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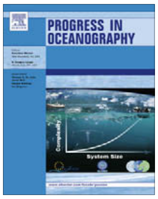

Top-down and bottom-up factors affecting seabird population trends in the California current system (1985–2006)

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ABSTRACT

To characterize the environmental factors affecting seabird population trends in the central portion of the California current system (CCS), we analyzed standardized vessel-based surveys collected during the late spring (May–June) upwelling season over 22 yr (1985–2006). We tested the working hypothesis that population trends are related to species-specific foraging ecology, and predicted that temporal variation in population size should be most extreme in diving species with higher energy expenditure during foraging. We related variation in individual species abundance (number km^{-2}) to seasonally lagged (late winter, early spring, late spring) and concurrent ocean conditions, and to long-term trends (using a proxy variable: year) during a multi-decadal period of major fluctuations in the El Niño-Southern oscillation (ENSO) and the Pacific decadal oscillation (PDO). We considered both remote (Multivariate ENSO Index, PDO) and local (coastal upwelling indices and sea-surface temperature) environmental variables as proxies for ocean productivity and prey availability. We also related seabird trends to those of potentially major trophic competitors, humpback (*Megaptera novaeangliae*) and blue (*Balaenoptera musculus*) whales, which increased in number 4–5-fold midway during our study. Cyclical oscillations in seabird abundance were apparent in the black-footed albatross (*Phoebastria nigripes*), and decreasing trends were documented for ashy storm-petrel (*Oceanodroma homochroa*), pigeon guillemot (*Cepphus columbus*), rhinoceros auklet (*Cerorhinca monocerata*), Cassin's auklet (*Ptychoramphus aleuticus*), and western gull (*Larus occidentalis*); the sooty shearwater (*Puffinus griseus*), exhibited a marked decline before signs of recovery at the end of the study period. The abundance of nine other focal species varied with ocean conditions, but without decadal or long-term trends. Six of these species have the largest global populations in the CCS, and four are highly energetic, diving foragers. Furthermore, three of the diving species trends were negatively correlated with the abundance of humpback whales in the study area, a direct competitor for the same prey. Therefore, on the basis of literature reviewed, we hypothesize that the seabirds were affected by the decreasing carrying capacity of the CCS, over-exploitation of some prey stocks and interference competition from the previously exploited, but now increasing, baleen whale populations. Overall, our study highlights the complexity of the ecological factors driving seabird population trends in the highly variable and rapidly changing CCS ecosystem.

1. Introduction

The marine environment has increasingly become subject to unprecedented and concurrent climatic and anthropogenic forcing (e.g., Levitus et al., 2001; Bovy, 2007; Österblom et al., 2007; Halpern et al., 2008). Perhaps as a result, many marine populations are experiencing monotonic changes (i.e., linear increases or decreases), rather than the cyclical patterns recorded in the archeological and historical records (e.g., Glantz and Thompson, 1981; Baumgartner et al., 1992; Horn and Stephens, 2006). Most contemporary analyses have concentrated on the climatic drivers of population variation, with an emphasis on long-term warming, decadal trends and regime shifts (e.g., Bograd et al., 2000; Sydeman et al., 2001; Batchelder et al., 2002; Field et al., 2006). Indeed, a warming trend over the last 50 yr has impacted the global ocean, including the highly productive California current system (CCS), by forcing an ecosystem shift from a productive sub-arctic regime towards a depopulated subtropical environment (Venrick et al., 1987; McGowan et al., 1998). This biogeographic transition has led to a shift from cold-water to warm-water communities of primary consumers (e.g., zooplankton), mid-level consumers (e.g., nekton) and upper-trophic predators (e.g., seabirds) (Peterson and Schwing, 2003; Hyrenbach and Veit, 2003; Brodeur et al.,

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2007). Because marine birds are highly mobile upper-trophic predators, they respond to short- and long-term oceanographic changes most readily; making them ideal indicators of changing ocean productivity and ecosystem structure (e.g., Veit et al., 1997; Oedekoven et al., 2001; Hyrenbach and Veit, 2003; Jahncke et al., 2008).

Recently documented decadal shifts in the zoogeographic affinity of seabird species in the CCS (Ainley et al., 1995a; Ainley and Divoky, 2001; Hyrenbach and Veit, 2003) are consistent with concurrent shifts in overall zooplankton biomass and species composition driven by ocean climate (Peterson and Schwing, 2003; Peterson et al., 2002; Hoof and Peterson, 2006; Ohman, 2006, 2007). Concurrently, the system has experienced the depletion of major trophic groups (e.g., rockfishes, sharks) due to over-fishing (Jackson et al., 2001; Worm et al., 2006; Heithaus et al., 2008), and the recovery from exploitation of once-harvested cetacean populations (cf. Tønnessen and Johnsen, 1982; Calambokidis and Barlow, 2004). To investigate a possible mechanism linking seabird population trends to changes in the zoogeography and the overall productivity of the CCS, as well as the recovery of potentially major trophic competitors (whales), we test the prediction that species-specific energetic costs of prey acquisition influence the numerical responses of seabird species to food variability (Ballance et al., 2009). Following previous studies, we use environmental conditions over both large (e.g., basin-wide) and small (e.g., central California) spatial scales as indirect indices of food availability, and classify seabird species according to their foraging mode into high- and low-energy life-styles (e.g., Ballance et al., 1997; Hyrenbach and Veit, 2003). Indeed, species that feed by subsurface prey pursuit only inhabit high prey availability and colder sub-arctic waters, while surface foragers and plungers dominate unproductive areas (i.e. warmer subtropical and tropical waters) (Ainley, 1977).

To investigate this hypothesis, we analyze trends of at-sea abundance of the marine avifauna in the central CCS during a 22 yr period (1985–2006), and relate changes in the abundance of 16 focal species to a suite of environmental variables that are proven proxies for ocean productivity and prey abundance (Ainley et al., 1995b; McGowan et al., 1998; Jahncke et al., 2008). We evaluate these "bottom-up" climate-driven fluctuations alongside "top-down" forcing, through trophic interference competition by the increasing numbers of humpback and blue whales (*Megaptera novaeangliae, Balaenoptera musculus*) in the study area. The whales appeared in the study area, increasing many fold in number during the space of just a couple of years, midway through the study; thus providing a "natural experiment" to investigate trophic effects, and likely interference competition. As we will explain, we believe the whale increase was the result of the return to traditional central California feeding grounds, decades after the cessation of shore-based whaling stations.

2. Methods

2.1. Study area

Data were collected during annual National Marine Fisheries Service rockfish recruitment surveys (NMFS – RRS) (Fig. 1), which sampled 47 standardized conductivity-temperature-depth (CTD) stations, spanning the continental shelf and upper slope (to 3000 m depth) from Bodega Bay (38.32°N) to Cypress Pt. (35.58°N), California. Southeast Farallon Island (SEFI) (37.7°N, 123°W), the largest seabird colony in the continental USA (NOAA, 2008), is located in the middle of the study area. A typical cruise-day was spent steaming between hydrographic stations, sampling eleven lines of CTD stations with 20 km spacing (Baltz, 1997), which interrupted survey effort for 20–60 min intervals depending on water depth (deeper water, longer station). This survey grid was surveyed yearly during 1–2 replicate sweeps in late spring (May–June) (Table 1).

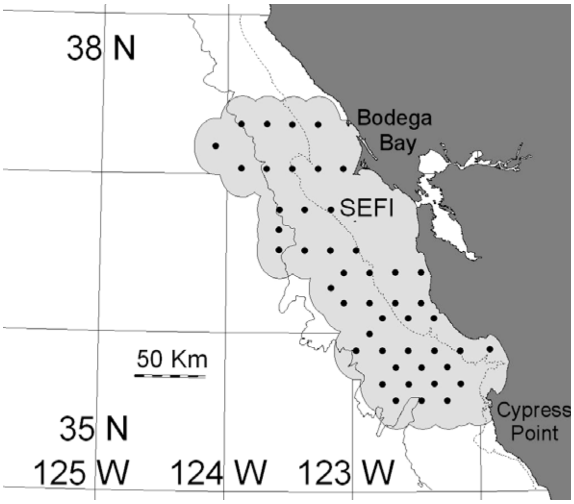

Fig. 1. Map of study area, showing the shelf-break (200-m isobath; dashed line), the bottom of the continental slope (3000-m isobath; solid line), Southeast Farallon Island (SEFI), and the extent of the 11 lines of conductivity-temperature-depth (CTD) stations sampled during cruises. The polygon encompasses the spatial extent of the study area, delineated by adding a 20-km buffer to each CTD station.

2.2. Surveys methods

Seabirds and marine mammals were surveyed using standardized strip transects (300 m for birds, Spear et al., 2004; 800 m for mammals, Keiper et al., 2005), modified to account for the relative flight speed and movement of flying birds (Spear et al., 1992) but not for slow-moving whales. Therefore, we gathered data to con-

Table 1
Survey effort during the early (1985–1994) and the late (1997–2006) study periods, showing the number of survey days, 15-min survey bins, and distance surveyed each year.

Survey dates			Survey effort		
Year	Start	End	Days	Bins	km
1985	5/31	6/22	22	164	647.67
1986	5/30	6/19	20	426	1953.17
1987	6/2	6/19	17	360	1513.97
1988	5/23	5/31	8	217	925.70
1989	5/31	6/11	11	273	1082.27
1990	5/29	6/11	13	395	1492.77
1991	5/28	6/11	14	541	2281.77
1992	6/3	6/18	15	460	1990.83
1993	6/3	6/12	9	346	1372.70
1994	6/11	6/18	7	268	1086.83
1997	5/14	5/19	6	216	907.53
1998	5/14	5/20	5	199	922.90
1999	5/10	6/3	24	422	1667.60
2000	5/30	6/6	7	226	906.70
2001	5/30	6/6	7	180	714.20
2002	5/29	6/3	5	144	556.70
2003	5/30	6/6	7	262	1002.10
2004	5/30	6/2	3	69	283.67
2005	5/25	5/31	6	181	721.47
2006	5/29	6/9	11	172	772.63
Summary					
Early period (1985–1994)			136	3450	14,347.67
Late period (1997–2006)			81	2071	8455.5
Total			217	5521	22,803.2

struct indices of relative abundance and not absolute population size. At least two observers, stationed on the flying bridge (12 m above sea surface), surveyed the strip simultaneously while the vessel was underway and recorded every seabird and mammal sighted within a 90° arc on the side of the track with least glare (Spear et al., 2004). Continuous counts were summed every 15 min ($\sim$4 km at the cruising speed of 9–10 kt, 16.7–18.6 km h^{-1}) and matched with the vessel's position. SST was interpolated to match the 4 km spatial scale of the 15-min seabird survey bins using the ArcView 3.2 geographic information system (GIS) software inverse distance-weighted method (Keiper et al., 2005).

For the sake of consistency, one observer (DGA) was present on almost every cruise. On the few instances when this was not possible, observers trained by DGA collected the data. During two years, 1995 and 1996, when this criterion could not be met, no seabird data were collected. To facilitate inter-annual comparisons, we constrained our analysis to the same 2-mo period (May 1–June 30) and geographic area (Fig. 1). A total of 22,803 km (yearly mean 1140 ± 529 km SD) were surveyed over 20 yr (early period: 1985–1994, late period: 1997–2006) with no effort in 1995 and 1996 (Table 1).

2.3. Environmental data-sets

We correlated seabird and whale abundance to five data-sets indicative of monthly ocean conditions: large-scale variability associated with the Pacific decadal oscillation (PDO) and the Multivariate El Niño Index (MEI); regional indices of coastal upwelling at two reference latitudes (39°N, 36°N); and local sea-surface temperature (SST) from cruise CTD casts. The PDO Index, defined as the leading principal component (PC) of monthly North Pacific SST poleward of 20°N, indicates large-scale atmospheric and water mass distributions in the North Pacific. In particular, positive and negative PDO values correspond to anomalously warm- and cold-water conditions in the CCS, respectively (Mantua et al., 1997; www.jisao.washington.edu/pdo). The MEI is based on the first PC describing ocean and atmospheric conditions in the tropical Pacific Ocean (30°S–30°N), seasonally-adjusted with respect to the 1950–1993 reference period. Negative values of the MEI represent La Niña (cold conditions), while positive values represent El Niño (warm conditions) (Wolter and Timlin, 1998; www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html).

We used the monthly upwelling index from the Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov/products/PFEL), for 36°N, 122°W and 39°N, 125°W, to identify the phasing and intensity of upwelling during cruises (Keiper et al., 2005; Thayer and Sydeman, 2007). To account for the multiple upwelling centers within the study area, we used the two regional upwelling indices. This approach provided complete spatial coverage of the study area (Fig. 2).

2.4. Environmental data analysis

Previous studies of the diet and productivity for seabird species breeding at SEFI have documented lagged responses to local (e.g., upwelling intensity) and remote (e.g., ENSO variability) oceanographic conditions (Ainley et al., 1993; Ainley et al., 1995a,b). Thus, we included antecedent environmental conditions as explanatory variables in our analysis of at-sea bird abundance. To account for time lags between oceanographic conditions and shifts in seabird distributions, we considered three distinct periods preceding the spring (May–June) surveys: Late Winter (January–February), Early Spring (March–April), and Late Spring (May–June). For each time period, we quantified four environmental conditions (MEI, PDO, upwelling south of the study area, upwelling north of the study area) by averaging the corresponding monthly data. This process yielded four time series of environmental variables preceding seabird surveys by 3–5, 1–3, and 0–1 mo, respectively. In addition, we used the mean value of the SST CTD data measured in situ during cruises to reflect local conditions during surveys.

Because oceanographic conditions are serially autocorrelated (i.e., current conditions are influenced by previous conditions; Steele, 1985) and cross-correlated with each other (i.e., basin-wide atmospheric patterns influence local conditions; Brodeur et al., 2000), we quantified the degree of auto and cross-correlation among the four environmental metrics. We used a 23-yr time series ($n = 276$ monthly records) spanning the study (October 1984–September 2007) and linear Pearson correlations to quantify the autocorrelation patterns for each individual variable and the pair-wise cross-correlations between variables (Table 2). We found significant pair-wise cross-correlations between the four environmental variables: PDO, MEI, upwelling at 36°N, upwelling at 39°N. Five of the six pair-wise tests yielded significant correlations (Pearson correlation, $n = 276$, $p < 0.001$). Briefly, El Niño coincided with the warm-phase of the PDO and with periods of seasonally higher coastal upwelling north and south of the study area. Yet, the strongest cross-correlations ($r > 0.4$) were observed for the two large-scale variables (MEI, PDO) and for the two regional variables (UP-36, UP-39).

Table 2
Pearson linear correlation coefficients (r) among environmental variables; $n = 276$ monthly values during 23 yr (October 1984–September 2007).

Correlation coefficient	*p*-Value			
	MEI	PDO	UP_S	UP_N
MEI	–	0.492	−0.150	−0.139
PDO	<0.001	–	−0.266	−0.234
UP_S	0.002–0.005	<0.001	–	0.593
UP_N	0.02–0.05	<0.001	<0.001	–

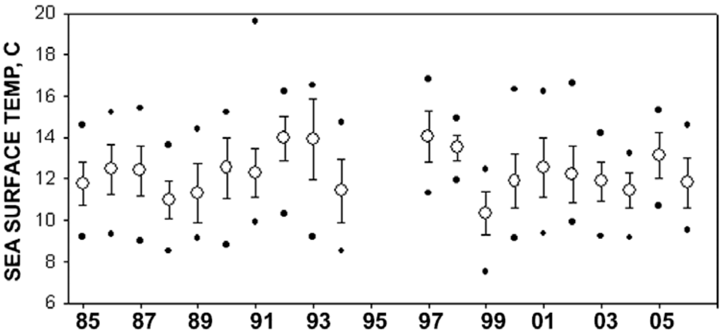

Fig. 2. Sea surface temperature (mean ± SD, range) sampled during seabird surveys, as indexed by the water temperature at the 15-min seabird survey bins surveyed within the study area each year.

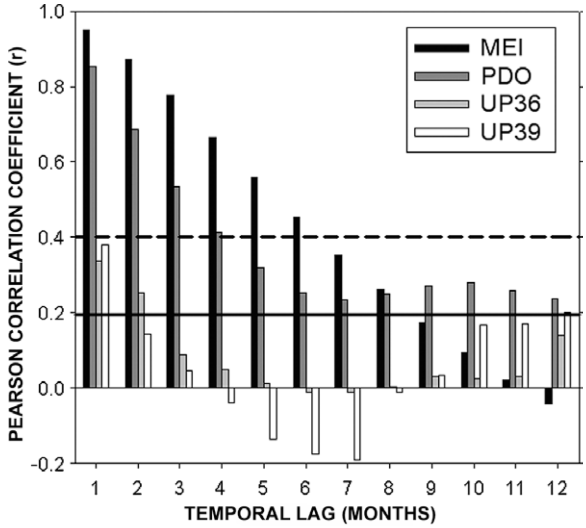

Fig. 3. Autocorrelations of four monthly environmental variables over a range of temporal lags from 1 to 12 mo. The horizontal lines indicate two levels of statistical significance defined by alpha = 0.001 (solid line) and 0.0001 (dashed line).

The autocorrelation analysis also revealed significant temporal patterns for all four environmental variables (Fig. 3). The two large-scale oceanographic variables were characterized by the largest temporal scales, with a loss of significant autocorrelation after a time lag of six (MEI) and four (PDO) months, respectively. The two regional upwelling indices showed considerably shorter time scales, with marginal cross-correlations ($0.4 < r < 0.2$) at a lag of one and two months.

To account for the co-variation of these oceanographic variables, we combined them into multi-variate environmental factors using principal component analysis (PCA). We only included four principal components (PCs) with eigenvalues >1 (Weichler et al., 2004; Ainley et al., 2005), which together explained 82.83% of the observed variance (Table 3). Using those variables with strong loadings (>0.5), we describe the factors as follows: PC1 was associated with MEI variability in all three time periods (late winter, early spring, late spring), with PDO conditions in spring (early, late) and during late spring (May–June) for both south and north of the study area; PC2 was associated with spring-time upwelling at both 36°N and 39°N; PC3 was associated with winter-time upwelling at both 36°N and 39°N; and PC4 was associated with PDO variability before the seabird surveys, in late winter and early spring (January–April).

We assessed temporal trends in these four multi-variate factors by testing for cross-correlations with the temporal proxy variable (year since the start of the study) using Spearman rank correlations ($df = 19$, r_s $critical = 0.433$). These tests indicated no trends in spring-time environmental conditions sampled during the study period: PC1 ($r_s = -0.195$, $0.50 > p > 0.20$), PC2 ($r_s = +0.238$, $0.50 > p > 0.20$), PC3 ($r_s = -0.005$, $p > 0.50$), and PC4 ($r_s = +0.018$, $p > 0.50$).

2.5. Seabird data analysis

We focused on those bird species that occurred on >50% of cruises and contributed at least 0.1% of all individuals recorded (Table 4; contains scientific names). We used Systat 11.0 (© 2002 SYSTAT Software Inc.) to examine the relationship between the abundance (bird density, birds km^{-2}) of 16 "common" species and five independent explanatory variables: the four orthogonal PC factors described above (indicative of environmental conditions) and the year since the start of the time series (a proxy variable to test for trends).

We used a multiple regression analysis, with a forward and backward fitting procedure, to relate the density of each focal seabird species to the explanatory variables. We initially entered all five variables into the model and used a step-wise procedure to remove insignificant terms sequentially in order of increasing *p*-value (Ainley et al., 2005; Hyrenbach et al., 2006). We retained those variables deemed marginally significant ($p < 0.10$), and report the performance (adjusted r^2) of the best-fit models. Seabird densities were log-transformed ($y' = \log\ (y + 0.01)$) to meet assumptions of normality, and the regression residuals were tested for normality (one-sample Kolmogorov–Smirnov tests, $n = 20$, $p < 0.05$).

In addition to the multiple regressions, we used generalized additive models (GAMs) with the Poisson link function to visualize year-to-year changes in the density of those species abundant enough to show significant ($p < 0.05$) responses to warm-water events (PC1 factor) and temporal trends (year since the start of the time series) (Clarke et al., 2003). We performed these analyses using the S + 2000 software (© 1999 MathSoft). To further quantify long-term changes in seabird abundance, we compared the log-transformed densities during the early (1985–1994) and the late (1997–2006) periods of our study using *t*-tests and the percent change in mean densities (Percent change) = [(late density − early density) $*$ 100/(early density)] (Hyrenbach and Veit, 2003).

2.6. Baleen whale data analysis

Cetaceans were tallied if they occurred within an expanded 800-m survey transect, and are expressed herein as the density

Table 3

Results of principal component analysis showing the loadings of the different components of the four dominant multi-variate environmental factors and the proportion of the observed variance explained by each factor. Those variables with large loadings (>0.5) are in bold font.

Process – time period	Variable	PC1	PC2	PC3	PC4
ENSO – winter	MEI$_1$	**+0.790**	+0.348	−0.145	+0.018
ENSO – early spring	MEI$_2$	**+0.840**	+0.398	−0.004	-0.122
ENSO – late spring	MEI$_3$	**+0.708**	+0.371	+0.400	-0.259
PDO – winter	PDO$_1$	+0.497	+0.092	−0.081	**+0.822**
PDO – early spring	PDO$_2$	**+0.757**	+0.172	−0.105	**+0.554**
PDO – late spring	PDO$_3$	**+0.762**	-0.207	+0.434	+0.232
Upwelling North – winter	UP-39$_1$	−0.396	-0.444	**+0.619**	+0.153
Upwelling North – early spring	UP-39$_2$	−**0.609**	**+0.572**	+0.164	+0.216
Upwelling North – late spring	UP-39$_3$	−**0.704**	**+0.513**	−0.078	+0.059
Upwelling South – winter	UP-36$_1$	−0.471	−0.166	**+0.643**	+0.288
Upwelling South – early spring	UP-36$_2$	-0.466	**+0.651**	+0.425	+0.011
Upwelling South – late spring	UP-36$_3$	−**0.785**	+0.373	−0.113	+0.146
Sea surface temp. – late spring	SST	**+0.685**	+0.236	+0.476	−0.356
Eigenvalues		5.78	1.91	1.64	1.42
Cumulative variance explained		0.44	0.59	0.72	0.83

Table 4
The 18 most abundant seabird species recorded during NMFS-RRS surveys in May–June 1985–2006, showing the occurrence (% of survey years observed) and the number and proportion of individuals of each species. The bold font denotes the "common" focal species included in this analysis. The species are classified according to their foraging mode (divers/surface foragers) and arranged in decreasing abundance.

	Occurrence (% cruises)	Individuals	
		Number	Proportion
Sooty shearwater *Puffinus griseus* (SHSO)	100	25,6963	60.97
Common murre *Uria aalge* (MUCO)	100	70,075	16.63
Cassin's auklet *Ptychoramphus aleuticus* (AKCA)	100	43,744	10.38
Brandt cormorant *Phalacrocorax penicillatus* (BRCO)	100	9308	2.21
Rhinoceros auklet *Cerorhinca monocerata* (AKRH)	95	2872	0.68
Pigeon guillemot *Cepphus columba* (GUPI)	100	648	0.15
Divers		*383,610*	*91.02*
Western gull *Larus occidentalis* (GUWE)	100	14,428	3.42
Red phalarope *Phalaropus fulicarius* (PHRE)	70	4904	1.16
Northern phalarope *Phalaropus lobatus* (PHRN)	45	3421	0.81
California gull *Larus californicus* (GUCA)	70	2686	0.64
Black-footed albatross *Phoebastria nigripenis* (ALBF)	100	2556	0.61
Pink-footed shearwater *Puffinus creatopus* (SHPF)	100	2135	0.51
Ashy storm-petrel *Oceanodroma homochroa* (STAS)	85	977	0.23
Northern fulmar *Fulmarus glacialis* (FUNO)	90	962	0.23
Brown pelican *Pelecanus occidentalis* (PELB)	95	770	0.18
Sabine's gull *Xema sabini* (GUSA)	75	548	0.13
Black-legged kittiwake *Rissa tridactyla* (KWBL)	5	546	0.13
Leach's storm-petrel *Oceanodroma leucorhoa* (STLE)	50	511	0.12
Surface foragers		*34,444*	*8.17*
Total (all species)		418,054	99.19

(number km^{-2}) encountered during a given cruise. Thus, this metric of relative whale abundance is not a corrected population size estimate based on line-distance methodology, for which the required sighting distance and angle data are not available. Yet, similar metrics of relative abundance have been previously used to characterize trends in whale abundance in the CCS (Larkman and Veit, 1998). We focused this analysis on the most abundant mysticete, the humpback whale, which accounted for approximately 78% of all the baleen whales sighted in the study area in spring, followed by the gray whale (*Eschrichtius robustus*), which accounted for 12% (Keiper et al., 2005). While we believe that blue whales are likely important consumers in this system (e.g., Croll et al., 2005; Schoenherr, 1991), they enter our study area several weeks after our cruises. Hence we collected no data on their distribution and abundance in the study area, even though they are present off central California in summer/fall (Croll et al., 2005; Schoenherr, 1991), well within the time period when they could directly affect foraging of the seabird species discussed. Conversely, the few gray whales that summer in our study area, feeding on benthic, infaunal invertebrates, would not be directly interacting with seabirds.

We related the log-transformed whale density data ($(y' = \log(y + 0.001))$) to the five environmental variables in the step-wise procedure as described above. To test for correlation between whale and seabird abundance, we related year-to-year variation in focal seabird abundance to concurrent whale abundance with linear regressions using Systat 11.0 (© 2002 SYSTAT Software Inc.). To further explore the correlation of increasing whale populations on seabird trends, we compared the performance (adjusted r^2) of the seabird models including only one explanatory variable: 'year' or 'whale density'. We tested all the regression residuals for normality (one-sample Kolmogorov–Smirnov tests, $n = 20$, $p < 0.05$).

3. Results

Observers recorded 418,054 birds belonging to 69 taxa during the surveys. While 18 seabird species met the abundance threshold, only 16 met the number-of-cruises criterion for inclusion in the analyses (Table 4). These 16 species fell into four groups, on the basis of their responses to environmental variables.

3.1. Seabird patterns in relation to environmental factors

3.1.1. No variable explained patterns

Analyses failed to yield significant results for four species: pink-footed shearwater, red-necked phalarope, black-legged kittiwake and California gull (Tables 5 and 6). The kittiwake and phalarope exhibited short-term (1–2 yr) pulses (Fig. 4a and b). In fact, the only incursion of the sub-arctic-breeding kittiwake took place during 1999, an anomalously cold-water year of enhanced spring upwelling; large numbers also occurred off southern California (33–36°N; Bograd et al., 2000). While the red-necked phalarope occurred more frequently (45% of cruises), their large inter-annual variability obscured any significant trends.

Pink-footed shearwater and California gull abundance did not change significantly (Fig. 4c and d), even though the shearwater's average density almost doubled (84% increase) over the long-term (Table 7).

Table 5
Abundance of focal species, showing the coefficient of variation (CV) in density across years and results of the test of residuals from best-fit multiple regressions (Kolmogorov–Smirnov test, $n = 20$). Diving and surface-foraging species are listed separately, in decreasing order of abundance. See Table 4 for definitions of the species acronyms.

	Density (number/km^2)			Regression residuals	
	Mean	Min–max	CV (%)	Max diff	p
SHSO	29.38	3.37–74.58	81.25	0.196	0.374
MUCO	6.88	0.77–13.20	55.12	0.120	0.901
AKCA	5.09	0.04–17.23	99.08	0.107	0.957
COBR	1.14	0.01–14.46	281.93	0.201	0.345
AKRH	0.33	0.00–1.29	94.67	0.124	0.880
GUPI	0.06	0.01–0.30	135.61	0.153	0.680
GUWE	1.53	0.45–4.57	78.51	0.160	0.631
PHRE	0.32	0.00–2.58	226.32	0.180	0.483
GUCA	0.35	0.00–2.90	220.22	0.095	0.985
ALBF	0.28	0.06–0.76	70.62	0.123	0.885
SHPF	0.28	0.03–1.66	136.43	0.158	0.646
STAS	0.09	0.00–0.50	160.14	0.128	0.860
FUNO	0.08	0.00–0.38	135.73	0.263	0.104
PELB	0.06	0.00–0.24	114.45	0.121	0.896
GUSA	0.05	0.00–0.31	175.99	0.169	0.561
STLE	0.05	0.00–0.71	312.27	0.147	0.724

Table 6
Results of multiple regression models of the relationship between seabird density and environmental variables. The total number of significant variables and the percent of variance explained (adjusted r^2) by the best-fit model are shown, alongside the associated p-values for each of the five independent variables considered. The sign (±) of the coefficients are shown for marginally significant ($p < 0.10$). Significant ($p < 0.05$) variables are highlighted in bold font. Highly significant variables, adjusted for multiple comparisons (*alpha* = 0.05/16 = 0.003), are underlined. Diving and surface-foraging species are listed separately, in decreasing order of abundance. See Table 4 for definitions of the species acronyms.

	Variables	r^2	PC1	PC2	PC3	PC4	Year
SHSO	2	22.5	0.375	−0.052	0.612	+0.095	0.971
MUCO	2	29.8	+0.020	−0.090	0.248	0.197	0.580
AKCA	**1**	**62.1**	**0.895**	**0.675**	**0.575**	**0.224**	−**0.001**
COBR	1	23.1	+0.018	0.161	0.970	0.703	0.490
AKRH	**1**	**20.4**	**0.800**	**0.492**	**0.411**	**0.520**	−**0.026**
GUPI	**2**	**58.8**	**0.005**	**0.437**	**0.939**	**0.949**	−**0.030**
GUWE	**3**	**58.2**	**0.450**	−**0.040**	**0.735**	**+0.091**	−**0.001**
PHRE	1	25.7	−0.013	0.329	0.729	0.954	0.120
GUCA	**0**	**0**	**0.218**	**0.867**	**0.798**	**0.344**	0.621
ALBF	**2**	**37.3**	**0.224**	**0.224**	**+0.056**	**0.264**	−**0.003**
SHPF	**0**	**0**	**0.174**	**0.792**	**0.558**	**0.529**	0.223
STAS	**1**	**19.0**	**0.335**	**0.106**	**0.843**	**0.428**	−**0.031**
FUNO	2	21.5	−0.091	+0.062	0.577	0.377	0.349
PELB	1	18.1	+0.035	0.552	0.628	0.295	0.641
GUSA	1	18.8	0.537	0.326	+0.032	0.675	0.877
STLE	1	21.9	+0.020	0.310	0.786	0.100	0.362

3.1.2. Patterns explained by year

Year explained important variation in trends for black-footed albatross, ashy storm-petrel, Cassin's auklet, rhinoceros auklet, pigeon guillemot and western gull (Fig. 4e–j, Table 6). All of these species, except the albatross, showed a peak in abundance before the early 1990s, followed by a decrease thereafter (Fig. 5). The albatross did not decrease over the long-term, but rather, exhibited two 'cycles' of high and low abundance (Figs. 4 and 6). In the case of three species, additional environmental variables contributed to the variation explained by year (Table 6). For the pigeon guillemot, abundance was further explained by the remote oceanographic factors associated with the MEI and PDO (PC1); for the albatross, winter upwelling was also important (PC3); and for western gull, spring upwelling and the PDO during winter were important (PC2, PC4).

3.1.3. Patterns explained by MEI/PDO

Not showing patterns related to long-term trends (Table 6) were the Leach's storm-petrel, brown pelican, Brandt's cormorant, and red phalarope (Fig. 4k–n). Yet, their abundance was significantly affected by basin-scale factors (MEI/PDO), as indicated by the importance of PC1 (Table 6). All but the phalarope exhibited a positive relationship with PC1, indicating higher densities during warm-water conditions (see also Fig. 6). Accordingly, for the two species where GAMs were feasible, density increased with higher PC1 values. Of these, the brown pelican breeds in a warmer area to the south and moves north during ENSO (NOAA, 2008). Brandt's cormorant, on the other hand, breeds locally as well as to the south (NOAA, 2008) and its initial increase in abundance, followed by a precipitous drop at higher PC1 values, may indicate different responses by locally-breeding and visiting birds during warm-water periods: while breeding success fails during warm-water periods, non-breeders move northwards in response to shifting prey distributions.

3.1.4. Patterns explained by multiple factors

The most complex abundance patterns were exhibited by northern fulmar, sooty shearwater, common murre, and Sabine's gull (Fig. 4o–r). Sooty shearwater showed the general trend of species whose variation was explained by year (more abundant in the 1980s), but the higher CV early-on precluded statistical significance (Fig. 4q), despite a 32% decline (Table 7). In its case, upwelling in spring (PC2, negative) and in winter (PC4, positive) were important factors (Table 6).

Common murre and northern fulmar abundance were best explained in opposite ways by PC2 and PC1 (Fig. 4o and p): the murre responded positively to PC1 and negatively to PC2, thus mirroring the pattern of pigeon guillemot, another locally-breeding diving species (Fig. 6). The fulmar showed the opposite response, with a significant positive correlation to PC2 (Table 6).

As for Sabine's gull, PC3 was the significant explanatory variable driving its fluctuations in abundance (Fig. 4r, Table 6). Therefore, stronger winter upwelling (i.e., ocean conditions before these gulls migrated through the study area) was critical. Yet, this species did not show significant changes in abundance over the long-term (Table 7).

3.2. Humpback whale abundance and trends

A total of 173 sightings and 322 humpback whales were recorded during this study (Fig. 7). The whales occurred during eight (80%) and 10 (100%) cruises, respectively, of the early (1985–1994) and the late (1997–2006) periods, and their abundance was significantly higher ($t = -4.309$, $df = 18$, $p < 0.001$) and less variable (F-test of equal variances, $F = 0.103$, $df = 9, 9$, $p = 0.002$) during the latter part of the time series (Table 8). In fact, their mean abundance (±SD), expressed as the number of whales sighted per 100 km^{-2} surveyed, increased six fold (percent chance = 645) during the study: from 0.56 ± 0.81 to 4.21 ± 2.54. Whale abundance was only significantly related to the proxy variable, time ($F = 16.145$, $df = 18, 1$, $p = 0.001$), suggesting there was a positive trend in abundance. This best-fit regression explained 44.4% (adjusted r^2) of the observed variance in whale abundance, and the regression residuals were normally distributed (Kolmogorov–Smirnov one-sample test, *Max_Diff* = 0.124, $n = 20$, $p = 0.882$). None of the other 13 variables was significant ($0.143 < p < 0.982$).

3.3. Comparison of diving and surface-foraging species

Our hypothesis predicted that seabird species with high energy requirements, namely diving species with high locomotion costs, would decline more markedly in response to both bottom-up (i.e., declining productivity) and top-down (i.e., enhanced competition with humpback whales) forcing in the central CCS.

Three divers (50%) and three surface foragers (30%) showed a significant decline in abundance over time, and no species showed a positive trend. When we compared the proportions of divers and surface foragers that exhibited significant increases, significant decreases, and no significant trends using a G-test (Zar, 1990), we detected a significant difference ($G = 8.402$, G *crit.* = 5.991, $df = 2$, $0.025 < p < 0.01$). Furthermore, five of the six diving species considered (all except the Brandt's cormorant, which doubled its mean abundance between the early and the late time periods) exhibited higher mean densities until the late 1980s, followed by a decrease thereafter: Cassin's auklet decreased 83%, pigeon guillemot 84%, rhinoceros auklet 56%, sooty shearwater 34%, and common murre 16%, ashy storm-petrel 76%, and western gull 58% (Table 7).

3.4. Diving species and whales

When we investigated the responses of seabird abundance to humpback whale densities, two divers, rhinoceros auklet and pigeon guillemot (33.3%), and no surface foragers showed a signifi-

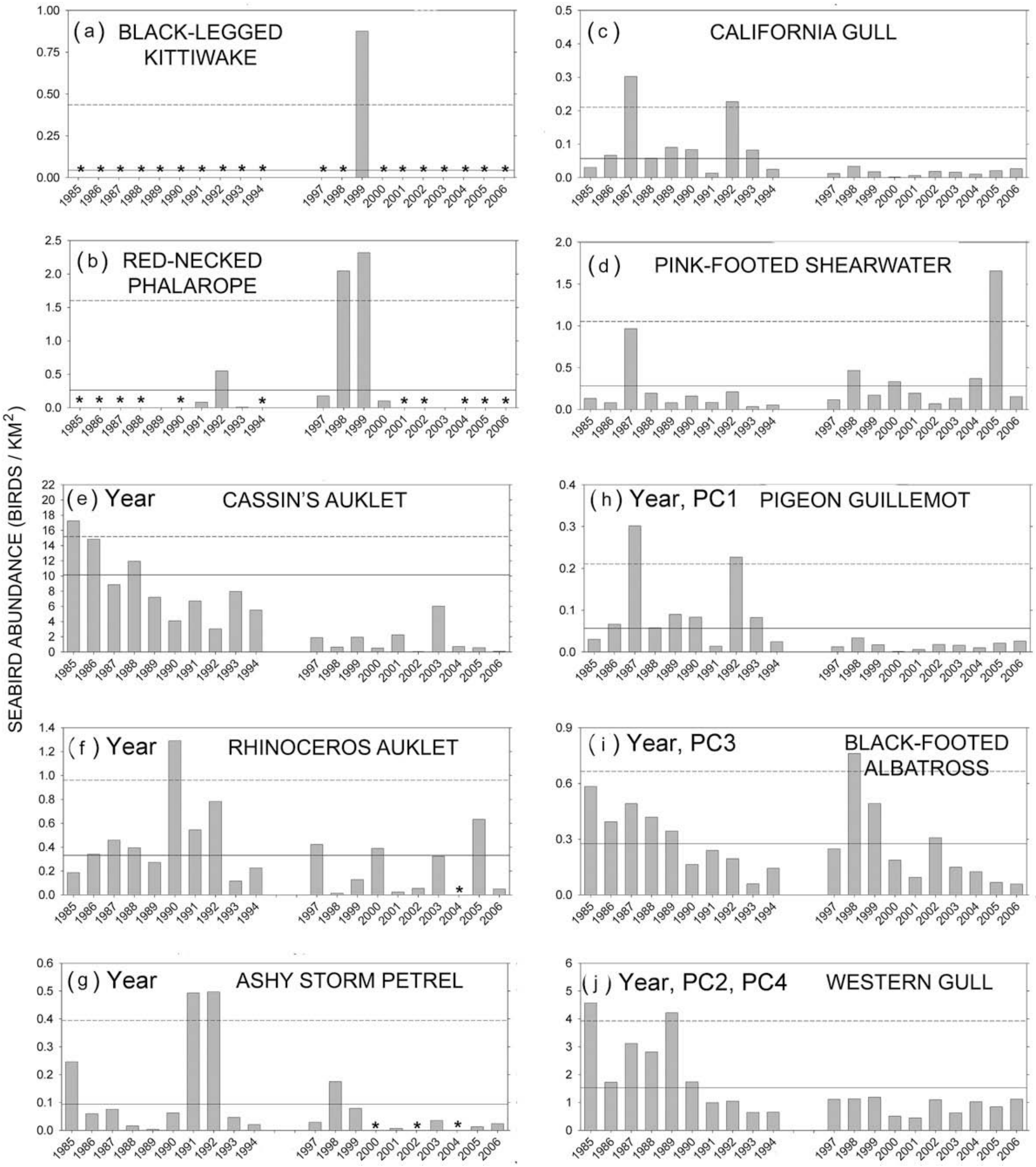

Fig. 4. Time series of abundance of 18 focal species during the early (1985–1994) and late (1997–2006) periods, compared to the long-term mean (solid line) ±1 SD (dashed lines): (a–d) species for which no patterns were discernible, (e–j) those for which "Year" was an important variable, (k–n) those for which PC1 was important, and (o–r) those for which a combination of factors were important. Years when species were not sighted are highlighted with an asterisk (∗).

cant negative response, with no species responding positively (Table 9). When we compared the proportions of divers and surface foragers that exhibited significant increases, significant decreases, and no significant trends using a G-test (Zar, 1990), we detected a significant difference ($G = 52.91$, $G\ crit. = 5.991$, $d = 2$, $p < 0.001$). In fact, in addition to the rhinoceros auklet and the pigeon guillemot, a third diving species (Cassin's auklet) showed a marginally significant ($p = 0.076$) negative response to humpback whale abundance. While the variable year explained a substantially higher amount of the observed variation (adjusted r^2) in seabird numbers than did the humpback whale densities for the Cassin's auklet (62.1 versus 11.9) and the pigeon guillemot (37.5 versus 16.5), the rhinoceros auklet variation was better explained by whale densities than by year (26.4 versus 20.4).

4. Discussion

4.1. Bottom-up forcing to explain patterns

The CCS is warming and becoming less saline; in accord, primary productivity, zooplankton biomass, and general carrying capacity have declined (Venrick et al., 1987; McGowan et al., 1998). As a result, warm-water subtropical seabirds are occurring with increasing frequency, while certain species more characteristic of colder sub-arctic waters are decreasing (Ainley et al., 1995a; Veit et al., 1997; Ainley and Divoky, 2001; Hyrenbach and Veit, 2003). In colder and more productive waters, prey resources are expected to be more abundant and concentrated (i.e., less patchy; see Ballance et al., 1997; Jahncke et al., 2008). Thus, these more

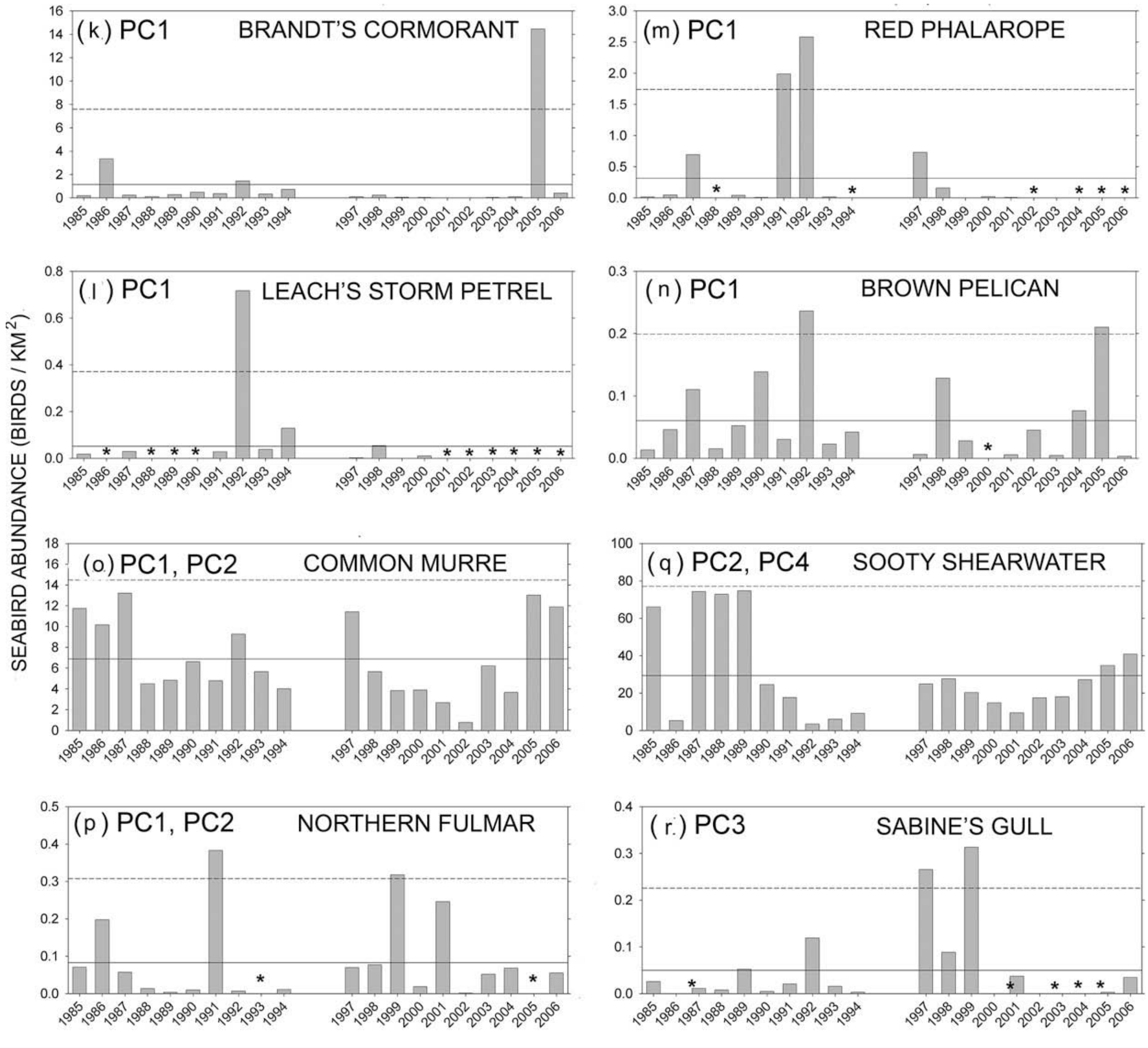

Fig. 4 (*continued*)

Table 7
Results of *t*-tests to assess differences in bird density during the early (1985–1994) and late (1997–2006) periods. The percent chance quantifies the magnitude of the shift in mean density across periods. Bold font highlights those species exhibiting significant long-term changes in abundance. Diving and surface-foraging species are listed separately, in decreasing order of abundance. See Table 4 for definition of species' acronyms.

	Early mean ± SD	Late mean ± SD	Change (%)	*t*-Test (*p*)
SHSO	35.32 ± 32.16	23.44 ± 9.49	−33.65	0.176 (0.862)
MUCO	7.47 ± 3.35	6.30 ± 4.29	−15.68	1.149 (0.266)
AKCA	8.72 ± 4.61	1.46 ± 1.79	−83.26	**4.805 (<0.001)**
COBR	0.74 ± 0.99	1.54 ± 4.54	107.05	1.888 (0.075)
AKRH	0.46 ± 0.35	0.20 ± 0.22	−55.88	**2.594 (0.018)**
GUPI	0.10 ± 0.09	0.02 ± 0.01	−83.62	**4.183 (0.001)**
GUWE	2.15 ± 1.45	0.91 ± 0.28	−57.78	**2.661 (0.016)**
PHRE	0.54 ± 0.95	0.09 ± 0.23	−82.87	1.386 (0.183)
GUCA	0.35 ± 0.91	0.34 ± 0.63	−1.79	1.366 (0.189)
ALBF	0.30 ± 0.17	0.25 + 0.22	−17.91	0.968 (0.346)
SHPF	0.20 ± 0.27	0.37 ± 0.47	84.11	1.551 (0.138)
STAS	0.15 ± 0.19	0.03 ± 0.05	−76.25	**2.143 (0.046)**
FUNO	0.07 ± 0.12	0.09 ± 0.10	20.41	0.789 (0.440)
PELB	0.07 ± 0.07	0.05 ± 0.07	−28.21	1.278 (0.217)
GUSA	0.03 ± 0.04	0.07 ± 0.12	186.12	0.536 (0.599)
STLE	0.09 ± 0.22	0.01 ± 0.01	−93.11	1.960 (0.066)

productive water masses can accommodate diving species, which at a higher energetic cost have lessened search/flight capabilities in favor of a greater ability to dive beneath the ocean surface in pursuit of prey (Ainley, 1977).

Our results reinforce previous research on the changing CCS fauna and carrying capacity, and support the ecological notion that seabirds, specifically, and marine communities, generally, respond to changes in overall ocean *productivity*. However, the entire "community" has not responded in concert. Declining abundance trends are evident mainly among diving species with high energy needs (4 of 7 species, including sooty shearwater, with "year" as a significant explanatory variable): Cassin's auklet, pigeon guillemot, rhinoceros auklet and sooty shearwater. Curiously, none of the alcids in this group, all of which nest locally, exhibited a long-term decline in breeding productivity at least through 1998 (see Sydeman et al., 2001). The decrease in Cassin's auklet and pigeon guillemot numbers is consistent with declines at their main breeding grounds, the Farallon Islands (see Lee et al., 2007; Warzybok and Bradley, 2007). As for the rhinoceros auklet, abundance in central California waters during spring exceeds the breeding population (cf. our Table 2; NOAA, 2008). Therefore, we contend that the decreasing at-sea population could, in part, have involved "floating individuals" in the demographic sense: an excess of mature indi-

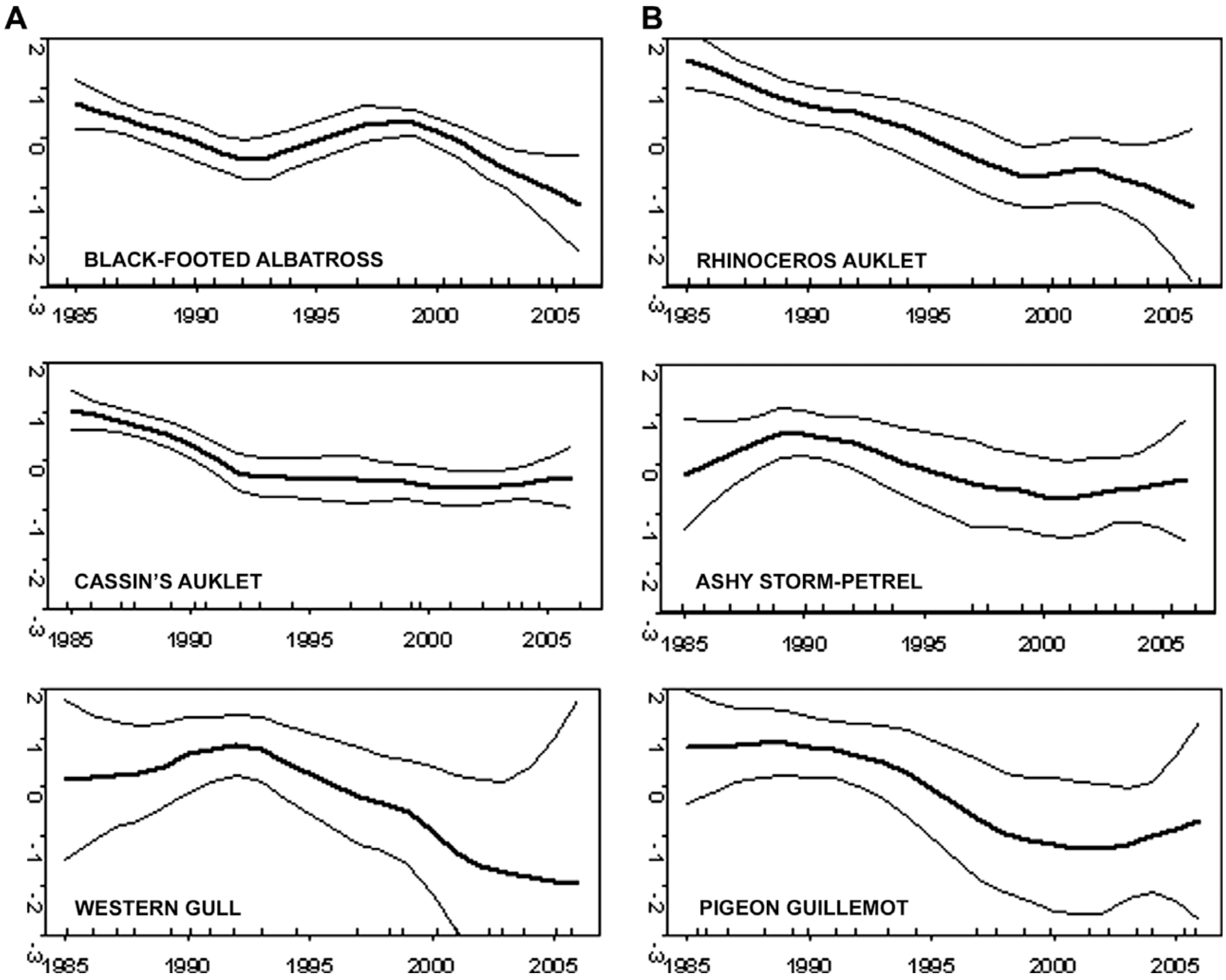

Fig. 5. Generalized additive models (GAM) relating seabird density (number km^{-2}) to the survey year 1985–2006. The best-fit loess function (thick line), the 95% confidence intervals (fine lines), and the distribution of surveys (vertical ticks) are shown. Shown are species that occurred in >75% of cruises: (A) Those with highly significant ($p < 0.003$) trends (cassin's auklet, western gull, black-footed albatross); (B) those with significant ($p < 0.05$) trends (rhinoceros auklet, ashy storm-petrel, pigeon guillemot).

viduals denied breeding by a lack of nest sites at Gulf of the Farallones colonies (Manuwal, 1974; see Ainley and Boekelheide, 1990, for further elaboration of this phenomenon in this region).

In the case of the sooty shearwater, confidence intervals around the observed variation in early years rendered their long-term decline statistically insignificant. However, the apparent decrease in abundance in the CCS from the early (1985–1994) to the late (1997–2006) period coincides with trends in other CCS sectors (Ainley et al.,1995a; Veit et al.,1997; Hyrenbach and Veit, 2003). Large numbers may have shifted to more productive waters elsewhere, but in the later cold-water years, they perhaps exhibited a return to the CCS (Spear and Ainley, 1999; Hyrenbach and Veit, 2003). The shearwater decrease is also consistent with decreases at distant breeding colonies in the southern hemisphere (Hamilton et al., 1997; Jones, 2000).

We believe that decreases in CCS seabirds, at least in part, reflect a climate-driven decrease in prey abundance (see references at the beginning of this section), especially for the locally-breeding species. The negative relationship with spring upwelling (PC2) and the positive relationship with the PDO (PC4) exhibited by the sooty shearwater might also indicate changes in their dispersal within the study area. Shearwaters are likely more prevalent during cold-water periods, but become more concentrated in localized areas in response to dynamic upwelling fronts (e.g., Briggs et al., 1987; Ainley et al., 2005). Therefore, their apparent abundance from year-to-year should be affected by the overlap between the rigid survey grid and those dynamic areas of concentration. In particular, previous analyses have revealed that these shearwaters, unconstrained to forage close to their breeding colonies, shift their distributions from year-to-year and occur in deep waters of the shelf-break and slope (e.g., Briggs et al., 1987; Oedekoven et al., 2001).

A "problem" with the previously offered bottom-up explanation for the decline of CC seabirds in accord with climate-driven decreasing zooplankton volumes (Veit et al., 1997) is that, as determined subsequently, the decrease involved only gelatinous zooplankton (Lavaniegos and Ohman, 2003), which seabirds do not eat, and did not involve euphausiids (Brinton and Townsend, 2003), which seabirds do eat in large quantities. Far more directly involved is likely to be the severe decrease in prevalence of rockfish (*Sebastes* spp.) and other demersal fish (Leet et al., 2001), the juveniles of which once formed the forage base for most upper-level predators in central California waters, including salmon (*Onchorhynchus* spp.), pinnipeds and seabirds (Lenarz, 1980; Ainley and Boekelheide, 1990; Sydeman et al., 2001). Thus, over-exploitation of rockfish spawning biomass, exacerbated by the positive PDO regime, appears to be the main factor behind this decrease (Clark, 2002; Ralston, 2002).

4.2. Top-down forcing to explain patterns

While we ascribe, in part, decreasing trends in certain seabird species to changes in CCS carrying capacity, other factors, besides

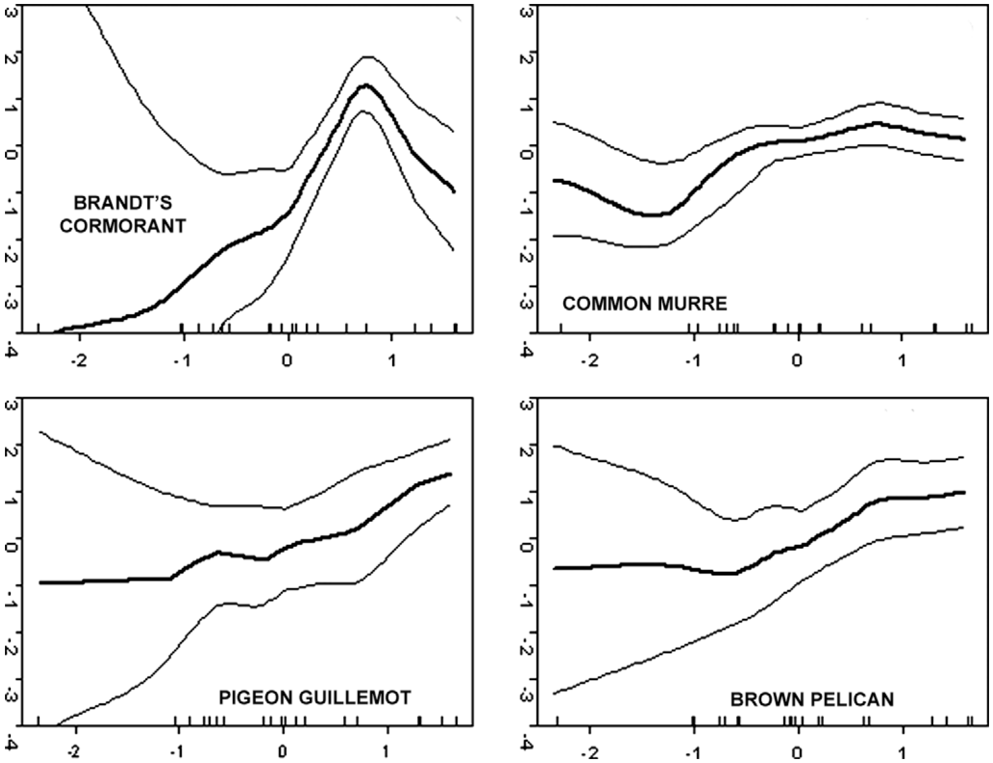

Fig. 6. Generalized additive models (GAM) relating seabird density (number km^{-2}) to PC1 scores. Only those species with significant responses ($p < 0.05$) which occurred in >75% of annual cruises are shown: brandt's cormorant, pigeon guillemot, common murre, brown pelican.

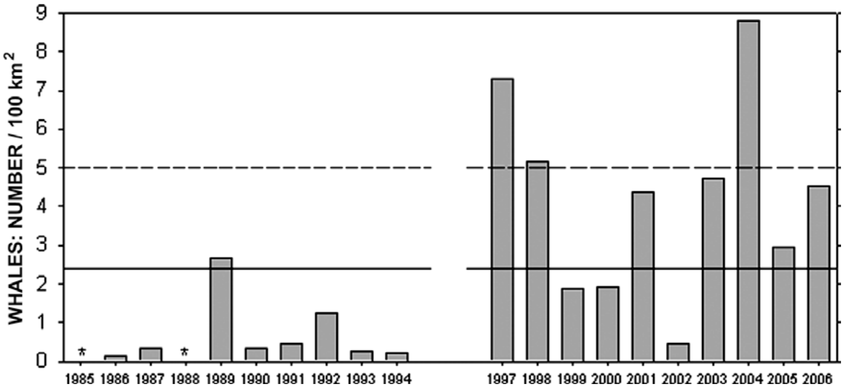

Fig. 7. Time series of humpback whale (*Megaptera novaeangliae*) abundance during the early (1985–1994) and late (1997–2006) study periods, compared to the long-term mean (solid line) ±1 SD (dashed lines). Years when whales were not sighted are highlighted with an asterisk (∗).

Table 8
Humpback whale observations during NMFS-RRS surveys in May–June 1985–2006, showing the occurrence (% of survey years observed) and the number of sightings and individuals recorded during the early and late time periods of the study. Whale abundance (mean, minimum, maximum, CV), calculated as the number of whales seen per 100 km^2 of survey area, is reported for both time periods.

	Occurrence (%)	Sightings	Individuals	Abundance (whales/100 km ^{2})		
				Mean	Min–max	CV
1985–1994	80	40	66	0.56	0.00–2.66	144.62
1997–2006	100	133	260	4.21	0.45–8.81	60.51

over-exploitation by humans, are likely involved in affecting food availability to these predators.

Concurrently with these seabird decreases, humpback whales, which feed on the same prey (euphausiids, forage fish) and in the same waters used by seabirds during the breeding season (see NOAA, 2008), have increased 3–9-fold in the study area from the late 1980s to the late 2000s (Fig. 5; see also Pyle and Gilbert, 1996). Because the step-increase in whale abundance in the study area contrasts the overall gradual trend for the species in the eastern North Pacific after the cessation of whaling (Calambokidis and Barlow, 2004), it likely involves a distributional shift suggestive of a return to a former 'tradition' of foraging over the CCS shelf (see

Table 9
Linear regression analysis of the relationship between seabird density and humpback whale density and results of the associated normality tests of the regression residuals (Kolmogorov–Smirnov test, $n = 20$). The percent of the variance explained by the best-fit models and the associated p-values are shown. The sign (positive/negative) of the coefficients are reported for marginally significant results ($p < 0.10$). Significant ($p < 0.05$) results are highlighted in bold font. Diving and surface-foraging species are listed separately, in decreasing order of abundance. See Table 4 for definition of species' acronyms.

	F	p	% Variance	Regression residuals	
			r^2	Max diff	p
SHSO	0.248	0.624	0	0.119	0.910
MUCO	0.380	0.849	0.2	0.129	0.850
AKCA	−3.554	0.076	11.9	0.196	0.377
COBR	1.276	0.273	1.4	0.132	0.830
AKRH	−7.823	0.012	**26.4**	0.100	0.976
GUPI	−4.760	0.043	**16.5**	0.136	0.807
GUWE	1.839	0.192	4.2	0.107	0.958
PHRE	0.024	0.879	0	0.235	0.186
GUCA	1.359	0.259	1.9	0.169	0.563
ALBF	1.094	0.309	0.5	0.128	0.858
SHPF	1.502	0.236	2.6	0.149	0.709
STAS	2.114	0.163	5.5	0.125	0.874
FUNO	0.954	0.342	0	0.122	0.893
PELB	0.410	0.530	0.1	0.129	0.849
GUSA	1.125	0.303	0.7	0.108	0.954
STLE	0.397	0.536	0	0.334	0.017

Whitehead, 2003, for a discussion of 'culture' and movement patterns in another cetacean species). Those traditional foraging grounds were vacated owing to harassment from shore-based whalers that persisted as late as the mid-1970s (Tønnessen and Johnsen, 1982; chapter on shore-based whaling on US West Coast). Moreover, another once-hunted species, the blue whale, has increased in a similar step-like fashion in shelf-break and slope waters of the CCS during summer. However, because they occur in the study area one or two months after our cruises, we have no direct data on their distribution and abundance (see graphs in Pyle and Gilbert, 1996; NOAA, 2004; Croll et al., 2005). The blue whales, which feed mainly on euphausiids (NOAA, 2008), are present during a critical period when the fledglings of locally-breeding seabirds are first beginning to forage and breeders are attempting to recover their body condition. Therefore, this is a critical time for the energetic recovery of breeding adults and the survival of both adults and fledglings.

While individual humpback whales can make a huge impact on prey stocks in North American coastal waters, by consuming on the order of 338–370 kg of prey per individual per day (Tynan, 2004; Witteveen et al., 2006), we are not arguing that exploitative competition between whales and seabirds is the main driver of prey availability to seabirds in the central CCS. Indeed, as noted above, while overall zooplankton has decreased in this system, the abundance of euphausiids has not; however, there have been marked decreases in the stocks of salmon, rockfish and whiting (*Merluccius productus*; Leet et al., 2001). Because these competitors have a diet similar to that of the seabirds and whales, their decreases conceivably have left a prey "surplus" (see Ainley et al., 2009, for a discussion of co-occurrence of whales, birds, salmon and their prey in coastal Northern California and Oregon). Rather, therefore, we argue that interference competition, whereby the whales would significantly reduce the number and density of near-surface prey schools, forcing the seabirds to increase their search time and diving depth. This increase in foraging effort would in turn have a negative impact on seabird energetics. The potential for close co-occurrence and interference competition (i.e., the birds and the whales are feeding side-by-side) has been documented in eastern North Pacific waters by the occasional inadvertent consumption of Cassin's auklets by co-foraging whales (Dolphin and McSweeney, 1983). Interestingly, a recent BBC video clip shows exactly what we are talking about: a "ball" of forage fish formed to defend against attack from below by diving seabirds (murres) and from above by aerial birds (gulls) is suddenly removed from the scene by one humpback whale gulp (http://news.bbc.co.uk/2/hi/science/nature/7940396.stm).

The observed decreases in the population size of diving species indirectly supports the hypothesis of Ballance et al. (2009) that the relationship between seabird breeding population size and food availability is mediated through the energetics of foraging. As noted previously, diving species have the highest foraging costs. Furthermore, higher metabolic costs of foraging have been documented in individuals breeding in the largest colonies, a pattern suggestive of intra-specific competition for food requiring longer foraging trips at larger colonies (Ballance et al., 2009). This model further predicts that maximum colony size within a species should vary owing to regional differences in prey availability. In the case of pigeon guillemot, Cassin's auklet and western gull (see below), study area colonies are, respectively, the largest in the world (Ainley and Boekelheide, 1990; NOAA, 2008). The observed decreases in large populations of locally-breeding seabirds as the productivity of the CCS has declined, with greater changes in diving species having an energetically costly foraging method, are consistent with the conjectures of Ballance et al. (2009).

The documented decrease in the western gull at-sea population, consistent with a long-term decrease in their reproductive output (Sydeman et al., 2001) and their Farallon breeding population (Warzybok and Bradley, 2007), can also be attributed to the declining prey availability mentioned above.

4.3. Other factors involved in seabird trends

Additional species-specific ecological factors influenced the observed trends for the other focal species. For instance, we contend that changes in breeding habitat at the main breeding site, SEFI, is likely the main factor regulating the ashy storm-petrel population (USFWS, 2007). Sydeman et al. (2001) detected a decline in this species' productivity but only beginning in the later 1990s, well after the decline in at-sea numbers. Thus, this timing argues against oceanographic population drivers. In fact, the storm-petrel is a surface forager with very efficient flight, not having the high energy needs of diving species.

Another species that was less abundant later in the study period is the California gull. Like the sooty shearwater, the observed lack of a statistically significant trend seems to be due to the large confidence intervals during the early period. Yet, this species' year-to-year variation was not explained by oceanographic factors. These abundance patterns are likely related to continental rather than marine factors, since this species nests inland in North America (see Wredge et al., 2006).

The remaining species exhibited a more complex relationship in both the patterns of their abundance, and to the environmental correlates. Leach's storm-petrel, brown pelican, Brandt's cormorant and common murre were more abundant at sea during ENSO (a higher PC1 score), likely because fewer individuals occupied breeding sites (Ainley and Boekelheide, 1990) and spent more time at sea. Red phalarope and northern fulmar showed the opposite relationship to PC1, indicating lower abundance in the study area during ENSO. Murre and fulmar prevalence was also affected by the extent of spring upwelling; the murre apparently spent more time at colonies and the fulmar more time in the study area when spring upwelling was stronger. None of these species exhibited overall trends in abundance at sea, although murre numbers at SEFI, their main colony, have been increasing (Warzybok and Bradley, 2007).

4.4. Final thoughts

Our study highlights the complexity of the responses of marine species, particularly far-ranging seabirds, to variations in environmental conditions affected by remote and local forcing operating at multiple temporal scales. We addressed seabird distributions during spring/early summer, a critical period of migration and reproduction for locally-breeding species. Other studies that have sampled the central CCS across seasons over multiple decades have documented long-term changes in water column structure, nutrient availability, and plankton and fish biomass, which are consistent with the seabird trends we report herein (e.g., Peterson and Schwing, 2003; Brodeur et al., 2007). On the other hand, our results suggest that additional ecological factors, such as inter- and intra-specific competition for food, are also important determinants of seabird trends. Additionally the plight of 'shifting baselines' in marine ecosystems, a major problem hindering the interpretation of historical trends and contemporary data, must be kept in mind as ecologically key species (i.e., whales), recover from earlier decimation (e.g., Pauly, 1995; Schrope, 2006).

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