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Climate–ecosystem change off southern California: Time-dependent seabird predator–prey numerical responses

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ABSTRACT

Climate change may increase both stratification and upwelling in marine ecosystems, but these processes may affect productivity in opposing or complementary ways. For the Southern California region of the California Current Ecosystem (CCE), we hypothesized that changes in stratification and upwelling have affected marine bird populations indirectly through changes in prey availability. To test this hypothesis, we derived trends and associations between stratification and upwelling, the relative abundance of potential prey including krill and forage fish, and seabirds based on the long-term, multi-disciplinary CalCOFI/CCE-LTER program. Over the period 1987 through 2011, spring and summer seabird density (all species combined) declined by ~2% per year, mostly in the northern sector of the study region. Krill showed variable trends with two species increasing and one deceasing, resulting in community reorganization. Nearshore forage fish, dominated by northern anchovy (*Engraulis mordax*) as well as offshore mesopelagic species, show declines in relative abundance over this period. The unidirectional decline in springtime seabird density is largely explained by declining nearshore fish abundance in the previous season (winter). Interannual variability in seabird density, especially in the 2000s, is explained by variability in krill abundance. Changes in the numerical responses of seabirds to prey abundance correspond to a putative ecosystem shift in 1998–1999 and support aspects of optimal foraging (diet) theory. Predator–prey interactions and numerical responses clearly explain aspects of the upper trophic level patterns of change in the pelagic ecosystem off southern California.

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1. Introduction

Ocean warming accompanied by increasing density stratification is projected by coupled atmosphere–ocean global climate models (Solomon et al., 2007). Generally, large-scale empirical observations support model predictions (Belkin, 2009; Levitus et al., 2009), but substantial spatial variability may be observed at smaller (e.g., regional) scales (Burrows et al., 2011). Eastern boundary current ecosystems, where upwelling-favorable winds may be enhanced by global warming (Bakun, 1990), provide an exception; in these regions upwelling intensification may lead to ocean cooling. While the global warming-upwelling intensification hypothesis remains equivocal, in some regions of the world observations of upwelling-favorable wind intensification are compelling (Narayan et al., 2010; García-Reyes and Largier, 2010).

Ecosystem responses to simultaneous changes in temperature/stratification and upwelling are difficult to predict. Upwelling

intensification could increase isopycnal shoaling and nutrient input leading to enhanced productivity, but excessive upwelling could also increase fish mortality via excessive turbulence or advection (Cury and Roy, 1989). Increased stratification could impede the efficacy of upwelling, thereby diminishing nutrient input and primary productivity (Roemmich and McGowan, 1995; Sarmiento et al., 2004), though in some upwelling regions stratification has been positively related to nitrate concentrations and proxies of phytoplankton biomass (Aksnes and Ohman, 2009, Kahru et al., 2012); these observations also have been supported by recent models (Rykaczewski and Dunne, 2010). To date, a few model experiments have addressed the ecosystem consequences of increasing stratification and upwelling (Auad et al., 2006; Di Lorenzo et al., 2005), but this interaction has yet to be adequately investigated using observations.

The California Current Ecosystem (CCE) is an eastern boundary current system where upwelling and stratification have been studied for decades and related to multiple trophic levels including phytoplankton (Aksnes and Ohman, 2009; Chavez and Messié, 2009; Venrick, 2012), zooplankton (Hooff and Peterson, 2006; Lavaniegos and Ohman, 2007), forage fish (Brodeur et al., 2006;
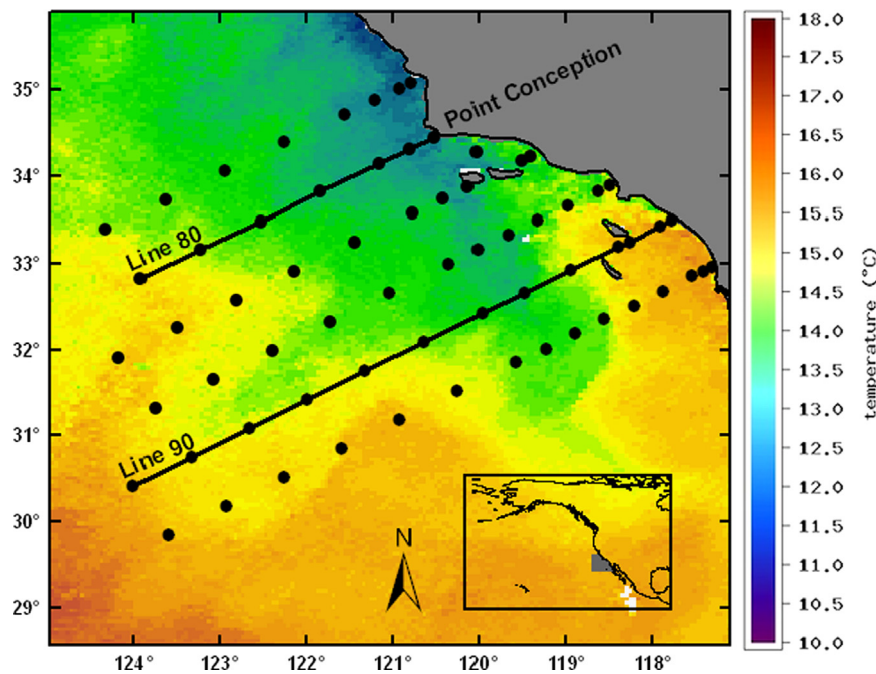
Fig. 1. Map showing CalCOFI/CCE-LTER grid overlaid on AVHRR SST image from 30 May 2000.

MacCall, 2009), and upper trophic level fish, seabirds, and marine mammals (Black et al., 2011; García-Reyes et al., 2013; Sydeman and Allen, 1999; Thompson et al., 2012). It is well known that upwelling in the CCE is spatially heterogeneous with major regional variation (Checkley and Barth, 2009; Bjorkstedt et al., 2011). One of the largest upwelling cells in the CCE is located off Point Conception, California, a large coastal promontory near the northern boundary of the Southern California Bight (SCB) region (Fig. 1). Cold, newly-upwelled waters deflected off Point Conception under northwesterly wind forcing spread southward in the vicinity of the Channel Islands, but typically remain well to the north of the California–Mexico border. Stratification in this region has increased over time (Roemmich and McGowan, 1995; Lavaniegos and Ohman, 2007; Aksnes and Ohman, 2009; see also Palacios et al., 2004 for the central California region), but it is unclear whether the pattern of change is best explained by trends in ocean warming or inter-decadal variability related to variation in the Pacific Decadal Oscillation and North Pacific Gyre Oscillation (Bograd and Lynn, 2003). Decadal-scale variability can be a dominant signal in the region (Di Lorenzo and Ohman, 2013). Because the SCB is characterized by spatial heterogeneity in water mass structure and a north–south ecotone where cold, upwelled waters meet warm and strongly stratified sub-tropical waters from the south (Hayward and Venrick, 1998), this region provides an unparalleled opportunity to study and resolve climate-related stratification and upwelling-ecosystem dynamics across physical and ecological boundaries where changes in pelagic ecosystems may be most apparent.

The California Cooperative Oceanic Fisheries Investigations (CalCOFI), supplemented recently by the California Current Ecosystem Long-Term Ecological Research (CCE-LTER) program, has been studying the pelagic ecosystem of the SCB since 1949, resulting in one of the longest-running multi-disciplinary, multi-trophic level studies in the world. Approximately 65 years of information (1949 through present) is available on physical oceanographic processes, hydrographic conditions, and plankton communities (Peña and Bograd, 2007). Studies of seabird communities were initiated in 1987 and now provide a 25-year time series for these taxa (Hyrenbach and Veit, 2003; Veit et al., 1996,

1997). Hyrenbach and Veit demonstrated that declines in various seabird populations, indexed by density at sea, were related to ocean warming, but these authors did not examine seabird numerical responses to variation in potential prey populations. More recently, Lavaniegos and Ohman (2007) showed that stratification negatively impacted zooplankton, specifically pelagic tunicates, in this region. Hsieh et al. (2009) showed negative relationships between an index of stratification and the abundance of larval mesopelagic fish in the region. Subsequently, Koslow et al. (2011, 2013) confirmed the decline in mesopelagic fish, which they attributed to shoaling of the oxygen minimum zone, and also demonstrated declines in many nearshore pelagic schooling species, including northern anchovy (*Engraulis mordax*). In this study, we hypothesize that changes in stratification and upwelling affect seabirds indirectly through intermediate trophic levels represented by zooplankton, specifically krill, and forage fish. To test this hypothesis, we derived trends and associations between upwelling, stratification, potential prey populations, and seabird density using the CalCOFI/CCE-LTER data set. Our specific questions are: (1) What are the temporal trends in seabird, krill, and forage fish populations? (2) Are trends and interannual variability in krill and forage fish related to changes in seabirds? (3) Are changes in seabirds and prey related to changes in stratification, upwelling, and the interaction between these variables? (4) Are changes in seabird abundance best explained by monotonic or cyclical changes in prey and/or physical properties? This study is important as understanding predator–prey relationships is key to the ecosystem-approach to fisheries management (Cury et al., 2011; Hunsicker et al., 2011; Smith et al., 2011).

2. Methods

The study region is located in the southern sector of the CCE. Six transect lines extending as far as 700 km offshore have been regularly sampled during the CalCOFI program, resulting in data that can be used to resolve spatial and temporal changes in the distribution and abundance of pelagic organisms and the environment simultaneously. Along these transects, permanent hydrographic and

plankton sampling stations are located at regular intervals ($\sim$74 km apart in the offshore domain, and $\sim$37 km or less in the nearshore domain). Details of sampling coverage by cruise are available from www.calcofi.org/catlist/232-coverage.html. At each station, ocean properties such as temperature and salinity are measured and the plankton community is sampled. The plankton samples contain both zooplankton and ichthyoplankton (fish larvae), which can be used as indicators of the abundance of the older age classes of fish eaten by seabirds, mammals, and large predatory fish (Koslow et al., 2011, 2013). As have others (Bograd and Lynn, 2003; Hyrenbach and Veit, 2003), we selected data from transect line 90 (Fig. 1; off Dana Point; 30.42°N, 124.0°W–33.48°N, 117.77°W) and line 80 (off Point Conception; 34.47°N, 120.49°W–32.82°N, 123.91°W) to represent the southern (sub-tropical) and northern (temperate) sectors of the study region. We selected these transects as they are located in the middle of these domains (Fig. 1). Time series of hydrographic data were derived from conductivity–temperature–depth (CTD) samples on these lines. Population data for seabirds, krill, and forage fish were derived from the study grid as a whole (seabirds) or significant portions of the entire grid (see Koslow et al., 2011, 2013 for forage fish; Lavaniegos and Ohman, 2007 for krill). We analyzed only the years 1987–2011 for consistency across all variables.

2.1. Physical data

Temperature and salinity were measured from the surface to 500 m or $\sim$10 m above the sea floor at stations where water depth was < 500 m. We calculated density stratification as the density difference between 100 m and 10 m (see also Bograd and Lynn, 2003) for winter (January–February) and spring (March–May). These months reflect CalCOFI sampling periods, and therefore differ somewhat from the upwelling calculations. For upwelling, we used the Bakun Upwelling Index (UI; m^3/s/100 m coastline), calculated by NOAA's Environmental Research Division. Data were downloaded from ftp://orpheus.pfeg.noaa.gov/outgoing/upwell/monthly/upindex.mon (accessed 1 May 2012). Monthly values for upwelling at 33°N, 119°W (Point Conception) were used in this study. We calculated seasonal averages in the UI (winter: December–February, spring: March–May) for each year.

2.2. Zooplankton and fish

Field methods and data summarization for zooplankton (including krill) are detailed by Lavaniegos and Ohman (2007) and Brinton and Townsend (2003). Abundance data (number $m^{-2}+1$) for all post-metanaupliar stages of three krill species (Euphausia pacifica, Thysanoessa spinifera, and Nyctiphanes simplex) were log$_{10}$ transformed for analysis.

Field methods and data summarization for larval fish abundance (number m^{-2}) are described by Hsieh et al. (2005, 2009) and Koslow et al. (2011, 2013). We used abundance of 11 species-groups, including anchovy, flatfish (Citharichthyes spp.), mesopelagic fish, jack mackerel (Trachurus symmetricus), rockfish (Sebastes spp.), and croakers (Family Sciaenidae). Fish species and groups

Table 1
Trends in stratification, upwelling, krill and larval forage fish abundance stratified by season, 1987-2011. See text for analytical details. Bold text indicates significant change for that season at $p < 0.05$.

	Season	n	F	Nominal p-value	r²	Coefficient sign	Monte Carlo significance
Physical variables							
Density stratification line 80	Winter	24	3.84	0.063	0.15	+	0.063
	Spring	25	0.02	0.888	0.00	+	0.887
Density stratification line 90	**Winter**	**24**	**10.27**	**0.004**	**0.32**	+	**0.005**
	Spring	25	0.40	0.534	0.02	+	0.532
Upwelling index 33°N	**Winter**	**25**	**5.48**	**0.028**	**0.19**	+	**0.027**
	Spring	25	0.07	0.790	0.00	+	0.788
Zooplankton							
Krill (sum spp.)	Spring	25	0.07	0.788	0.00	+	0.788
E. pacifica	Spring	25	4.11	0.055	0.15	+	0.055
T. spinifera	**Spring**	**25**	**27.03**	**< 0.001**	**0.54**	+	**< 0.001**
N. simplex	**Spring**	**25**	**48.94**	**< 0.001**	**0.68**	–	**< 0.001**
Fish							
Hake	**Winter**	**23**	**18.96**	**< 0.001**	**0.47**	–	**< 0.001**
	Spring	25	0.88	0.359	0.04	–	0.355
Sardine	**Winter**	**23**	**4.50**	**0.046**	**0.18**	–	**0.046**
	Spring	**25**	**6.85**	**0.015**	**0.23**	+	**0.015**
Nearshore fish	**Winter**	**23**	**32.70**	**< 0.001**	**0.61**	–	**< 0.001**
	Spring	**25**	**13.07**	**0.002**	**0.36**	–	**0.002**
Anchovy	**Winter**	**23**	**53.47**	**< 0.001**	**0.72**	–	**< 0.001**
	Spring	**25**	**24.65**	**< 0.001**	**0.52**	–	**< 0.001**
Croakers	**Winter**	**23**	**6.99**	**0.015**	**0.25**	–	**0.015**
	Spring	25	0.24	0.631	0.01	–	0.634
Flatfish	Winter	23	2.15	0.158	0.09	–	0.156
	Spring	25	0.51	0.482	0.02	–	0.478
Rockfish	Winter	23	4.13	0.055	0.16	–	0.052
	Spring	25	0.70	0.410	0.03	–	0.415
S. jordani	**Winter**	**23**	**11.68**	**0.003**	**0.36**	–	**0.002**
	Spring	25	2.15	0.156	0.09	–	0.154
Offshore fish	**Winter**	**23**	**10.20**	**0.004**	**0.33**	–	**0.005**
	Spring	**25**	**7.23**	**0.013**	**0.24**	–	**0.014**
Mackerel	Winter	23	0.19	0.667	0.01	+	0.724
	Spring	25	1.33	0.261	0.05	–	0.266
Mesopelagic fish	**Winter**	**23**	**10.21**	**0.004**	**0.33**	–	**0.005**
	Spring	**25**	**6.83**	**0.016**	**0.23**	–	**0.017**

were initially selected if their average annual abundance for the period 1951 though 2011 was greater than 2.0 fish m^{-2} (Koslow et al., 2013, updated to 2011 for this paper). We created a rockfish group from all *Sebastes* spp. In addition to a general rockfish group, we used *S. jordani* as a focal species because of its importance as prey for seabirds (Sydeman et al., 1997). Two species of the genus *Sebastolobus* were excluded. Seven myctophid, species were grouped into the "mesopelagic" fish group. One species, *Protomyctophum crockeri*, was excluded from the mesopelagic group though it fit our initial selection criteria because as a non-vertical migrator, it is essentially unavailable to seabirds as prey. Species-groups were also combined into "nearshore" and "offshore" groups for analysis. The nearshore fish category included flatfish, anchovy, croakers, rockfish, and *S. jordani*, while offshore fish included mesopelagic fish and jack mackerel. Two other species, sardine (*Sardinops sajax*) and hake (*Merluccius productus*), were not included in either of these groups because they occur in both nearshore and offshore habitats (Hsieh et al., 2005). Finally, total fish abundance was calculated from the sum of mesopelagic fish, hake, sardine, anchovy, croakers, flatfish, rockfish, *S. jordani*, and mackerel. Seasonal mean larval fish abundance were transformed prior to analysis of trends and interrelationships (ln (abundance+1); 1 was added to abundances to ensure positive values after transforming). We used ichthyoplankton data from winter and spring surveys to correlate with seabird density from spring.

2.3. Seabirds

From 1987 – present, we collected data on seabird abundance for 23 focal species-groups; field methods are summarized by Hyrenbach and Veit (2003) and Yen et al. (2006). We used data from spring surveys in this paper. The dominant species included black-footed albatross (*Phoebastria nigripes*), brown pelican (*Pelecanus occidentalis*), Cassin's auklet (*Ptychoramphus aleuticus*),

California gull (*Larus californicus*), Cook's petrel (*Pterodroma cookii*), Leach's storm-petrel (*Oceanodroma leucorhoa*), pink-footed shearwater (*Puffinus creatopus*), western gull (*Larus occidentalis*), red phalaropes (*Phalaropus fulicarius*), red-necked phalaropes (*Phalaropus lobatus*), and dark shearwaters (mostly sooty shearwaters (*Puffinus griseus*), also short-tailed shearwaters (*P. tenuirostris*)). We combined the abundances of these and all other species into total seasonal counts, and used these data in analyses. Given the prevalence of dark shearwaters in spring, we examined trends and associations with prey populations with and without this group. Our focus is on the total seabird community and its changes in abundance through time. We standardized count data to density by dividing survey counts by the area surveyed (birds km^{-2}). We use density in illustrations, but analyzed seabird data using the original count data with the area surveyed included as a covariate to account for variation in observation effort (see below). Unlike fish, we did not combine species-groups into "nearshore" and "offshore" groups for analysis as the nearshore abundance dominates the pattern of abundance.

Table 2
Trends in seabirds for (A) all seabird species combined and (B) all species excluding dark shearwaters, 1987–2011. Significant values $p < 0.05$ are bold. See text for modeling procedures. Summer is included simply as a confirmation of the trends for spring, but that season is not a focus of this paper.

	Predictor entered	df	χ^2	Coefficient sign	p-Value
(A)					
Spring					
Step 1	Area	1	0.00	–	0.947
2	**Date**	1	**21.65**	+	**< 0.001**
3	**Year**	1	**12.73**	–	**< 0.001**
4	Year^2	1	1.81	+	0.172
Summer					
1	Area	1	0.56	+	0.455
2	Date	1	2.80	+	0.096
3	**Year**	1	**8.59**	–	**0.001**
4	Year^2	1	1.55	+	0.205
(B)					
Spring					
Step 1	Area	1	0.17	–	0.680
2	**Date**	1	**18.03**	+	**< 0.001**
3	**Year**	1	**10.03**	–	**< 0.001**
4	Year^2	1	1.87	+	0.164
Summer					
1	Area	1	0.21	+	0.645
2	Date	1	0.13	+	0.722
3	**Year**	1	**12.21**	–	**< 0.001**
4	Year^2	1	3.44	+	0.055

Table 3
Results of negative binomial regression between spring seabird community abundance and spring prey abundance. Base models (including area surveyed) (km^2) and year (linear term) were followed by individual models on krill or fish. (A) Total community abundance. (B) Community abundance minus dark shearwaters. $N=23$ years. Bold indicates significance at $p < 0.05$.

Model	Predictor entered	df	LRS	Coefficient sign	Nominal p-value
(A)					
Base	Area	1	0.00	–	0.947
	Year	1	**10.85**	–	**0.000**
Krill	*N. simplex*	1	2.47	+	0.105
	E. pacifica	1	3.22	–	0.056
	T. spinifera	1	**4.82**	+	**0.019**
	E. pacifica*+*T. spinifera	1	**4.99**	+	**0.014**
Fish	**Mesopelagics**	1	**8.90**	–	**0.002**
	Rockfish	1	0.58	–	0.441
	S. jordani	1	2.96	–	0.081
	Mackerel	1	0.11	+	0.740
	Flatfish	1	0.82	+	0.361
	Anchovy	1	0.65	–	0.409
	Hake	1	2.84	–	0.086
	Sardine	1	1.57	–	0.213
	Croakers	1	0.60	–	0.428
	Total	1	2.04	–	0.144
	Nearshore	1	0.00	–	0.982
	Offshore	1	**6.07**	–	**0.011**
(B)					
Base	Area	1	0.17	–	0.680
	Year	1	**10.59**	–	**0.000**
Krill	*N. simplex*	1	2.44	+	0.107
	E. pacifica	1	1.38	+	0.225
	T. spinifera	1	2.01	+	0.143
	E. pacifica+*T. spinifera*	1	2.11	+	0.127
Fish	**Mesopelagics**	1	**11.88**	–	**0.000**
	Rockfish	1	1.18	–	0.263
	S. jordani	1	**3.69**	–	**0.049**
	Mackerel	1	0.07	+	0.785
	Flatfish	1	1.12	+	0.286
	Anchovy	1	1.62	–	0.186
	Hake	1	**4.55**	–	**0.027**
	Sardine	1	1.79	–	0.185
	Croakers	1	1.26	–	0.244
	Total	1	3.47	–	0.054
	Nearshore	1	0.36	–	0.536
	Offshore	1	**8.77**	–	**0.002**

2.4. Statistical analyses

For winter and spring, trends in physical conditions, krill, and fish were tested using simple linear regression; to account for possible autocorrelation in the time series, the significance in trends was confirmed using bootstrap Monte Carlo randomization procedures (Manly, 2007; Table 1). In no case did the significance of the p-value determined by Monte Carlo randomization differ substantially from nominal p-values. Trends in seabird abundance were tested using negative binomial regression with survey area, survey mid-day of year, year and year^2 as predictor variables (Table 2). In this analysis, each variable was entered sequentially, and the step-specific Likelihood Ratio Statistic (LRS, distributed as Chi^2) was used to evaluate significance. The potential effects of krill and forage fish on springtime seabird abundance were examined using negative binomial regression. The base model included survey area and year (linear) as this model accounted for the trend in seabird abundance through time (Table 3). Subsequently, we entered data on each species of krill ($n=3$) and species-groups of larval fish ($n=12$) as predictors. Due to the relatively small sample of years for these analyses ($n=21$ and $n=23$ for winter–spring and spring–spring comparisons, respectively), in order to maintain adequate degrees of freedom we initially tested effects of each prey species separately. As above, we evaluated the statistical significance of each prey species using a LRS calculated for the last step in the modeling process, and confirmed p-values using bootstrap and Monte Carlo tests (10,000 randomizations of the data were performed and mean Pearson correlation coefficient, r^2 and p-values were estimated to determine strength of association between variables). Spring seabird abundance data were compared to winter as well as spring fish data to investigate possible lagged effects.

3. Results

3.1. Trends in stratification, upwelling, and potential prey populations

Density stratification increased in winter, but not in spring (Table 1, Fig. 2). The changes in density stratification were similar on lines 80 and 90, but the rate of increase was slightly greater on line 90. Upwelling intensity increased in winter and showed no change in spring. The abundance of *E. pacifica* and *T. spinifera* increased, while *N. simplex* abundance decreased (Table 1, Fig. 3). The upward trend for *E. pacifica* was modest, whereas the changes in abundance for the other species were substantial, though contrasting sharply. Owing to the corresponding changes in abundance of *T. spinifera* and *N. simplex*, overall there was no change in summed krill abundance in the study region. Sardine, anchovy, rockfish, *S. jordani*, and mesopelagic fish declined in the winter, and few trends were observed in spring (Table 1, Fig. 4). Anchovy declined in both seasons, whereas sardine declined in winter but increased in spring. Summed rockfish declined in winter but showed no change in spring. There were essentially no changes in the abundance of flatfish, croakers, or mackerel (Table 1).
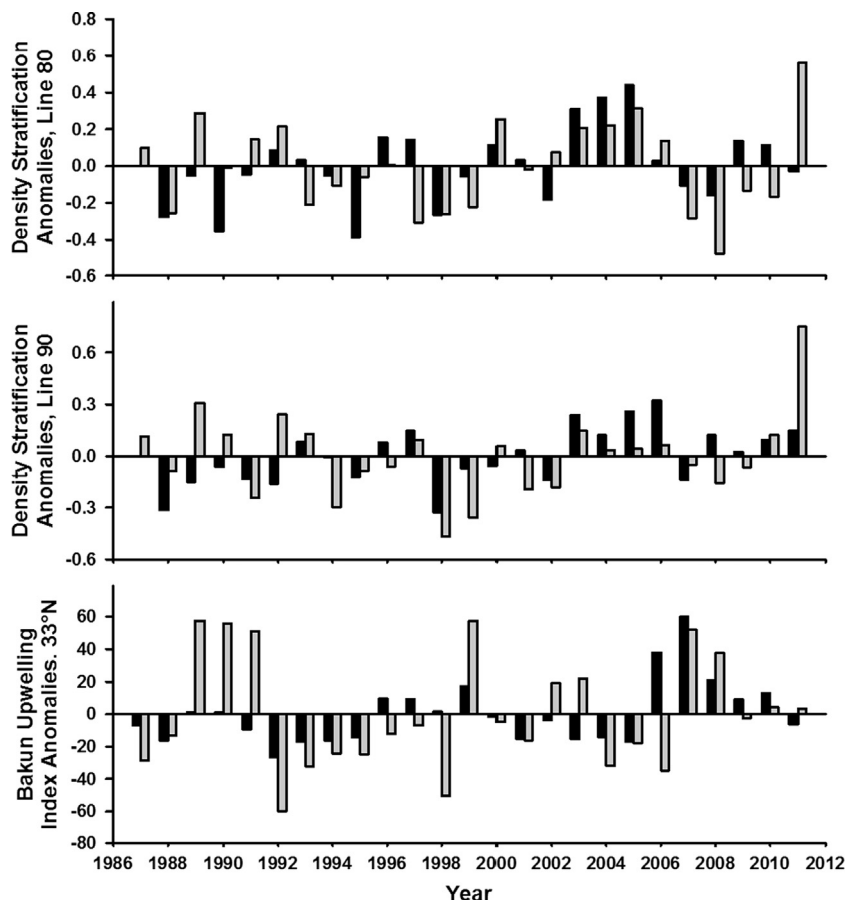

Fig. 2. Interannual variation (seasonal mean) of density stratification on Lines 80 and 90 (see Fig. 1 for locations) and the Bakun Upwelling Index at 33°N, 1987–2011. Black=winter and gray=spring.

3.2. Trends in seabird density

Seabird density at sea decreased (Table 2A, Fig. 5A). The model for spring shows a significant effect of date, with greater seabird abundance observed when spring surveys were conducted at a later date, coincident with the influx of migratory species,

primarily shearwaters, in May rather than April. The overall rate of decline over the 25 years was -2.2% per annum. In the late spring and especially summer, the dominant species in the Southern California region are sooty and short-tailed shearwaters, both trans-hemispheric migrants that breed in Chile, New Zealand, Australia, and other sub-Antarctic locations (Shaffer et al., 2006). When we eliminate these dark shearwaters from the total bird density estimates, we still find a log-linear decline in abundance over the 25-year period (Table 2B). The overall rate of decline for all species without dark shearwaters was -1.9% per annum. The decline in seabirds, however, was restricted to the northern sector of the study area (Fig. 5B). Seabird density from 35 to 33°N declined in a log-linear fashion over the period, whereas seabird density from 32 to 30°N did not change appreciably. Shearwaters and other species with sub-arctic zoogeographic affinities preferentially inhabit the cooler waters of the northern portion of the study area (Hyrenbach and Veit, 2003; Yen et al., 2006).

3.3. Seabird–prey associations

Springtime seabird density was related positively to the abundance of springtime krill, primarily *T. spinifera*, and negatively related to springtime mesopelagic fish (Table 3A). As there are numerous studies documenting the importance of krill as primary prey for seabirds in the CCE (Briggs and Chu, 1987; Abraham and
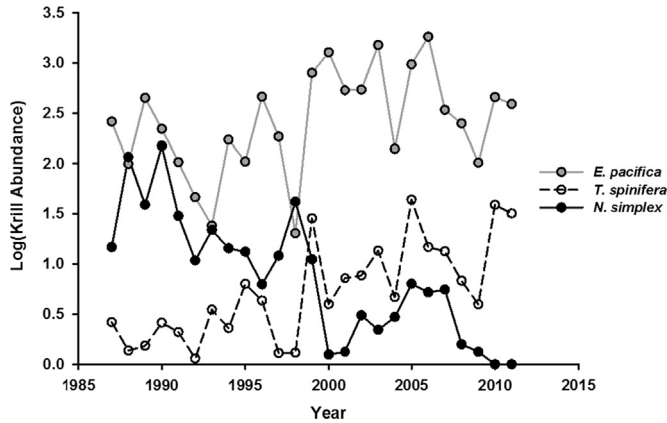

Fig. 3. Interannual variability in abundance of three species of euphausiid crustacean (Log(No. $m^{-2}+1$)), 1987–2011.

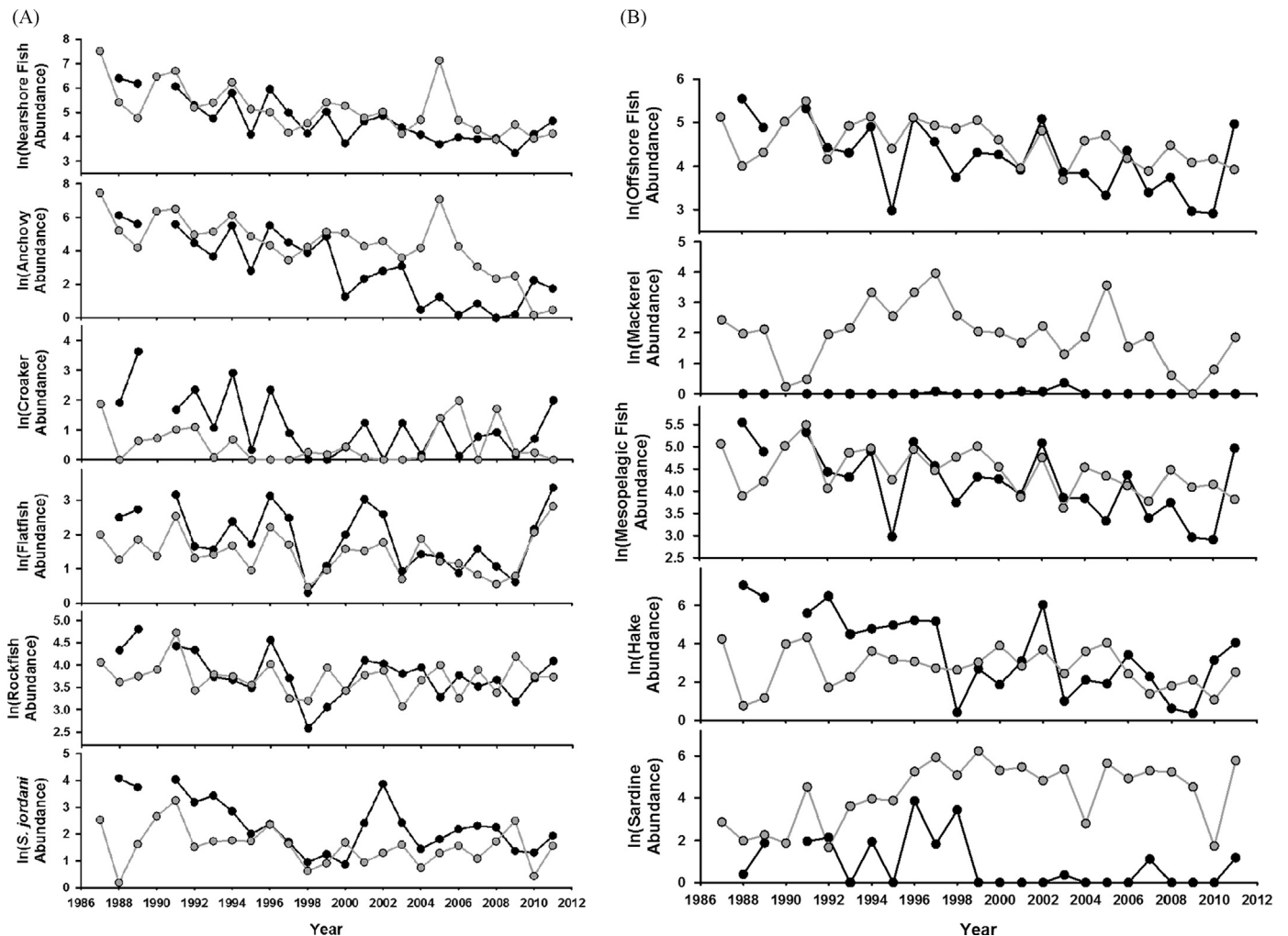**Fig. 4.** Interannual variability in abundance of larval fish (ln(No. m^{-2}), 1987–2011: (A) nearshore fish group and species (flatfish, anchovy, croakers, rockfish, and *S. jordani*) and (B) offshore fish group and species (jack mackerel and mesopelagic fish), as well as hake and sardine, which were not grouped into either the nearshore or offshore fish categories. Black=winter and gray=spring.
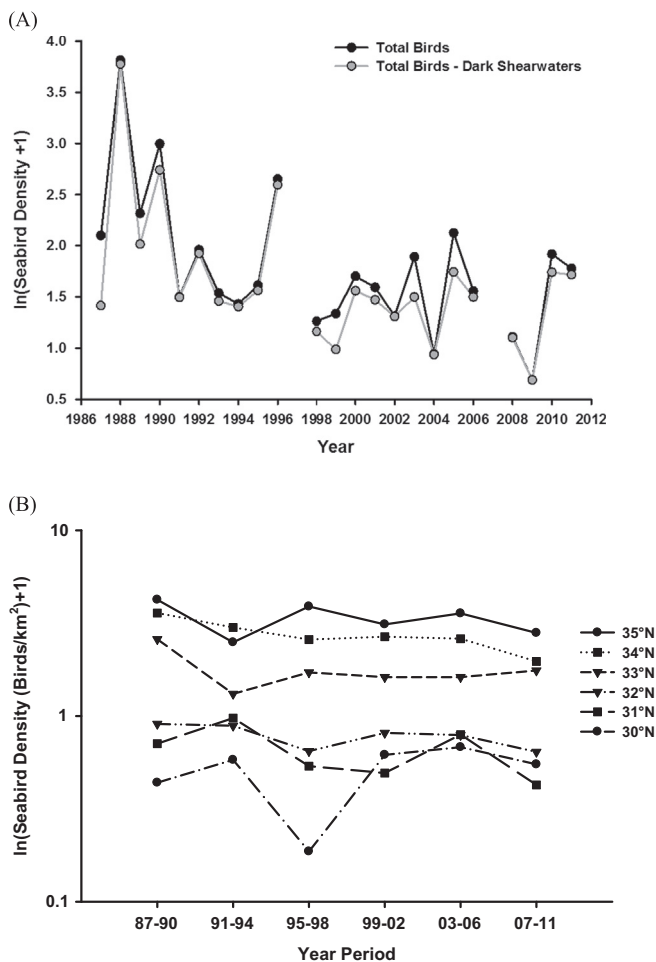
(A)

(B)

Fig. 5. (A) Interannual variability in the abundance of total seabirds recorded at sea in spring, with and without dark shearwaters, 1987–2011. (B) Seabird density by latitude over 4-year periods (with the exception of 2007–2011).

Sydeman, 2004; Smith et al., 2011), we consider the seabird–krill relationship reflective of key predator–prey interactions in the system. The best model for krill included a combination of the species *E. pacifica* and *T. spinifera* and explained ∼20% of the interannual variability in seabird density (Fig. 6A). This result is confirmed by bootstrap and Monte Carlo randomization test ($r=0.46$, $r^2=0.24$, $p=0.03$). The variance explained by krill is low due to one outlier: 1988 when seabird density was exceptionally high. In 1988, phalarope abundance accounted for 88% of the total number of birds, which was considerably greater than in any other year of study. When we exclude 1988 from this numerical response model, the variance explained increases to 31%.

Spring mesopelagic fish were inversely related to seabird density (both including and excluding dark shearwaters), indicating that seabirds tend to be less abundant when mesopelagics are more abundant (Table 3A,B, Fig. 6B). This result is confirmed by bootstrap and Monte Carlo randomization test (total bird density: $r=-0.420$, $r^2=0.21$, $p=0.03$; excluding dark shearwaters: $r=-0.423$, $r^2=0.22$, $p=0.03$). When the seabird density outlier year 1988 is removed, however, the variability explained by this relationship decreases from 20% to 6%; therefore, the relationship between springtime mesopelagic fish and seabirds is likely to be spurious. When both mesopelagic fish and krill (*E. pacifica* + *T. spinifera*) are considered in a model, both were significantly

related to springtime seabird density (not shown). *Sebastes* and hake were also negatively correlated, but in the presence of mesopelagics, these species groups were not significant (not shown).

Given that the seabirds feed primarily on older age classes of these fish (i.e., juvenile rather than larval forms), we investigated lagged relationships between seabirds and prey by correlating wintertime larval fish relative abundance against springtime seabird density. Notably, for all species except mackerel and sardine, which showed no relationship at all, all of the relationships were positive, including those for mesopelagic species, hake, and *Sebastes* spp. (Table 4). The best model was based on a combination of all nearshore fish species (Fig. 6C); this relationship explained 17% of the variance in seabird density and was confirmed by bootstrap and Monte Carlo randomization test ($r=0.40$, $r^2=0.19$, $p=0.06$). However, removing 1988 decreased the variance explained to 13%. When considering the seabird density without dark shearwaters, the best models included hake and all forage fish species combined (Table 4B, Fig. 6D; $r=0.51$, $r^2=0.28$, $p=0.02$). In summary, springtime krill (*E. pacifica* + *T. spinifera*) and wintertime nearshore larval fish (dominated by anchovy) appear to best explain springtime seabird density in the CalCOFI/CCE-LTER study region.

3.4. Temporal variability in predator–prey relationships

We examined the time series for temporal trends in seabird (predator) – prey numerical responses. It is clear that seabird–prey interactions changed through time. For example, the krill–seabird relationship was inconsistent or out of phase prior to 1998–1999. After 1999, when the seabird community decreased and the krill species composition shifted towards a cool-water community, the relationship strengthened and was mostly in phase (Fig. 7A). This shift in the numerical response was supported statistically, with no relationship between seabirds and krill prior to 1998, and a strong relationship after 1999 (Table 5). A similar observation was obtained for the mesopelagic fish, except the time period of association was reversed. Mesopelagic fish and seabirds were inversely related prior to 1998, but this relationship was inconsistent during the latter half of the study period. This change also was supported statistically, with a significant negative interaction between seabird community abundance (minus dark shearwaters) and mesopelagics prior to 1998, and no relationship in the period after 1999.

4. Discussion

From their major assessment of seabird – ocean temperature relationships, Hyrenbach and Veit (2003) concluded that long-term changes in seabird populations in southern California were related to changes in prey populations. Other studies of seabirds in elsewhere in the California Current (Ainley and Hyrenbach, 2010) have come to a similar conclusion that ocean climate effects are mediated by prey availability. Importantly, previous authors also highlight the importance of seabird responses to ocean variability on multiple time scales, from seasons to years and decades (Hyrenbach and Veit, 2003; Sydeman et al., 2009; Ainley and Hyrenbach, 2010). In this study, we addressed the hypothesis that stratification and upwelling affect seabirds indirectly through changes in prey availability. To test this hypothesis, we considered numerical responses between seabird densities at sea and indices of abundance for three species of krill and nine taxa of forage fish over multiple time scales, years to decades. We consider krill and forage fish "potential prey" as seabirds are known to consume most of these taxa, but direct evidence for this is generally not available for the southern California region. We also assume that
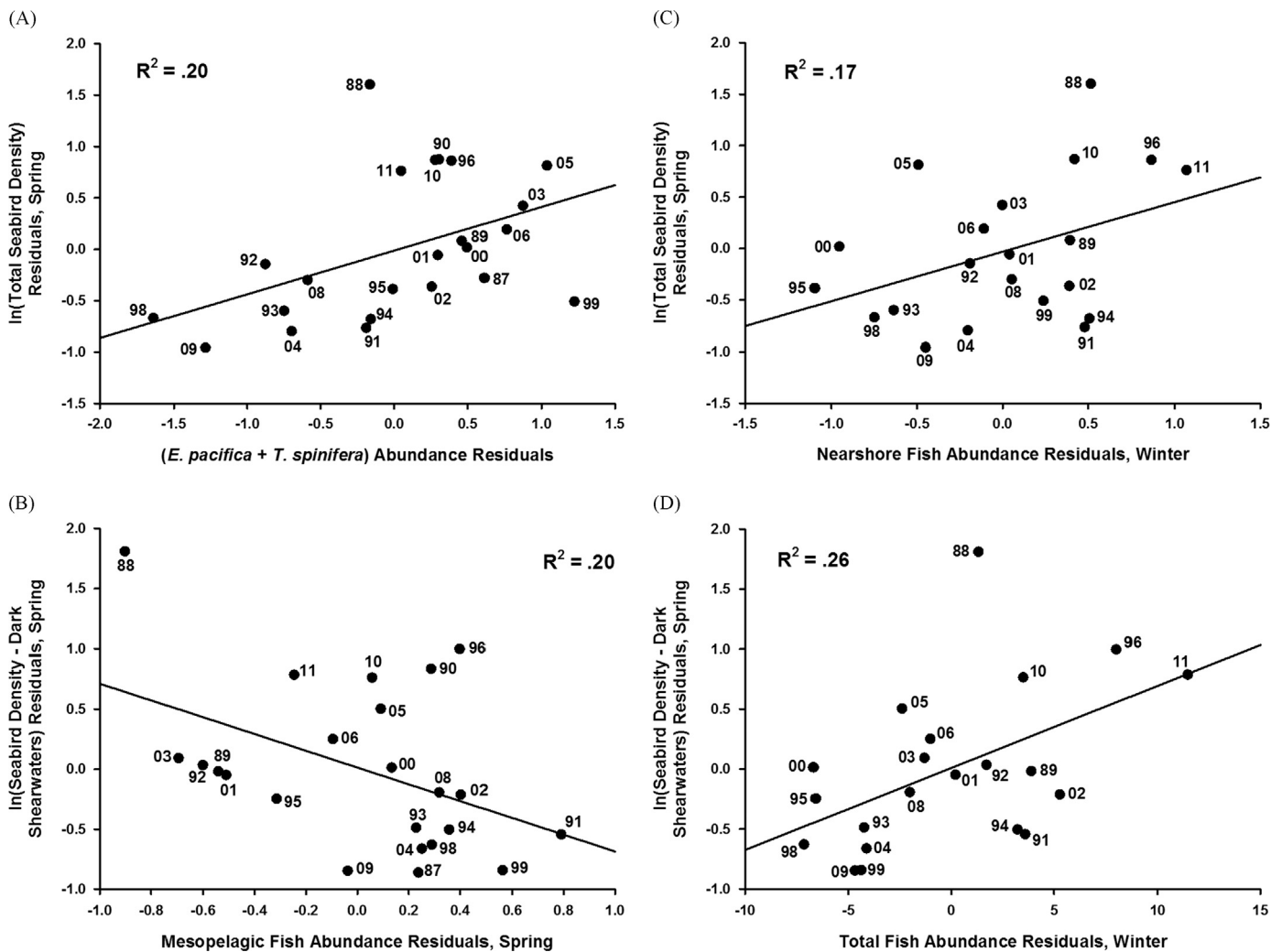
Fig. 6. Relationships between spring total seabird abundance and potential prey resources. (A) *E. pacifica+T. spinifera*, (B) spring mesopelagic fish abundance, (C) winter nearshore fish abundance, and (D) winter total fish abundance. All data are residuals. Points are labeled with 2-digit year.

larval forms constitute a proxy for the juvenile and older age classes consumed by the birds. Koslow et al. (2011) showed that this assumption is valid as larval abundance is related to standing stock biomass for both anchovies and sardines. Because many seabird populations in the region have declined (Hyrenbach and Veit, 2003), we examined each prey time series for trends in relative abundance. Subsequently, we investigated whether the residuals in prey abundance were related to residuals in seabird density (i.e., trends removed for both). Last, focusing on the prey species that related to the birds, we investigated whether stratification and upwelling explained variation in these populations. In this discussion, we therefore focus primarily on two inter-related questions: (1) how do changes in prey availability explain seabird population declines and variability, especially in the northern sector of the study region where the seabird declines occurred?, and (2) how do changes in upwelling and stratification explain variation in prey populations, hence the availability of prey to seabirds?

4.1. Trends in seabirds and prey

The northern sector of the southern California Current Ecosystem is an abundance "hotspot" for krill (Santora et al., 2011a), and select seabirds and marine mammals (Yen et al., 2006). Despite evidence of modest upwelling intensification in this region that could support increased phytoplankton productivity, we found that the seabird population decline previously described (Sydeman et al., 2009; Hyrenbach and Veit, 2003; Veit et al., 1996) continued through 2011, with no apparent leveling-off in recent years (Table 2). This pattern of decline was found in both spring and summer and was not simply related to the precipitous decline in dark (sooty and short-tailed) shearwaters (Veit et al., 1996, 1997). In this new analysis, we adjusted for the mid-date of the surveys, a covariate not considered in previous analyses, but one that could mask or accentuate population trends. We showed that later spring surveys were associated with greater seabird abundance (due to an influx of shearwaters later in the spring), but when survey date was included in negative binomial regression models, a substantial population decline was evident. The overall rate of seabird decline in the study area was −2.2% per year and was centered in the cooler, northern region of the study area where seabird densities were an order of magnitude higher than in the warmer, subtropical sector. This conclusion corresponds with the species-specific population trends reported by Hyrenbach and Veit (2003); in their study substantial declines occurred in dark shearwaters, Cassin's auklet (*Ptychoramphus aleuticus*), and rhinoceros auklet (*Cerorhinca monocerata*), all species with cold-water affinities and found in the northern sector of the study area.

Long-term trends also were apparent for potential prey, but with considerable variability among species. For example, over the

Table 4
Result of negative binomial regression between spring community abundance and winter prey abundance. Base models (area, year) were followed by models on individual fish taxa. (A) Total seabird community. (B) Community abundance minus dark shearwaters. N=21 years. Bold indicates significance of $p < 0.05$.

Model	Predictor entered	df	LRS	Coefficient sign	Nominal p-value
(A)					
Base	Area	1	0.01	+	0.936
	Year	**1**	**9.30**	**−**	**0.001**
Fish	Mesopelagics	1	2.12	+	0.141
	Rockfish	**1**	**3.58**	**+**	**0.041**
	S. jordani	1	1.52	+	0.201
	Mackerel	1	0.18	+	0.677
	Flatfish	1	3.57	+	0.054
	Anchovy	1	3.09	+	0.068
	Hake	**1**	**4.66**	**+**	**0.022**
	Sardine	1	0.04	−	0.842
	Croakers	**1**	**4.21**	**+**	**0.034**
	Total	**1**	**4.92**	**+**	**0.022**
	Nearshore	**1**	**4.90**	**+**	**0.018**
	Offshore	1	2.12	+	0.140
(B)					
Base	Area	1	0.10	−	0.754
	Year	**1**	**10.65**	**−**	**0.000**
Fish	**Mesopelagics**	**1**	**3.61**	**+**	**0.049**
	Rockfish	**1**	**5.39**	**+**	**0.010**
	S. jordani	1	2.32	+	0.109
	Mackerel	1	0.01	+	0.899
	Flatfish	**1**	**4.74**	**+**	**0.025**
	Anchovy	1	2.55	+	0.098
	Hake	**1**	**7.07**	**+**	**0.003**
	Sardine	1	0.00	−	0.946
	Croakers	**1**	**4.13**	**+**	**0.036**
	Total	**1**	**6.45**	**+**	**0.008**
	Nearshore	**1**	**5.99**	**+**	**0.008**
	Offshore	**1**	**3.62**	**+**	**0.049**

25-year period, we found a substantial increase in the krill species *T. spinifera,* a modest increase in *E. pacifica*, and a substantial decline in *N. simplex* (Fig. 3). By 1999, *T. spinifera* replaced *N. simplex* as the second most abundant euphausiid in the ecosystem, resulting in the euphausiid community being comprised of species with sub-arctic/transition zone zoogeographic affinities (Brinton, 1962). This finding is based on the chosen period of analysis (1987 – present). We chose this period to overlap with the seabird data, but the CalCOFI zooplankton and larval fish database extends back to ~1950 (Lavaniegos and Ohman, 2007; Koslow et al., 2013). Based on the full time series, it is clear that *N. simplex* has both increased and decreased over the past 60 years, with increases after the 1976–1977 regime shift and an abrupt decline from 1999 to the present (Brinton and Townsend, 2003). In a recent study, Di Lorenzo and Ohman (2013; see also Ohman et al., 2013) attributed these changes to variation in North Pacific climate mediating advection of this species into southern California waters from sub-tropical regions. Some parallel increases and decreases have been documented with fishes (Koslow et al., 2013). Many trends in larval fish were also established, including substantial declines in northern anchovy (*E. mordax*) and mesopelagic species (mostly myctophids) from 1987 – present. Similar to our assessment of trends in *N. simplex*, however, variation in these dominant "nearshore" and "offshore" fish species has actually varied over the long-term, with increasing numbers through the 1970s and 1980s and decreasing abundance in the more recent decades (Hsieh et al., 2005, 2009; Koslow et al., 2011, 2013). Nonetheless, the decline in anchovy and mesopelagic fish from 1987 to the present is compelling.

4.2. Prey abundance and seabird density

Rarely has seabird abundance at sea been related to contemporaneous prey data, and when they are relationships are typically scale-dependent with few significant relationships at large spatial scales (e.g., Fauchald et al., 2011). In this case, the decline in seabird density can be explained by declines in potential prey, especially those that comprise a significant proportion of the seabird diets. This leads us to focus on the possible relationships between seabirds and *N. simplex*, northern anchovy (as the main contributor to the nearshore forage fish community), and mesopelagic species. While the decline in *N. simplex* could be related to the seabird decline, we find this unlikely because (i) the seabird decline occurred in the northern sector of the study area where this euphausiid is typically rare (Brinton and Townsend, 2003), (ii) *N. simplex* generally comprises < 10% of the diet of the principal seabird species in the community (Sydeman et al., 1997, 2001; Thayer and Sydeman, unpublished data), hence is unlikely to have demographic consequences, and (iii) when we examined residuals of seabird density against residuals of *N. simplex*, no correlation was found (Table 3A). Therefore, while it remains possible that the decline in *N. simplex* could possibly affect some sub-tropical bird species in the region (e.g., black-vented shearwater, *Puffinus opisthomelas*), it cannot be considered a major factor in the overall seabird decline.

In comparison, changes in anchovy and perhaps other nearshore forage fish have the potential to cause major impacts on seabirds. The nearshore fish community constitutes well-known and major proportions of the seabird prey (Miller and Sydeman, 2004; Mills et al., 2007; Robinette et al., 2007; Thayer and Sydeman, 2007; Sydeman et al., 2009). For breeding seabirds on the Farallon Islands, ~400 km north of the CalCOFI/CCE-LTER study site, anchovy, in particular, was a primary food resource in the 1990s after juvenile rockfish declined from the 1970s to 1980s (Sydeman et al., 2001). Importantly, the residuals of nearshore species (and anchovy) abundance in winter were significantly positively related to changes in the abundance of seabirds in spring (Fig. 6C). Therefore, we think the anchovy decline probably accounts for much of the long-term decline in the seabirds in the region. Hsieh et al. (2005) demonstrated a shoreward contraction of "coastal species", primarily anchovy, in the northern sector of the study area where the seabird decline was most pronounced. This region is also a "hotspot" of abundance for many seabird species including dark shearwaters (Yen et al., 2006). Finally, preliminary spatial analyses of seabirds in this sector from 1987 to 2012 shows a similar shoreward contraction in distribution (Sydeman, unpublished data).

The abundance of offshore fish also declined during the study period and could explain some of the seabird population trend. The relationships between the residuals of seabird abundance and mesopelagic fish, though, were inconsistent, being positive in winter, but negative in spring. The inverse relationship in spring was due to a single year (1988) and is likely spurious. While some seabirds are known to consume lanternfish (Myctophidae) off southern California, in almost all cases they comprise a relatively small part of the diet and are therefore unlikely to have substantial effects on the seabird community. Regarding these "oceanic species", Hsieh et al. (2009) suggested northward and shoreward expansions, which appear spatially and temporally congruent with the decline and shoreward contraction of the nearshore fish. Koslow et al. (2011) attributed changes in mesopelagic fish to shoaling of the oxygen minimum zone (OMZ). Putting these observations together, it seems probable that the northward and shoreward expansion of mesopelagic species was related to the decline and shoreward contraction of nearshore species, with both trends related to oceanographic processes and possibly shoaling of
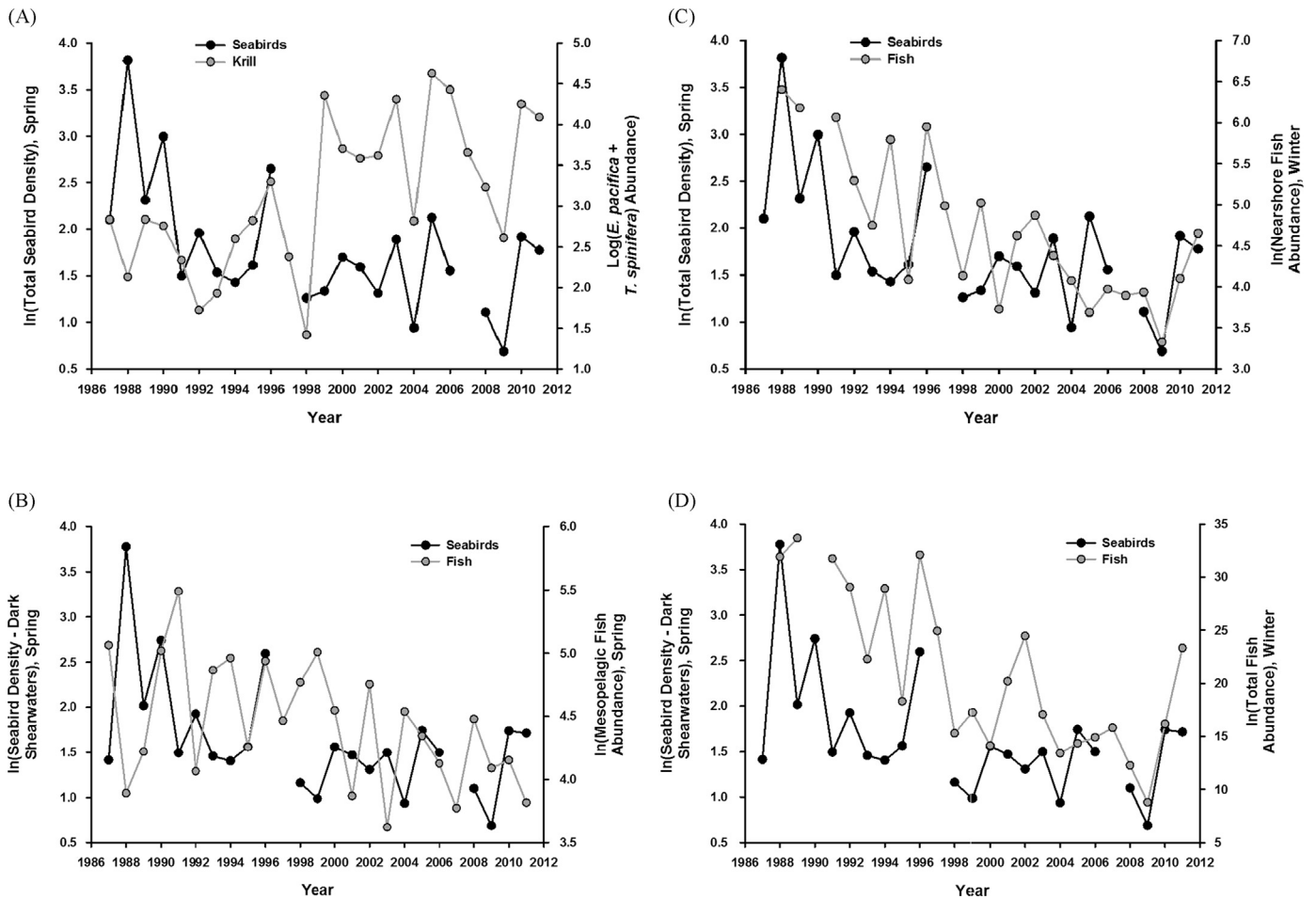
(A)

(C)

(B)

(D)

Fig. 7. Interannual variability in time series of seabird community relative abundance and prey abundance. (A) *E. pacifica* + *T. spinifera*, (B) spring mesopelagic fish abundance, (C) winter nearshore fish abundance, and D. winter total fish abundance. Shown are the raw data for seabirds and prey.

Table 5
Spring birds and prey, pre-1998 and post-1999. Bold text indicates significance of $p < 0.05$.

Dependent	Predictor entered	Pre-1998					Post-1999				
		N	df	LRS	Coefficient sign	Nominal *p*-value	N	df	LRS	Coefficient sign	Nominal *p*-value
Total birds	Area	10	1	0.30	−	0.568	**11**	**1**	**5.92**	**+**	**0.006**
	Year	**10**	**1**	**4.06**	**−**	**0.024**	11	1	0.19	+	0.657
	E. pacifica + *T. spinifera*	10	1	0.00	−	0.955	**11**	**1**	**21.20**	**+**	**0.000**
Bird Abundance – Sooty Shearwaters	Area	10	1	0.32	−	0.553	**11**	**1**	**5.22**	**+**	**0.010**
	Year	10	1	2.72	−	0.073	11	1	0.21	+	0.654
	Mesopelagic fish	**10**	**1**	**6.01**	**−**	**0.006**	11	1	0.04	−	0.848

the OMZ. If so, the positive relationship between winter mesopelagic fish abundance and seabird density (Fig. 6B) could actually be explained by the nearshore fish, which we think have driven the interdecadal patterns of seabird density in this region of the SCB. Understanding the spatial distribution of predators and prey is needed to evaluate this possibility. There may also be particular seabird species that favor greater abundance of mesopelagic species (e.g., shearwaters, albatrosses, rhinoceros auklets), but from the total seabird community perspective, changes in the nearshore fish and primarily anchovy is probably the most important factor explaining seabird numbers in the CalCOFI/CCE-LTER region.

While contemporaneous trends in potential prey must play a role in accounting for seabird population trends, interannual variability in seabird density could be related to any potential prey irrespective of their time trends. On this time-scale, variation in krill, particularly the relative abundance of *T. spinifera*, appears to be a primary explanatory factor for variation in seabird numbers. Directly or indirectly (e.g., if krill form an important part of the diet of forage fish), krill form an integral part of the diet of most seabirds in the region. Krill constitute a very large proportion of the diet of dark shearwaters (Briggs and Chu, 1987), ~80% of Cassin's auklet diet (Sydeman et al., 2001; Abraham and Sydeman, 2004), and are key for rhinoceros auklets early in the breeding season (Ito et al., 2009). Krill have been related directly to seabird demographic parameters (Sydeman et al., 2006, 2013) as well as seabird numbers at sea in the central (Santora et al., 2011b, 2012) and central-northern portions of the

California Current (Ainley et al., 2009). The relationship between krill and seabirds was largely, but not entirely, driven by the importance of krill to dark shearwaters – without dark shearwaters the relationship with krill, though still positive, was insignificant (Table 3B). The relationship between *T. spinifera* and *E. pacifica* and seabirds bears closer analysis by focusing on specific subregions such as the Point Conception area and other coastal hotspots (Yen et al., 2006; Santora et al., 2011a) that may be regions of enhanced predator–prey interactions. A caveat is that the r^2 values are lower than desired, but some were quite a bit higher when stratifying the time series by time (see below). Moreover, numerical relationships between seabirds and prey may be best represented by non-linear equations, a topic for future modeling investigations.

4.3. Temporal changes in upwelling and stratification

We found indications that both density stratification and upwelling increased in winter, but not in spring over the 25-year period. Both variables also showed substantial interannual variation, e.g., upwelling was unusually strong in winter and spring in 2006–2008 and stratification was particularly high in 2011 (Fig. 2). Upwelling intensification has also been demonstrated in other regions of the CCE for similar time periods (e.g., García-Reyes and Largier, 2010), as has increasing stratification (Aksnes and Ohman, 2009; Palacios et al., 2004; McGowan et al., 2003). Not surprisingly, the increase in stratification was greater on Line 90, within the warmer region of the CalCOFI/CCE-LTER study region. Seabird density, however, did not change appreciably in this region (Fig. 5B). Hsieh et al. (2005) examined a direct measure of stratification, buoyancy frequency along Line 90, and also found an increasing trend. Most previous authors attributed changes in stratification to inter-decadal climate variability and in particular the ecosystem shift of 1976–1977. Bograd and Lynn (2003) compared thermal stratification of two time periods and documented significant variation between 1950–1976 and 1977–1999, especially in the Santa Barbara Basin to the southeast of the Point Conception upwelling cell. They interpreted their findings in relation to low-frequency climate variability (i.e., PDO), but their time series ended in 1999. Here, we have considered upwelling and stratification through 2011. Some authors have considered the period following the transition years of 1998–1999 as representative of another ecosystem shift (Bond et al., 2003; Peterson and Schwing, 2003; deYoung et al., 2008). Our data on upwelling and stratification in southern California do not clearly demonstrate an ecosystem transition at that time.

4.4. Shift in predator–prey interactions?

Though upwelling and stratification in the study region did not transition substantially starting in 1999, it is quite obvious that the numerical response of seabirds to prey abundance did change. In particular, the correlation with the residuals of krill (sum of *E. pacifica* and *T. spinifera* summed) shifted from one of relative unimportance prior to 1998 (1987–1997: $r^2=0.28$, $p=0.12$) to great significance post-1999 (2000–2011, $r^2=0.57$, $p=0.007$). There was not, however, a similar shift in numerical responses for residuals in springtime seabird density and residuals of winter nearshore fish (1987–1997, $r^2=0.19$, $p=0.28$; 2000–2011: $r^2=0.12$, $p=0.29$). Instead, the effect of nearshore fish was long-term (not interannual), with 34% of the variation in seabird density accounted for by nearshore fish abundance (neither with trend removed). Therefore, this study provides evidence for a potential shift in seabird numerical responses with shifts in the availability of alternative prey species. As the nearshore fish (mostly anchovy) community declined, apparently the seabirds began to rely on the

increasing abundance of krill or changes in the krill community composition (i.e., relatively more *T. spinifera* and less *N. simplex*). This indicates a possible threshold response to alternative prey availability, in accordance with optimal foraging (diet) theory (Sih and Christensen, 2001). While it is beyond the scope of this paper to determine the threshold(s) where shifts in abundance of nearshore fish and/or krill trigger a response in the seabirds, we are unaware of other papers demonstrating similar changes in predator–prey numerical responses that may be related to suggested ecosystem shifts. In the central California Current, the putative ecosystem shift of 1989–1990 impacted the food habits of seabirds, but no change in predator–prey numerical (breeding success) response were noted (Sydeman et al., 2001). As contemporaneous predator and prey abundance data are rare, it is not surprising that numerical responses have been infrequently reported in the ecosystem shift literature (deYoung et al., 2008), although such changes in predator–prey relationships must be a typical consequence of ecosystem shifts. Fisheries-induced ecosystem shifts, such as those of the Scotian shelf (Frank et al., 2005) have documented numerically important changes to predators resulting from changes in tropho-dynamics, but that is quite different than what we have described here as a probable ecosystem feature of low-frequency climate variability.

5. Conclusion

Multi-trophic level investigations of climatic impacts on pelagic ecosystems are rare, but seabird studies have often led the way in establishing trophic connections (e.g., Frederiksen et al., 2006; Watanuki et al., 2009; Sydeman et al., 2012). One of the first studies to relate climate to potential prey to seabirds was that of Aebischer et al. (1990), who linked time series on weather, phyto- and zooplankton biomass, forage fish (represented by herring (*Clupea harengus*)), and seabirds (kittiwakes (*Rissa tridactyla*)) in a manner similar to our approach here. Their parallel trends across trophic levels were taken as evidence of climate change impacts on the North Sea ecosystem. Similarly, we have identified parallel trends across trophic levels and evidence of association between forage fish, krill, and seabirds in the Southern California region over a 25-year period. These patterns of change in populations are matched, but equivocally, by weak changes in stratification and upwelling (both increasing in winter). However, these changes should not be attributed to unidirectional climate change as patterns of change in krill and fish have been shown to vary over time, and predator–prey interactions and numerical responses may be best explained by low-frequency climate variability. Nonetheless, deriving predator–prey numerical response relationships is clearly of great value to understanding climatic impacts on pelagic ecosystems and the management of upper trophic level organisms (fish, seabirds, and mammals) of conservation concern.

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