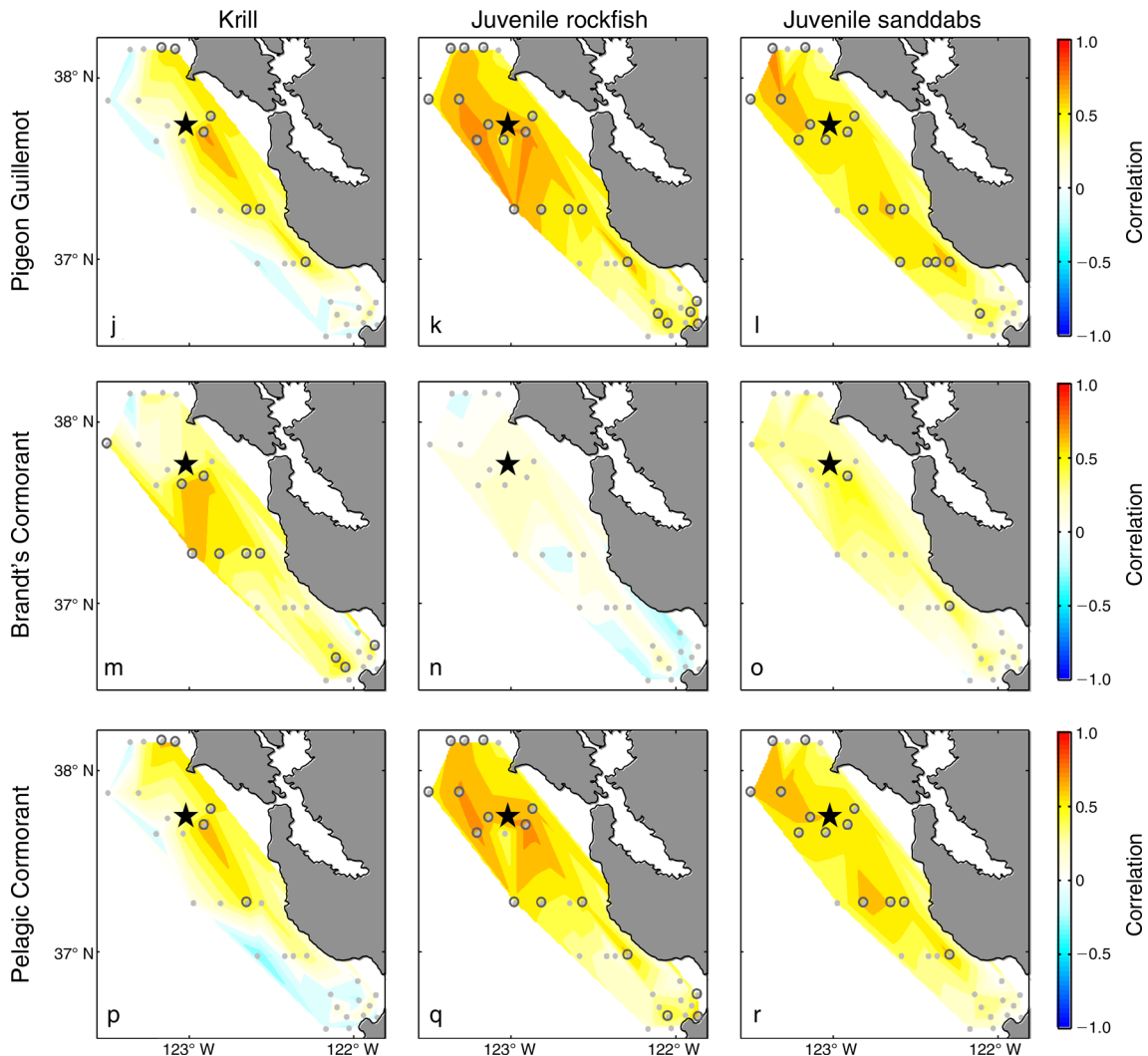


FIG. 6. Continued.

taxa (e.g., juvenile rockfish) may exhibit reduced availability, and are clearly a favored prey when juvenile rockfish are less available, and (4) demographic responses among seabirds to forage taxa are generally nonlinear and indicate the importance of multiple forage taxa, as well as their availability within shelf and oceanic regions to seabirds that exhibit complex prey-switching behavior.

Our results are important for at least three reasons: (1) from the population dynamics perspective, local prey spatial availability (where and how much) is a direct driver of seabird production and is critical to population viability (Anderson et al. 1980, Piatt et al. 2007, Ainley and Hyrenbach 2010, Lewison et al. 2012, Velarde et al. 2013); (2) predator-prey interactions within marine ecosystems are inherently patchy, so spatial assessments of trophic transfer will benefit food web modeling (Yodzis 1994, Winder et al. 2001, Hunsicker et al.

2011); and (3) establishing spatially explicit thresholds between seabird reproduction and important forage species provide reference points that could be useful in fisheries management and marine spatial planning (Yodzis 1994, Cury et al. 2011, Grantham et al. 2011). Moreover, given the high level of spatio-temporal variance and coherence observed in this study, we provide new insights on the spatial ecology of this region, which complements our previous larger-scale work on predator-prey hot spots and oceanographic determinants of micronekton assemblages in the central California Current (Santora et al. 2011b, 2012a, b). In short, we demonstrate that to be of benefit for central place foraging predators, the ecosystem approach to forage fish management should consider how environmental conditions drive subregional to habitat-specific variations in prey abundance and distribution. We discuss below how interannual hydrographic dynamics

TABLE 2. Results of generalized additive models between seabird breeding success and habitat-specific (shelf, oceanic) abundance of krill and forage fish.

Seabird	Krill		Rockfish		Sanddab		Anchovy
	Shelf <i>P</i> , <i>r</i> ² adj., % deviance	Oceanic <i>P</i> , <i>r</i> ² adj., % deviance	Shelf <i>P</i> , <i>r</i> ² adj., % deviance	Oceanic <i>P</i> , <i>r</i> ² adj., % deviance	Shelf <i>P</i> , <i>r</i> ² adj., % deviance	Oceanic <i>P</i> , <i>r</i> ² adj., % deviance	Shelf <i>P</i> , <i>r</i> ² adj., % deviance
Common Murre	< 0.001 , 0.79 , 82.00%	< 0.001 , 0.64 , 69.40%	0.09, 0.23, 29.90%	0.058, 0.21, 25.80%	0.003 , 0.59 , 65.90%	0.08, 0.21, 26.70%	0.15, 0.12, 16.80%
Cassin's Auklet	0.04 , 0.24 , 28.10%	0.26, 0.29, 53.40%	0.02 , 0.31 , 35.50%	0.01 , 0.47 , 54.90%	0.003 , 0.45 , 48.10%	0.01 , 0.35 , 39.20%	0.006 , 0.42 , 46.90%
Rhinoceros Auklet	0.01 , 0.63 , 76.90%	0.34, 0.26, 51.70%	0.28, 0.20, 38.60%	0.06, 0.25, 30.80%	0.21, 0.08, 13.80%	0.05 , 0.41 , 54.50%	0.43, 0.09, 23.80%
Pigeon Guillemot	0.002 , 0.47 , 49.60%	0.53, 0.02, 11.30%	0.002 , 0.46 , 49.10%	0.006 , 0.54 , 56.50%	0.03 , 0.51 , 66.10%	0.01 , 0.33 , 37.40%	0.14, 0.20, 29.90%
Brandt's Cormorant	0.07, 0.39, 54.30%	0.03 , 0.39 , 49.70%	0.72, 0.04, 2.20%	0.76, 0.04, 1.70%	0.23, 0.07, 13.00%	0.29, 0.05, 10.60%	0.59, 0.005, 7.03%
Pelagic Cormorant	0.005 , 0.41 , 44.80%	0.64, 0.02, 3.30%	0.01 , 0.50 , 61.70%	0.004 , 0.43 , 46%	0.01 , 0.35 , 38.80%	0.02 , 0.30 , 34.30%	0.12, 0.14, 19.20%

Notes: Values in boldface type indicate significant models; *r*² adj. is the adjusted *r*², and % deviance is the percentage of deviance explained for the model fit. See Fig. 7 and the Appendix for additional detail. Note that anchovy models were for shelf habitat only because of zero catches in oceanic areas; all relationships between anchovy and seabird reproduction yielded negative relationships (Appendix: Fig. A8).

influences the *preyscape*, which in turn shapes the demographic response of locally breeding seabirds.

Hydrographic control of the preyscape

Hydrodynamics underlie the distribution and abundance of marine organisms. Physical variables examined here characterized the ambient conditions when krill and forage fish were sampled. The spatio-temporal variability of these physical variables are proxies for upwelling (subsurface temperature, salinity, depth of the 26.1 isopycnal) or conditions that might affect the efficacy of upwelling (stratification). Our PC1 of ocean conditions clearly resolved the expected “warm/weak upwelling” and “cool/strong upwelling” states regularly observed in Eastern Boundary Current ecosystems (Chavez et al. 2003, Mackas et al. 2007, Cury et al. 2008). Basin-scale climate variability associated with the El Niño-Southern Oscillation (ENSO) cycle was evident in our study, with our PC1 Physics exhibiting maximum and minimum values during the 1992–1993 and 1997–1998 El Niño and 1998–1999, 2007–2008 La Niña events, respectively. The year 2005 also was characterized by high-temperature, low-salinity values, deep 26.1 isopycnal depths, but was not an official El Niño (Schwing et al. 2006, Sydeman et al. 2006). Weak upwelling at the start of the upwelling season in winter (January–February) and weak upwelling in May is considered a primary factor leading to poor productivity in the region in that year (Sydeman et al. 2006, Schroeder et al. 2013). Similarly, 2006 was a year of poor productivity (i.e., low krill, rockfish,

sanddab, and bird production; Fig. 4), but this year was not studied as intensively as 2005. In 2006, upwelling at the spring transition and into May appeared to be normal (Goericke et al. 2007), but other variables were not considered, including stratification. As we have indicated here (Fig. 2d), waters in the Gulf of the Farallones region were unusually highly stratified during May–June 2006. While we cannot determine if this was the cause or consequence of poor upwelling, it undoubtedly led to poor nutrient influx into the euphotic zone, which could have led to low production across trophic levels. However, stratification may not reflect an equilibrium response to local wind forcing, but it could be related to remote wind forcing integrated over some window of time (e.g., winter months) preceding the measurement period (Schroeder et al. 2013). To our knowledge, this study is one of the first to highlight high stratification within the GoF/MB during 2006 and its probable impacts on ecosystem productivity, including the relative abundance of krill and forage fish.

We demonstrated higher abundances of krill, juvenile rockfish, and sanddab during strong/cool upwelling years and higher anchovy abundance during warm/weak upwelling years. Furthermore, interannual fluctuations of the forage species were greater on the shelf compared to offshore. This onshore–offshore variability was particularly distinct for krill. The principal krill species in the region is *E. pacifica*, which dominates oceanic and shelf-slope waters, whereas the neritic *T. spinifera*

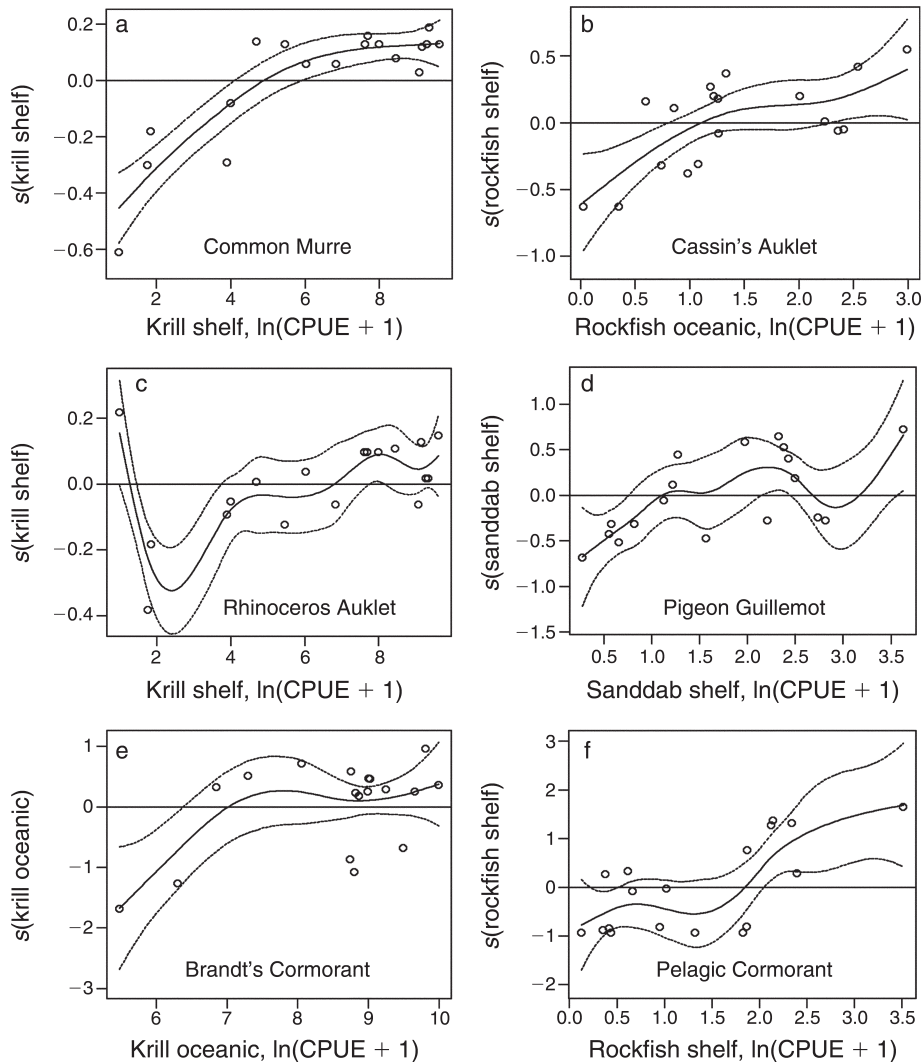


FIG. 7. Results of generalized additive models for assessing the numerical (production) response between seabird reproductive success and habitat-derived abundance of forage species, 1990–2007: (a) Common Murre, (b) Cassin's Auklet, (c) Rhinoceros Auklet, (d) Pigeon Guillemot, (e) Brandt's Cormorant, and (f) Pelagic Cormorant. Here the best model (highest r^2 and deviance explained) is selected for each seabird–prey species interaction (see Appendix: Table A1); all other relationships between seabird reproductive success and forage species are presented in the Appendix: Figs. A2–A8. Dashed lines indicate the 95% confidence limits. The parameter s is the smoothing function.

dominates on the shelf (Santora et al. 2012a). Our index of oceanic krill abundance (presumably *E. pacifica*) was relatively stable compared to shelf krill (likely *T. spinifera*), which fluctuated strongly relative to upwelling (Fig. 5). Unfortunately, krill were not identified to species until 2002, so we cannot examine habitat-based indices in detail.

Interannual variability of juvenile rockfish and sanddabs were significantly correlated and similarly represented across the study area, showing strong spatial coherence. Although the juvenile rockfish assemblage includes a large number of species, the most abundant species have strong numerical coherence over time (Field et al. 2010, Ralston et al. 2013). The pelagic juvenile

sanddab assemblage comprises two species, *Citharichthys sordidus* and *C. stigmaeus*, with the former at least an order of magnitude more abundant than the latter. The early life history stages of these two species exhibit subtle differences in their distribution patterns (Sakuma and Larson 1995), but the prolonged 200–250 day pelagic juvenile stage results in their widespread dispersal and availability to predators during years of peak abundance. The abundance of pelagic juvenile rockfish and sanddabs are significantly correlated with krill abundance in the shelf region, which should not be surprising given that they typically forage on krill and other zooplankton (Pearcy and Hancock 1978, Reilly et al. 1992). By contrast, the variable abundance of

northern anchovy, which are typically encountered at relatively lower levels during this season, are likely to be a greater reflection of their local availability in response to variable ocean conditions, as their distribution at the time of this survey is typically more strongly associated with the availability of potential spawning habitat throughout the California Current than it is associated with their coastwide abundance (Parrish et al. 1985, MacCall 1990).

Despite the temporal covariance demonstrated by krill–rockfish–sanddabs (hereafter KRS), we found the strongest coherence occurred between hydrographic conditions and krill. Although the Physics PC1 index is a good measure of regional processes (upwelling) and conditions, it may fail to capture important fine-scale physical features, such as hydrographic fronts that are important to these juvenile fish. Fronts provide an important mechanism for concentrating krill and other prey for these epipelagic forage fish, although the extent to which such aggregation is a direct result of advective processes or in response to concentrated prey abundance is unknown (Bakun 2010). For example, upwelling fronts have been used to successfully describe the distribution patterns of larval rockfish (Bjorkstedt et al. 2002) and juvenile stages of rockfish and other groundfish (Sakuma et al. 2013). The tendency for elevated catches of some species at frontal structures and potential for fronts to aggregate prey suggest that future studies should investigate the role of finer-scale physical processes in affecting the distribution and abundance of predators and prey, as has been done for seabirds elsewhere (e.g., Hunt et al. 1998).

Influence of the preyscape on seabird reproduction

Little is known about how the spatial availability of prey affects seabird breeding success, and this is particularly true for finer scales (e.g., 1–10 km). In their comprehensive study, Cury et al. (2011) developed threshold numerical response models for 14 seabird species within seven different ecosystems, finding remarkable coherence in their numerical production response curves. However, these authors used indices of prey abundance (CPUE or biomass) estimated over large spatial scales (e.g., the entire North Sea or Benguela Current) that were then related to seabird breeding success at specific colonies. In doing so, aspects of prey availability at smaller spatial scales that could be important determinants of breeding success may have been missed. The rationale for incorporating finer-scale spatial dynamics of prey in seabird demographic response models is also supported by optimal foraging theory. During the breeding season when seabirds are provisioning food for offspring, they forage to and from a central place (Orians and Pearson 1979, Burke and Montevercchi 2009), and are thus dependent on the prey availability within specific foraging ambits from the colonies. Foraging ambits vary between species, dependent on the flight capacities and foraging behavior of the

birds, a point that we return to later. To investigate the importance of prey in different spatial configurations, we used spatial correlation maps across all habitats to quantify and visualize the coherence between KRS and seabird breeding success (Fig. 6). One important caveat with this approach is that the spatial correlation maps are limited to the stations that were sampled. The station sampling was stratified rather than uniform, with clusters of stations located in the Gulf of the Farallones, and the others aligned in cross-shelf transects (Sakuma et al. 2006). To mitigate this problem to some extent, we calculated habitat-specific averages (e.g., shelf, oceanic) and related these values to seabird breeding success. We omitted Monterey Bay from this latter analysis because, with the exception of the Rhinoceros Auklet (Ford et al. 2004), the seabirds studied forage primarily between the 200-m depth contour and shore. As expected, the demographic responses we derived between seabird breeding success and prey abundance by region indicated spatially explicit nonlinear numerical response relationships, many showing the classic Type II curve (Cury et al. 2011). While some of the curves may have appeared more complex than an exponential rise to maximum, none of these models were supported to any greater substantial degree than log-linear relationships.

An item to consider is the role of anchovy in this study. In general, anchovy abundance was negatively associated (out of phase) with the KRS abundance. Nonetheless, anchovy is an important prey resource for breeding seabirds in the region (e.g., Ainley et al. 1981, Sydeman et al. 2001), especially when juvenile rockfish are unavailable (Ainley and Boekelheide 1990, Thayer and Sydeman 2007). Anchovy became the primary prey for seabirds (Sydeman et al. 2001) when juvenile rockfish abundance decreased throughout most of the 1990s to a low point in 2005–2006 (see Fig. 4 and Ralston et al. 2013). Furthermore, anchovy is preyed upon more frequently later in the seabird breeding season after rockfish settle to deeper habitats and become inaccessible (Ainley et al. 1996b). For Rhinoceros Auklets, Thayer and Sydeman (2007) showed that while rockfish abundance determined breeding success, anchovy abundance drove variability in chick growth. Brandt's Cormorant breeding success also increased over the 1990s and 2000s (Sydeman et al. 2009) until the anchovy population abruptly went into decline starting in 2008–2009 (Fig. 4). Despite the importance of anchovy to these seabirds, this study yielded only negative relationships between anchovy CPUE and seabird breeding success (Appendix: Table A1, Fig. A8). Undoubtedly, this is due to the fact that juvenile rockfish were the preferred prey during most years in this study, and because anchovy were abundant during weaker upwelling years when seabird reproduction is generally lower. This indicates that anchovy are likely a critical prey item for seabirds during suboptimal years when KRS are less available. Furthermore, anchovy may avoid strong, active upwelling areas off central California, but may



PLATE 1. Key components of the Central California pelagic ecosystem sampled by the Rockfish Recruitment and Ecosystem Assessment Survey Center. Clockwise from upper left corner: Pacific sea nettle (*Chrysaora fuscescens*), Rhinoceros Auklet (*Cerorhinca monocerata*) with juvenile northern anchovy (*Engraulis mordax*) in bill, krill (*Thysanoessa spinifera*), juvenile cowcod rockfish (*Sebastes levis*), longfin dragonfish (*Tactostoma macropus*), California market squid (*Doryteuthis opalescens*) with myctophid (*Myctophidae*), and juvenile Pacific sanddab (*Citharichthys sordidus*). Artwork by Sophie Webb (<http://sophiewebb.com/>).

enter these areas after upwelling relaxes (Parrish et al. 1985, MacCall 1990). If so, our relative abundance index of anchovy could be biased, as the RREAS was conducted during the main upwelling period off central-northern California (May–June). An important caveat is that the net employed and the timing of our survey may not provide a adequate relative abundance index of anchovy that relates to what seabirds are experiencing during this brief part of their breeding season. Further research is needed to understand how the occurrence of anchovy in this region is related to their production and as a distributional response to upwelling.

Regarding the individual forage taxa, there were a number of interesting results including substantial variability between seabird species, not only in their correlations with particular species of prey, but also in location of the strongest seabird–prey correlations (Fig. 6). First, it is clear that relationships between KRS and breeding success were not compelling for Rhinoceros Auklet and Brandt’s Cormorant, considering shelf-based averages in prey abundance (Table 2) or station-specific values (Fig. 6). Second, moderately compelling demographic response relationships were

found for Cassin’s Auklet and Pelagic Cormorant. Surprisingly, however, despite the importance of krill to Cassin’s Auklet (Ainley et al. 1996a, Abraham and Sydeman 2006, Sydeman et al. 2013) and the positive relationship indicated here, auklet breeding success was not well correlated with krill abundance on either habitat or station scales. This may have been due to averaging krill species abundance. Although Cassin’s Auklets consume and feed their young the two dominant krill species in the region, its breeding success is primarily related to the abundance of *T. spinifera* (Ainley et al. 1996a, Abraham and Sydeman 2006, Sydeman et al. 2013). The krill abundance index used here represents all euphausiid species of the region and comprises *Nyctiphanes simplex* and *Nematocelis difficilis* as well as *T. spinifera* and *E. pacifica*. Inclusion of these other species may have masked the influence attributable to *T. spinifera* that drives variation in auklet breeding success. Unfortunately, krill were not identified and enumerated at the species level until 2002. Cassin’s Auklets also forage on juvenile rockfish and sanddab (Ainley et al. 1996a), particularly during the month of May. Therefore, it is not surprising that the auklet’s breeding success was well correlated, at

both the habitat and station-specific levels, with the abundance of these forage taxa (assuming that the juvenile abundance is representative of the larval abundance consumed by the auklets). Abraham and Sydeman (2006) described prey switching in the auklet population and demonstrated a shift from use of *E. pacifica* early in the breeding season to consumption of *T. spinifera* later in the offspring rearing period. This switch occurs in May, and coincides with the period when they begin to forage more on larval rockfish and sanddab (Ainley et al. 1996a); this mid-late May switch also corresponds to the timing of the surveys. Therefore, we consider the relationships between auklets' breeding success and juvenile rockfish and sanddab to be important and substantiated by diet and prey-switching behavior. This is the first paper to relate auklet breeding success to juvenile rockfish and sanddab in the region.

Pelagic Cormorant is piscivorous, known to consume juvenile rockfish and sanddab (Ainley et al. 1981), so it is not surprising that its breeding success related well to the abundance of these prey species. However, these cormorants, unlike the widely ranging Brandt's, are neritic, rarely foraging farther than ~10 km from the colony (Ford et al. 2004). Habitat and station-specific data reveal strong correlations throughout the entire region, although the strongest correlations were clearly found for rockfish in the Gulf of the Farallones closest to the colony. However, across prey species, shelf-based relationships were strongest, supporting this species' limited foraging ambit and behavior.

Finally, particularly compelling demographic responses were revealed for Common Murre and Pigeon Guillemot. The murre is wide ranging and omnivorous, feeding on krill, rockfish, sanddabs, and anchovy, whereas the guillemot, like the Pelagic Cormorant, has a limited foraging ambit and is known to feed on rockfish and sanddabs (Ainley et al. 1996b, Sydeman et al. 1997, 2001, Robinette et al. 2007). When KRS are not available, murre switch to anchovies or other forage species if available, while Pigeon Guillemots shift to benthic species such as sculpins. The murre demographic response was strongest for krill and sanddabs in the northern half of the study area. Similarly, station data indicated the strongest correlation with Pigeon Guillemot breeding success in the north, but with rockfish and sanddabs rather than krill as the drivers.

Collectively, our results indicate that KRS are key to the breeding success of the Gulf of the Farallones seabirds. As seabirds in the central-northern California Current region exhibit broad diet breadths and complex prey switching behaviors based on prey availability (Ainley et al. 1996a, b, Abraham and Sydeman 2006, Thayer and Sydeman 2007), this conclusion is not surprising, and highlights the need for multispecies demographic response modeling. Indeed, aside from the special case of wasp-waist ecosystems with one or few species in the forage fish community (Cury et al. 2000), it

is unlikely that single forage species are critically important to seabird breeding success in most systems (van Baalen et al. 2001). Notably, the importance of sanddabs has not been previously appreciated in this region (but see Robinette et al. 2007). However, results generally indicate that prey availability in the shelf region of the entire study area is of importance to the birds. There were clearly stronger correlations and demographic response relationships from stations in the northern sector (i.e., closer to the principal breeding colony). Nonetheless, based on this fixed-station array, we cannot delineate essential foraging areas that promote seabird breeding success. Moreover, when KRS are not abundant, seabirds switch to other prey that may be distributed differently. Therefore, to protect the forage fish vital for seabird breeding success in the Gulf of the Farallones, the best options will likely relate to the implementation of protective zones based on the foraging ambits of the birds. Had the sampling design been uniform or random, it might have been possible to more appropriately contour the area to provide smaller-scale conservation units.

Implications for ecosystem-based fisheries management

In recognition of the integral role of krill in the marine food web, commercial krill fishing is currently banned in U.S. waters.⁶ There are also no fisheries for juvenile rockfish and juvenile sanddabs, although fisheries for adults of these fishes may have an effect on juvenile abundance by virtue of reduction of adult spawning potential (Field et al. 2010). Anchovy fisheries, while generally small (i.e., <15 000 metric tons harvested/year for the entire State of California), are localized (PFMC 2013); in theory, this could impact central-place foraging predators in areas where both the fisheries and foraging by predators overlap. Importantly, understanding the spatio-temporal dynamics of forage taxa and seabirds provides a valuable baseline that may be extended to commercially exploited and endangered species of the region (e.g., Chinook salmon *Oncorhynchus tshawytscha*; blue whale; *Balaenoptera musculus*). As demonstrated by Wells et al. (2012) and Sydeman et al. (2013), variability in the abundance and distribution of krill and forage fish when salmon smolts are migrating into the coastal ocean can have great effects on salmon abundance and subsequent catches in future years when they enter the fishery. Additional research steps to improve protection and conservation of central-place foraging seabirds are needed and may include multispecies demographic response modeling, tracking seabirds during chick provisioning, random spatial sampling of prey species, and understanding the spatial organization of multispecies prey patches. Our results indicate that temporal variance in this system is

⁶ www.pcouncil.org

substantial, and future syntheses and monitoring will benefit from long-term sampling of multiple trophic levels. A challenge for marine spatial management of forage taxa and top predators includes integrating spatial occurrence of forage hot spots (Santora et al. 2011*b*, 2012*a, b*) along with the temporal dynamics of predator–prey numerical responses within ecologically important areas. These next steps would provide much needed information for spatially explicit ecosystem-based management (Grantham et al. 2011) and help gain a mechanistic understanding between physics and prey with linkages through primary and secondary production.

Empirical relationships between forage abundance and seabird demography (Anderson et al. 1980) have also been influential in the development of management strategies for forage species in the California Current, by providing the basis for a biomass threshold for species such as northern anchovy and Pacific sardine, below which harvest rates are forced to approach zero (PFMC 2013). However, spatial management of fisheries removals may also be necessary to ensure that foraging grounds utilized by central-place predators are not disturbed. As DeMaster et al. (2001) discuss, the future of marine resource management is likely to be one in which competitive interactions between fisheries and predators are considerably more common than they are currently, with localized depletion and spatial considerations of foraging ranges providing a unique set of challenges to marine resource managers with respect to how fisheries and conservation needs are balanced. Clearly, the human demand and influence on coastal marine resources will continue to rise in the future. Regional linkages among ocean physics, forage taxa, and demographic responses of seabirds presented in this study represent an important step in melding marine spatial ecology with temporal dynamics, and may be used to guide protection and conservation of coastal marine ecosystems in the California Current and elsewhere in the world.

ACKNOWLEDGMENTS

We thank the members of the Rockfish Recruitment and Ecosystem Assessment Survey team. We appreciate the feedback and discussion from Valerie J. Loeb, Nate Mantua, Keith Sakuma, and Stephen Ralston. We are grateful for the feedback and comments provided by two anonymous reviewers, which greatly improved this paper. Partial funding for this synthesis was provided by NOAA's Integrated Ecosystem Assessment (IEA) program. Seabird breeding success on the Farallon Islands was monitored by Point Blue Conservation Science, with financial support from the U.S. Fish and Wildlife Service and others.

LITERATURE CITED

- Abraham, C. L., and W. J. Sydeman. 2004. Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychoramphus aleuticus*. *Marine Ecology Progress Series* 274:235–250.
- Abraham, C. L., and W. J. Sydeman. 2006. Prey-switching by Cassin's auklet *Ptychoramphus aleuticus* reveals seasonal climate-related cycles of *Euphausia pacifica* and *Thysanoessa spinifera*. *Marine Ecology Progress Series* 313:271–283.
- Abrams, P. A. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31:79–105.
- Ainley, D. G., D. W. Anderson, and P. R. Kelly. 1981. Feeding ecology of marine cormorants in southwestern North America. *Condor* 83:120–131.
- Ainley, D. G., and R. J. Boekelheide. 1990. Seabirds of the Farallon Islands: structure and dynamics of an upwelling system community. Stanford University Press, Stanford, California, USA.
- Ainley, D. G., and K. D. Hyrenbach. 2010. Top-down and bottom-up factors affecting seabird population trends in the California Current System (1985–2006). *Progress in Oceanography* 84:242–254.
- Ainley, D. G., L. B. Spear, and S. G. Allen. 1996*a*. Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. *Marine Ecology Progress Series* 137:1–10.
- Ainley, D. G., L. B. Spear, S. G. Allen, and C. A. Ribic. 1996*b*. Temporal and spatial patterns in the diet of common murre in California waters. *Condor* 98:691–705.
- Ainley, D. G., W. J. Sydeman, and J. Norton. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. *Marine Ecology Progress Series* 118:69–79.
- Anderson, D. W., F. Gress, K. F. Mais, and R. R. Kelly. 1980. Brown pelicans as anchovy stock indicators and their relationships to commercial fishing. California Cooperative Oceanic Fisheries Investigations Reports 21:54–61.
- Bakun, A. 2010. Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: conceptual templates and schematic constructs. *Journal of Marine Systems* 79:361–373.
- Bjorkstedt, E., et al. 2010. State of the California Current 2009–2010: Regional variation persists through transition from La Niña to El Niño (and back?). California Cooperative Oceanic Fisheries Investigations Reports 51:39–69.
- Bjorkstedt, E. P., L. K. Rosenfeld, B. A. Grantham, Y. Shkedy, and J. Roughgarden. 2002. Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. *Marine Ecology Progress Series* 242:215–228.
- Burke, C. M., and W. A. Montevocchi. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology* 278:354–361.
- Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5:261–271.
- Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and C. M. Niguen. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299:217–221.
- Checkley, D. M., and J. A. Barth. 2009. Patterns and processes in the California Current System. *Progress in Oceanography* 83:49–64.
- Chelton, D. B. 1982. Large-scale response of the California Current to forcing by the wind stress curl. *CalCOFI Reports* 23:130–148.
- Collins, C. A., J. T. Pennington, C. G. Castro, T. A. Rago, and F. P. Chavez. 2003. The California Current system off Monterey, California: physical and biological coupling. *Deep-Sea Research II* 50:2389–2404.
- Cury, P., A. Bakun, R. J. M. Crawford, A. Jarre, R. A. Quñones, L. J. Shannon, and H. M. Verheye. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science* 57:603–618.
- Cury, P., et al. 2011. Global seabird response to forage fish depletion—one-third for the birds. *Science* 334:1703–1706.
- Cury, P., Y.-J. Shin, B. Planaque, J. M. Durant, J. Fromentin, S. Kramer-Schadt, N. C. Stenseth, M. Travers, and V.

- Grimm. 2008. Ecosystem oceanography for global change in fisheries. *Trends in Ecology and Evolution* 23:338–346.
- DeMaster, D. P., C. W. Fowler, S. L. Perry, and M. F. Richlen. 2001. Predation and competition: the impact of fisheries on marine-mammal populations over the next one hundred years. *Journal of Mammalogy* 82:641–651.
- Edwards, M., G. Beaugrand, G. C. Hays, J. A. Koslow, and A. J. Richardson. 2010. Multi-decadal oceanic ecological datasets and their application in marine policy and management. *Trends in Ecology and Evolution* 25:602–610.
- Fauchald, P., K. E. Erikstad, and H. Skarsfjord. 2000. Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* 81:773–783.
- Field, J. C., A. D. MacCall, R. W. Bradley, and W. J. Sydeman. 2010. Estimating the impacts of fishing on dependent predators: a case study in the California Current. *Ecological Applications* 20:2223–2236.
- Ford, R. G., D. G. Ainley, J. L. Casey, C. A. Keiper, L. B. Spear, and L. T. Balance. 2004. The biogeographic patterns of seabirds in the central portion of the California Current. *Marine Ornithology* 32:77–96.
- Furness, R. W., and M. L. Tasker. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* 202:253–264.
- Goericke, R., et al. 2007. The state of the California Current, 2006–09: Regional and local process dominate. *California Cooperative Oceanic Fisheries Investigations Reports* 48:33–66.
- Grantham, H. S., et al. 2011. Accommodating dynamic oceanographic processes and pelagic biodiversity in marine conservation planning. *PLoS One* 6(2):e16552
- Haury, L., J. McGowan, and P. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions. Pages 277–327 in J. Steele, editor. *Spatial pattern in plankton communities*. Plenum Press, New York, New York, USA.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.
- Hunsicker, M. E., et al. 2011. Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecology Letters* 14:1288–1299.
- Hunt, G. L., R. W. Russell, K. O. Coyle, and T. Weingartner. 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series* 167:241–259.
- Hunt, G. L., P. J. Stabeno, S. Strom, and J. M. Napp. 2008. Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. *Deep-Sea Research II* 55:1919–1944.
- Lewison, R., et al. 2012. Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research* 17:93–2012.
- Link, J. S. 2010. *Ecosystem-based fisheries management*. Cambridge University Press, Cambridge, UK.
- MacCall, A. D. 1990. *Dynamic geography of marine fish populations*. University of Washington Press, Seattle, Washington, USA.
- Mackas, D. L., S. Batten, and M. Trudel. 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. *Progress in Oceanography* 75:223–252.
- Mills, K. L., T. Laidig, S. Ralston, and W. J. Sydeman. 2007. Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current System. *Fisheries Oceanography* 16:273–283.
- Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155–177 in D. J. Horn, G. R. Stairs, and R. Mitchell, editors. *Analysis of ecological systems*. Ohio State University Press, Columbus, Ohio, USA.
- Pacific Fishery Management Council (PFMC). 2013. *Pacific Coast Fishery Ecosystem Plan for the U.S. Portion of the California Current Large Marine Ecosystem*. <http://www.pfmcouncil.org/ecosystem-based-management/fep/>
- Parrish, R. H., D. L. Mallicoate, and K. F. Mais. 1985. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. *Fishery Bulletin* 83:483–496.
- Pearcy, W. G., and D. Hancock. 1978. Feeding habits of dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; and Pacific sanddab, *Citharichthys sordidus*, in a region of diverse sediments and bathymetry off Oregon. *Fishery Bulletin* 76:641–651.
- Peterson, W. T., and F. B. Schwing. 2003. A new climate regime in northeast pacific ecosystems. *Geophysical Research Letters* 30. <http://dx.doi.org/10.29/2003/GL017528>
- Piatt, J. F., A. M. A. Harding, M. Shultz, S. G. Speckman, T. I. van Pelt, G. S. Drew, and A. B. Kettle. 2007. Seabirds as an indicator of marine food supplies: Cairns revisited. *Marine Ecology Progress Series* 352:221–234.
- R Development Core Team. 2014. R: A language and environment for statistical computing (mgcv package version 1.7-29). R Foundation for Statistical Computing, Vienna, Austria.
- Ralston, S., and D. F. Howard. 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. *Fisheries Bulletin* 93:710–720.
- Ralston, S., K. M. Sakuma, and J. C. Field. 2013. Interannual variation in pelagic juvenile rockfish (*Sebastes* spp.) abundance—going with the flow. *Fisheries Oceanography* 22:288–308.
- Reilly, C. A., T. Wiley-Echeverria, and S. Ralston. 1992. Interannual variation and overlap in the diets of pelagic juvenile rockfishes (genus *Sebastes*) off central California. *Fisheries Bulletin* 90:505–515.
- Robinette, D. P., J. Howar, W. J. Sydeman, and N. Nur. 2007. Spatial patterns of recruitment in a demersal fish as revealed by seabird diet. *Marine Ecology Progress Series* 352:259–268.
- Sakuma, K. M., E. P. Bjorkstedt, and S. Ralston. 2013. Distribution of pelagic juvenile rockfish (*Sebastes* spp.) in relation to temperate fronts off central California. *California Cooperative Oceanic Fisheries Investigations Reports* 54:167–179.
- Sakuma, K. M., and R. J. Larson. 1995. Distribution of pelagic metamorphic-stage sanddabs *Citharichthys sordidus* and *Citharichthys stigmaeus* within areas of upwelling off Central California. *Fishery Bulletin* 93:516–529.
- Sakuma, K. M., S. Ralston, and V. G. Weststad. 2006. Interannual and spatial variation in the distribution of young-of-the-year rockfish (*Sebastes* spp.): expanding and coordinating a survey sampling frame. *California Cooperative Oceanic Fisheries Investigations Reports* 47:127–139.
- Santora, J. A., J. C. Field, I. D. Schroeder, K. A. Sakuma, B. K. Wells, and W. J. Sydeman. 2012a. Spatial ecology of krill, micronekton and top predators in the central California Current: implications for defining ecologically important areas. *Progress in Oceanography* 106:154–174.
- Santora, J. A., S. Ralston, and W. J. Sydeman. 2011a. Spatial organization of krill and seabirds in the central California Current. *ICES Journal of Marine Science* 68:1391–1402.
- Santora, J. A., W. J. Sydeman, I. D. Schroeder, C. S. Reiss, B. K. Wells, J. C. Field, A. M. Cossio, and V. J. Loeb. 2012b. Krill space: a comparative assessment of mesoscale structure in polar and temperate marine ecosystems. *ICES Journal of Marine Science* 69:1317–1327.
- Santora, J. A., W. J. Sydeman, I. D. Schroeder, B. K. Wells, and J. C. Field. 2011b. Mesoscale structure and oceanographic determinants of krill hotspots in the California Current: implications for trophic transfer and conservation. *Progress in Oceanography* 91:397–409.

- Schroeder, I. D., B. A. Black, W. J. Sydeman, S. J. Bograd, E. L. Hazen, J. A. Santora, and B. K. Wells. 2013. The North Pacific High and wintertime pre-conditioning of California Current productivity. *Geophysical Research Letters* 40. <http://dx.doi.org/10.1002/grl.50100>
- Schroeder, I. D., W. J. Sydeman, N. Sarkar, S. A. Thompson, S. J. Bograd, and F. B. Schwing. 2009. Winter pre-conditioning of seabird phenology in the California Current. *Marine Ecology Progress Series* 393:211–223.
- Schwing, F. B., N. A. Bond, S. J. Bograd, T. Mitchell, M. A. Alexander, and N. Mantua. 2006. Delayed coastal upwelling along the U.S. West Coast in 2005: a historical perspective. *Geophysical Research Letters* 33:L22S01.
- Smith, A. D. M., et al. 2011. Impacts of fishing low-trophic level species on marine ecosystems. *Science* 333:1147–1150.
- Steger, J. M., F. B. Schwing, C. A. Collins, L. K. Rosenfeld, N. Garfield, and E. Gezgin. 2000. The circulation and water masses in the Gulf of the Farallones. *Deep-Sea Research II* 47:907–946.
- Sydeman, W. J., R. W. Bradley, P. Warzybok, C. L. Abraham, J. Janhcke, K. D. Hyrenbach, V. Kousky, J. M. Hipfner, and M. D. Ohman. 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: unusual atmospheric blocking? *Geophysical Research Letters* 33:L22S09.
- Sydeman, W. J., M. M. Hester, J. A. Thayer, F. Gress, P. Martin, and J. Buffa. 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current System. *Progress in Oceanography* 49:309–329.
- Sydeman, W. J., K. A. Hobson, P. Pyle, and E. B. McLaren. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. *Condor* 99:327–336.
- Sydeman, W. J., K. L. Mills, J. A. Santora, S. A. Thompson, D. F. Bertram, K. H. Morgan, M. A. Hipfner, B. K. Wells, and S. G. Wolf. 2009. Seabirds and climate in the California Current—a synthesis of change. *CalCOFI Reports* 50:82–104.
- Sydeman, W. J., J. A. Santora, S. A. Thompson, B. Marinovic, and E. Di Lorenzo. 2013. Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. *Global Change Biology* 19:1662–1675.
- Sydeman, W. J., S. A. Thompson, M. Garcia-Reyes, M. Kahru, W. T. Peterson, and J. L. Largier. 2014. Multivariate ocean-climate indicators (MOCI) for the central California Current: environmental change, 1990–2010. *Progress in Oceanography*. <http://dx.doi.org/10.1016/j.poccean.2013.10.017>.
- Talley, L. D., G. L. Pickard, W. J. Emery, and J. H. Swift. 2011. *Descriptive physical oceanography, an introduction*. Sixth edition. Academic Press, Oxford, UK.
- Thayer, J. A., and W. J. Sydeman. 2007. Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. *Marine Ecology Progress Series* 329:253–265.
- van Baalen, M., V. Krivan, P. C. J. van Rijn, and M. W. Sabelis. 2001. Alternative food, switching predators, and the persistence of predator-prey systems. *American Naturalist* 157:512–524.
- Velarde, E., E. Ezcurra, and D. W. Anderson. 2013. Seabird diets provide early warning of sardine fishery declines in the Gulf of California. *Scientific Reports*. <http://dx.doi.org/10.1038/srep01332>
- Wells, B. K., J. A. Santora, J. C. Field, R. B. MacFarlane, B. B. Marinovic, and W. J. Sydeman. 2012. Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. *Marine Ecology Progress Series* 457:125–137.
- Winder, L., C. J. Alexander, J. M. Holland, C. Wooley, and J. N. Perry. 2001. Modeling the dynamic spatio-temporal response of predators to transient prey patches in the field. *Ecology Letters* 4:568–576.
- Wood, S. N. 2006. *Generalized additive models: an introduction with R*. Taylor and Francis Group, Boca Raton, Florida.
- Yodzis, P. 1994. Predator–prey theory and management of multispecies fisheries. *Ecological Applications* 4:51–58.

SUPPLEMENTAL MATERIAL

Appendix

A table showing correlation coefficients among krill and forage fish within shelf, oceanic, and Monterey Bay regions, a correlation matrix showing detailed relationships–covariance among regional physical variables, and figures showing results of generalized additive models for assessing relationship between seabird reproductive success and regionalized abundance of forage species, 1990–2007 (*Ecological Archives* A024-203-A1).