LONG- AND SHORT-TERM FACTORS AFFECTING SEABIRD POPULATION TRENDS IN THE CALIFORNIA CURRENT SYSTEM 1985-2006

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Abstract. We analyzed trends in abundance of the most abundant marine bird species in the northern California Current System (CCS) during the upwelling season (May-June) over a 22-year period 1986-2007. Standardized seabird survey data were collected during annual cruises that ranged from Bodega Bay (38.32° N) to Cypress Point (35.58° N), and within this latitudinal range from the coast to the bottom of the continental slope (3000-m isobath). Indices of large-scale (basin-wide), regional (CCS), and local (study area) oceanographic data were used to characterize the response of seabird densities (number km $^{-2}$) to environmental variability. The study occurred during a period of major fluctuations of El Niño-Southern Oscillation conditions (ENSO), and longer-term Pacific Decadal Oscillation variability (PDO). We related variation in species' abundance, with three seasonal lags: Late Winter (January – February); Early Spring (March – April); and Late Spring (May – June), to a suite of physical ocean and climate factors: Multivariate ENSO Index, PDO, coastal upwelling indices and sea-surface temperature. We detected cyclical trends in the abundance of the Black-footed Albatross (*Phoebastria nigripes*), and decreasing trends for Sooty Shearwater (*Puffinus griseus*), Pigeon Guillemot (*Cepphus columbus*), Rhinoceros Auklet (*Cerorhinca monocerata*), Cassin's Auklet (*Ptychoramphus aleuticus*), and Western Gull (*Larus occidentalis*) in the study area. A decrease in Ashy Storm-petrel (*Oceanodroma homochroa*) numbers may have been related to a loss of nesting habitat. No long-term pattern was evident in the numbers of Northern Fulmar (*Fulmarus glacialis*), Pink-footed Shearwater (*P. creatopus*), Leach's Storm-Petrel (*O. leucorhoa*), Common Murre (*Uria aalge*), Red Phalarope (*Phalaropus fulicarius*), Brandt's Cormorant (*Phalacrocorax pennicillatus*), Brown Pelican (*Pelecanus occidentalis*), and Sabine's Gull (*Xema sabinii*). Species varied in the degree to which remote versus local environmental factors explained annual variation in numbers. We hypothesize that decreasing trends, and even some of the short-term variability, was related to changes in ocean productivity and food availability. On the other hand, increasing trophic competition from baleen whales, which as suggested by a step-like pattern of population increase apparently rediscovered the study area where not long ago they had been harassed by whalers, may have been involved in some of the seabird trends as well; also involved likely were changes in characteristics of nesting grounds. Overall, our study points to the complexity of marine species' responses, particularly among far-ranging seabirds, to variation in the physical attributes of their habitat, which are in turn affected by remote and local climatic forces operating at multiple temporal scales.

Key words: bottom-up forcing, California Current, climate change, ENSO, baleen whales, PDO, seabird, top-down forcing, upwelling

INTRODUCTION

The California Current System (CCS) is highly dynamic, with its biota, including economically-important fish, invertebrate and marine mammal populations, fluctuating in abundance on decadal and longer temporal scales in response to climatic forcing (e.g., Baumgartner et al. 1992, Field et al. 2006). While these natural fluctuations are known to have occurred before the onset of human interference, marine populations have increasingly become subject to unprecedented and concurrent climatic and anthropogenic forcing during the last 250 years (e.g., Bovy 2007, Newsome et al. 2007). Yet, the factors currently impacting pelagic portions of marine communities appear linear in nature, rather than the cyclical changes documented in the archeological and historical record (e.g., Glantz and Thompson 1981; Baumgartner et al. 1992). Many changes in substrate-related portions are apparently non-linear (e.g. Sagarin et al. 1999, Helmuth et al. 2002).

In regard to human interference with pelagic communities of the CCS, first was the commercial extraction of top predators, the fur seals and whales (Doughty 1974, Tønnessen and Johnsen 1982), followed by the mid-level predators (sardines *Sardinops sagax*, anchovies *Engraulis mordax*, whiting *Merluccius productus*, salmon *Oncoryincus* spp., rockfish *Sebastes* spp., blue sharks *Prionace glauca* and albacore tuna *Thunnus alalunga*) (Leet et al. 1992, OEUVRE 1998). Increased warming of the ocean in the last 50 years has further impacted the CCS by forcing a shift from a productive subarctic towards a depopulated subtropical environment (Venrick et al. 1987, Veit et al. 1997, McGowan et al. 1998). This biogeographic transition has led to concurrent increases in warm-water species and declines in cold-water species (Moser and Smith 1993, Hyrenbach and Veit 2003).

How the quintessential epipelagic, and highly mobile seabird component has responded to these changes is difficult to surmise, as few historical records precede the modern era (see Ainley and Lewis 1974). This makes it difficult, for one thing, to determine whether seabirds once played an important ecological role in this ecosystem. However, three lines of evidence suggest that the seabird community of the CCS could well have exerted a significant downward pressure on food web structuring: (i) the avifauna is dominated by numerous diving, heavy-bodied species with high energetic requirements, some of which - like murres (*Uria aalge*) and shearwaters (*Puffinus griseus*) - are capable of exploiting the entire neritic water column (e.g., Hodum et al. 1998, Ainley et al. 2002); (ii) these species once numbered in untold millions (e.g., Ainley and Lewis 1974, Briggs et al. 1987) and (iii) largely feed on euphausiids (*Euphausia pacifica, Thysanoessa spinifera*), clupeid fish (e.g., sardines, anchovies) and the juveniles of larger fish (e.g., salmon, rockfish) that currently sustain the CCS marine food web (e.g., Ainley 1977, Sydeman et al. 2001).

Highly capable of switching among these several prey species, depending on availability (Chu 1984, Ainley and Boekelheide 1990, Ainley et al. 1996), avian populations respond successfully to short-term ecosystem fluctuations, such as El Niño-Southern Oscillation (ENSO; e.g., Ainley et al. 1995b) and longer-term oceanographic variability, such as the Pacific Decadal Oscillation (PDO; e.g., Irons et al. 2008). In the case of ENSO, seabird responses involve short term (< 1 year) shifts in at-sea distributions and failures in breeding success, due to nest abandonment and chick mortality (e.g., Ainley et al. 1995a, b). These short-term fluctuations do not usually impact seabird populations, for these are long-lived species with delayed maturity and high adult survivorship rates (Ainley and Boekelheide 1990). Skipping a year of breeding has little consequence. Nowadays, however, these

populations are also being impacted simultaneously by human activities directly (e.g., oil pollution, fisheries by-catch, egging, direct 'harvest', disturbance of breeding sites) and indirectly (e.g., loss of prey due to competition with fisheries, global warming) (Ainley et al. 2002, Bovy 2007). Together, all of these anthropogenic and climatic impacts are making it increasingly difficult for K-selected seabirds to recover from short-term oceanographic variability (Ainley and Divoky 2001).

In a system where top-down structuring is no longer a significant factor due to the removal of upper-trophic predators (Heithaus et al. 2007), seabird populations are expected to respond to bottom-up climate forcing, associated with inter-annual, decadal and longer-term warming of the CCS (e.g., Ainley et al. 1995b, Ainley and Divoky 2001, Hyrenbach and Veit 2003). Whether or not avian populations, without the buffering provided by an intact food web (e.g., McCann et al. 1998, Post et al. 2000, Terbrogh et al. 2001, Soulé et al. 2005), now respond more dramatically to climate fluctuation is a matter for discussion. It seems likely that this is so (e.g., Post et al. 2000; Finke and Denno 2005; Wilmers et al. 2006a, b; Sala 2006). In any case, to further our understanding of seabird population patterns in the modern era, we present here a summary and analysis of the trends exhibited by the major components of the neritic avifauna in the central portion of the CCS during a 22-year period (1985-2006). We relate changes to a suite of climatic factors, which are easier to track in this system than changes to the food web brought by direct and indirect anthropogenic influences on prey availability. Yet, the crucial assumption underlying this analysis is that these changes in oceanographic conditions influence the productivity and ecosystem structure of the CCS. We also suggest that biological factors, i.e. top-down forcing and indirect effects of changes to nesting grounds, may be involved in seabird trends as well.

METHODS

Study Area

Data on seabird distribution and abundance were collected during National Marine Fisheries Service rockfish recruitment assessment (NMFS – RRS) cruises onboard the *NOAA Ship David Starr Jordan*. These cruises sample a series of 31 net tow stations and 47 conductivity-temperature-depth (CTD) stations, extending from Bodega Bay (38.32° N) to Cypress Pt.(35.58° N), near Monterey, California. Net tow stations are scattered across the continental shelf – upper slope (depth <1000m) and the CTD stations are arranged along 11 lines with a 20-km spacing, spanning from the coast out to up to ~ 100 km from the coast (Schwing et al. 1991). This station grid has been repeatedly surveyed yearly (1986–1994 1997–2006) during 1-2 replicate sweeps in the late spring (May–June).

While cruises sampled the most intense portion of the upwelling season (May – June) (Schwing et al. 1991, Baltz 1997), the timing and survey track-lines of individual sweeps varied slightly from year to year. To facilitate annual comparisons, we standardized the survey effort by constraining analysis to the same two-month time period (May 1 – June 30) and geographic area (Fig. 1). We focused on the area extending from the shore to the offshore edge of the grid of hydrographic stations, defined using a 20-km buffer around each CTD station. A total of 6841 km^2 (yearly mean 342 ± 159 km^2 SD) were surveyed over 20 years (early period: 1985-1994, late period: 1997-2006) with no effort in 1995 and 1996 (Table 1).

Southeast Farallon Island (SEFI) (37.7 ^{o} N, 123 ^{o} W), the largest seabird colony in the continental USA, is located in the middle of the study area (Fig. 1). Eleven seabird species breed here (March – July) (Ainley and Boekelheide 1990). A subset of these species breeds on other smaller islands, islets and headlands in the study area (NOAA 2008).

Survey protocol

Seabirds (and marine mammals) were surveyed using standardized 300-m strip transects (Spear et al. 2004; 800 m for mammals, see Keiper et al. 2005), modified to account for the relative flight speed and movement of flying birds (Spear et al. 1992). At least two observers, stationed on the flying bridge (12 m asl), surveyed the strip simultaneously while the vessel was underway and recorded every seabird (and mammal) sighted within a 90^{o} arc on the side of the track with least glare (Spear et al. 2004). Continuous seabird counts were summed every 15 min (~ 4 km at the cruising speed of 9 – 10 kt, 16.7 – 18.6 km hr $^{-1}$) and matched with the vessel's position and with the sea surface temperature (SST) from the closest CTD station during a given survey sweep. 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).

Environmental data-sets

We used five environmental data sets indicative of monthly oceanographic conditions in the eastern North Pacific: large-scale variability associated with the Pacific Decadal Oscillation (PDO) and the El Niño Southern Oscillation Index (ENSO) indices (Fig. 2); regional indices of coastal upwelling at two reference sites (39^{o} N, 36^{o} N); and local SST conditions from CTD casts during annual cruises (Fig. 3).

The PDO Index, defined as the leading principal component (PC) of monthly North Pacific SST poleward of 20^{o} 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). These data are available online (www.jisao.washington.edu/pdo). The Multivariate ENSO Index (MEI) is based on the first PC of six combined fields (sea-level pressure, zonal and meridional surface winds, SST, surface air temperature, and total cloudiness fraction of the sky) for the tropical Pacific Ocean (30^{o} S – 30^{o} N), seasonally-adjusted with respect to the 1950-1993 reference period. Negative values of the MEI represent La Niña (cold), while positive values represent El Niño (warm; Wolter and Timlin 1998). These data are available online (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 two regional upwelling indices from reference locations centered to the south (36° N) and to the north of the study (39° N). This approach provided complete spatial coverage of the study area. Furthermore, because upwelling is highly seasonal, we used site-specific monthly anomalies to account for shifts in timing and magnitude from year to year. We also quantified local SST conditions during annual cruises, as indexed by the water temperature interpolated at the 15-min survey bins surveyed within the study area.

Data analysis

Environmental data. —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 used to quantify large-scale and regional oceanographic conditions. 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 for all pair-wise cross-correlations between variables.

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, 1995a, b). Thus, we included antecedent environmental conditions as explanatory variables in our analysis of at-sea seabird abundance. We lagged each time series by up to 12 mo and quantified the "temporal patch scale" of each time series as the point along the time domain where the correlogram first became insignificant (Sokal and Oden 1978). Because we attempted a total of 54 correlations (12 lags * 4 variables, 6 pair-wise cross-correlations), we adjusted our alpha level accordingly. Thus, we considered statistical ($r > 0.2$, $p < 0.001$) and biological significance ($r > 0.4$, $p < 0.0001$) using more conservative levels than the standard alpha = 0.05 (Hyrenbach and Veit 2003, Ainley et al. 2005).

To account for the time lags between changes in large-scale / regional oceanographic conditions and shifts in seabird distributions, we considered three distinct time periods preceding the spring (May – June) seabird surveys: Late Winter (January – February); Early Spring (March – April); and Spring (May – June). For each of these time periods, we quantified four environmental conditions (MEI, PDO, upwelling south of the study area, upwelling north of the study area) by averaging the monthly data for two consecutive months listed above. This process yielded four time series of environmental variables preceding seabird surveys off central California by 0-1, 1-3 and 3-5 mo, respectively. In addition to these oceanographic variables, we used the mean value of the SST data measured in-situ during the May – June surveys, to reflect the local conditions surveyed by the ship during each cruise.

Overall, we considered a total of 13 environmental variables in our analysis. 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 those principal components with large eigenvalues (>1) in the model, and varimax-rotated the axes to facilitate interpretation of the results (Weichler et al. 2004, Ainley et al. 2005).

Seabird data. — We focused our analysis on the most "common" seabird species: those found consistently (> 50% of cruises) and accounting for at least 0.1% of all the birds sighted during the study period (Table 2; which also contains scientific names for avian species). We used Systat 11.0 (© 2002 SYSTAT Software Inc.) to examine the relationship between the abundance (bird density) of 16 "common" species and five independent explanatory variables: four principal components (PCs) from the multi-variate analysis of the oceanographic variables (see results) and one temporal variable (year since start of the time series) designed to account for linear time trends in seabird abundance.

We used a multiple regression analysis, with a backward and forward fitting procedure, to relate the density (birds km^{-2}) of each focal seabird species to the five explanatory

variables described above. 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 ($p \leq 0.10$), and report the performance (adjusted r^2) of the best-fit models. Seabird densities were log-transformed 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 showing 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 density (PC) = [(late density - early density) * 100 / (early density)] (Hyrenbach and Veit 2003).

Whale data. — In the latter part of the paper, when commenting on trends in certain seabird species, we make reference to the increase of Humpback Whales (*Megaptera novaeangliae*) that occurred during the study. Cetaceans were tallied if they occurred within the seabird survey transect expanded out to 800 m, and are expressed herein as the number of whales seen per cruise day for each year, thus to compensate for variable lengths of cruises. A cruise day was generally steaming between CTD stations, the latter interrupting transit for 20-60 min intervals depending on depth. Thus, this is just an index of relative whale abundance, and not a corrected population estimate based on line-distance methodology, for which the required sighting distance and angle data are not available.

RESULTS

Relationships among environmental variables

Correlations. —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, $n = 275$, $p < 0.001$). 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 and PDO) and for the two regional variables (UP-36 and UP-39) (Table 3).

The autocorrelation analysis revealed significant temporal patterns for all four environmental variables (Fig. 4). The two large-scale oceanographic variables were characterized by the largest temporal patch 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 patch scales, with marginal cross-correlations ($0.4 < r < 0.2$) at a lag of one and two months.

Principal component analysis. —To account for the co-variation of environmental variables, we combined them into four principal components (PC) with eigenvalues >1, which together explained 82.83% of the variance (Table 4). Using those variables with strong loadings (>0.5), we describe these 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^{o} N and 39^{o} N; PC3 was associated with winter-time upwelling at both 36^{o} N and 39^{o} 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 a temporal variable (year since the start of the time series) using Spearman rank tests (df = 19, r_s critical = 0.433). These correlations were not significant, indicating no trends in spring-time environmental conditions sampled during the study: 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). Therefore, we included five independent variables in our analysis of seabird abundance: the four orthogonal PC factors and the year since the start of the time series.

Seabird species composition and abundance

Over 20 years of surveys, observers recorded 45,894 sightings of 418,054 birds belonging to 69 taxa. This analysis focuses on "common" species, as defined above. While 18 species met the abundance threshold, only 16 met the number-of-cruises criterion (Table 2). Herein, we report interannual patterns of abundance for 18 species, but perform statistical analyses for only 16, owing to statistical constraints related to sample size (Table 5).

We combined the focal species into five categories, on the basis of their long-term responses in abundance over the study period (1985-2006):

Species for which no variable explained patterns. — The multiple regression analysis failed to yield significant results for four species considered in this analysis: Pink-footed Shearwater, Red-necked Phalarope, Black-legged Kittiwake, California Gull (Tables 6, 7). The kittiwake and phalarope exhibited what appeared to be 'flight years', an ornithological term used to describe isolated short-term (1 – 2 yr) re-distributions of large numbers of birds (Fig. 5a, b). Coincidentally, the only incursions of the subarctic (breeding in Alaska) kittiwake took place during the 1999, an anomalously cold-water year of enhanced spring upwelling and large numbers of these birds also occurred off southern California (33 – 36 ^{o} N) in 1999 (Bograd et al. 2000). While the phalaropes occurred in the study area more frequently (45% of cruises), they were too variable to show any significant trends between the early (1987-1994) and late (1997-2006) study periods, despite a 83% proportional decline (Table 7).

The shearwater and the gull did not change significantly in abundance (Fig. 5c, d), even though the average density of the shearwater almost doubled (84% increase) from the early (1987-1994) to the late (1997-2006) periods (Table 7). The shearwater, a subtropical species that breeds in Chile and ventures into the eastern North Pacific during the boreal spring and summer, has increased significantly off southern California, as well (1987-1998) (Hyrenbach and Veit 2003).

Species for which patterns were explained by year. — Black-footed Albatross, Ashy Storm-petrel, Cassin's Auklet, Rhinoceros Auklet, Pigeon Guillemot, and Western Gull all showed trends in which year was the model factor that explained important variation (Fig. 5e-j). In the case of the five locally-breeding species, the pattern was one of higher mean densities in the late 1980s, and a gradual decrease to a lower mean density by the early 1990's. Overall, these species declined by at least 50%: Cassin's Auklet (83%), Pigeon

Guillemot (84%), Ashy Storm-petrel (76%), Rhinoceros Auklet (56%), and Western Gull (58%). The only far-ranging visitor among these species, Black-footed Albatross, did not decline significantly over the long-term, though its average density dropped by 18% from the early (1985-1994) to the late (1997-2006) time periods (Table 7)**.** Rather, it exhibited a repeating pattern of two 'cycles' of high and low abundance (Fig. 5i), with peaks in 1985 and in 1998. The GAMs helped to visualize these trends in seabird abundance over time (Fig. 6).

In the case of three species, other factors contributed to the variation explained by year (Table 6). For Pigeon Guillemot, variation in abundance was further explained by the remote oceanographic factors associated with the MEI and PDO (PC1); for Black-footed Albatross, winter upwelling was also important (PC3); and for Western Gull, spring upwelling and the PDO during winter were important (PC2, PC4)..

Species for which patterns were explained by MEI / PDO. —Not showing any patterns related to long-term trends (Table 7) were Leach's Storm-petrel, Brown Pelican, Brandt's Cormorant, and Red Phalarope (Fig. 5k-n). The abundance of these species was significantly affected by basin-scale environmental fluctuation (MEI / PDO), as indicated by the importance of PC1 in explaining their variation (Table 6). All but the Red Phalarope exhibited a positive relationship with the PC1 variable, suggesting higher densities in the study area during warm-water conditions. The GAMs helped to visualize responses to variation in the PC1 Factor, except for those species where this analyses was inhibited by small sample sizes (occurrence in < 75% of cruises) (Fig. 7). For the two species where GAMs were feasible, we documented increases in density during years with higher PC1 values (warm-water conditions). The Brown Pelican breeds exclusively south of the study area (in Southern and Baja California) and moves north during ENSO years (Ainley et al. 1995a, NOAA 2008). The Brandt's Cormorant breeds within and to the south of the study area, including the Farallones (NOAA 2008). Thus its initial increase in abundance, followed by a precipitous drop at higher PC1 values, is suggestive of different responses by locally-breeding and visiting birds during warm-water periods: non-breeders have more freedom to move elsewhere.

Species for which patterns were explained by a complex of factors. —The most complex patterns in abundance variation were exhibited by Northern Fulmar, Sooty Shearwater, Common Murre, and Sabine's Gull (Fig. 5o-r). The Sooty Shearwater showed the same general trend exhibited by the other species whose variation was explained by year (more abundant in the 1980s), but the higher variation (CV) early on precluded statistical significance (Fig. 5q), despite a 32% decline in average densities from the early (1985-1994) to the late (1997-2006) periods (Table 7). In its case, spring (PC2, negative) and winter (PC 4, positive) upwelling were the critical factors involved (Table 6). Previously, Sooty Shearwaters were shown to have declined off central (1985-1994) and southern (1987-1998) California (Oedekoven et al. 2001, Hyrenbach and Veit 2003).

Variation in the abundance of Common Murre and Northern Fulmar were best explained by PC2 and PC1 (Fig. 5o, p), but in opposite ways: the murre showed a positive relationship to PC1 and a negative response to PC2. The response of the murre mirrors that of the Pigeon Guillemot, another locally-breeding seabird with a positive response to PC1 (Fig. 8). The fulmar showed the opposite response, with a significant response to PC2.

In the case of Sabine's Gull, PC3 was the significant explanatory variable driving its fluctuations in abundance (Fig. 5r, Table 6). Therefore, stronger winter upwelling (i.e.,

conditions before these gulls passed through the study are in migration) was critical. Yet, this species did not show significant changes in abundance over the long-term (Table 7).

DISCUSSION

Bottom-up forcing to explain patterns

Noted above (Introduction) is the well-agreed upon fact that the CCS is warming, as well as becoming less saline; in accord, primary productivity and zooplankton biomass has declined as well (Venrick et al. 1987, McGowan et al. 1998). As a result, warmer-ocean species, including seabirds, have begun to appear at increasing frequency or have become more prevalent (see references above). Certain species more characteristic of colder, more productive waters have been declining (Ainley et al. 1995, Veit et al. 1997). In colder, more productive waters, resources (prey) are expected to be more abundant and concentrated (i.e., less patchily distributed). Thus these water masses favor diving species, which have lessened flight capabilities in favor of a greater ability to dive beneath the ocean surface in pursuit of prey (Ainley 1977, Spear and Ainley 1998, Hyrenbach and Veit 2003).

The results of our study reinforce previous research on the changing CCS fauna, and support the ecological notion that seabird species, specifically, and marine communities, in general, respond to changes in the productivity of the system. Declining abundance trends were evident in the at-sea populations of several diving species: Cassin's Auklet, Pigeon Guillemot, Rhinoceros Auklet, and Sooty Shearwater. Curiously, none of the alcids in this group exhibited a long-term decline in breeding productivity at least through 1998 (see Sydeman et al. 2001), although a more recent reproductive failure occurred in 2006 and 2007 due to unusual atmospheric and oceanographic conditions (Goericke et al. 2007). The decline in the at-sea population of Cassin's Auklet is consistent with modeled declines at their main breeding grounds, SEFI (see Lee et al. 2007), but no data are available on population trends of the other two alcids in the above group. However, it is obvious to us that at times there are far more, for example, Rhinoceros Auklets at sea in central California waters than there are breeders (cf. our Table 2 and NOAA 2008). Therefore, we conjecture that the declining populations we documented at sea at least in part involved 'floating individuals' (in the demographic sense). Namely, we believe this includes excesses of mature individuals denied breeding by a lack of nest sites (see also below). Among central California colonies, Rhinoceros Auklets and Pigeon Guillemots are constrained largely to nest in natural cavities, there clearly being a lack of soil for digging burrows. Each of these three species of alcids compete for any natural cavities at SEFI and elsewhere in the study area (see for example, Manuwal 1974); indeed, the larger guillemot and auklet expel from the larger cavities the smaller Cassin's Auklet, which attempts to nest earlier (Ainley and Boekelheide 1990).

In the case of the shearwater, confidence intervals around variation early in the study period rendered statistical significance to their apparent decline somewhat problematic. However, the trends we observed are consistent with those reported for other sectors of the CCS from waters off southern California to Washington State (33 – 48^{o} N) (Ainley et al. 1995b, Veit et al. 1997, Hyrenbach and Veit 2003). The shearwater's decline in the CCS is consistent, too, with declines detected at breeding colonies (Hamilton et al. 1997, Jones 2000; see also Lyver et al. 2001). We believe that the declines of the shearwater and the other species discussed above are, at least in part, indicative of a climate-driven decrease in localized prey abundance (e.g., zooplankton volumes, forage fish abundance; see references

above). The negative relationship to spring upwelling (PC2) and the positive relationship to the PDO (PC4) exhibited by the shearwater might be indicative of changes in their dispersion in the study area. Perhaps they are more prevalent in general during cooler periods, but more concentrated in local areas in response to upwelling fronts (e.g., Ainley et al. 2005). Therefore, their relative abundance one year to the next would be affected by the success at surveying areas of concentration.

Top-down forcing to explain patterns.

While clearly there must be a relationship of decreasing trends in certain species to changes in the carrying capacity of the CCS (as noted above), this likely is not the only factor involved in affecting food availability to seabirds. At the same time that the above seabirds have been declining in our study area, humpback whales, which prey on the same zooplankton and forage fish as these birds in the same waters during the seabirds' breeding season, have increased dramatically (Fig. 8; see also Pyle and Gilbert 1996). The whale increase in the study area is much more dramatic than the overall gradual trend of the species in the eastern North Pacific as it recovers from whaling (Calambokidis and Barlow 2004), and therefore must represent a return to a former 'tradition' of foraging over the central California shelf, a tradition vacated in response to harassment from shore-based whalers that ended in the study area only as late as the mid-1970s (Tønnessen and Johnsen 1982). Moreover, but a month or two after our cruises, another once-hunted baleen whale, the blue whale (*Balaenoptera musculus*), has increased in a similar step-increase fashion in shelf-break and slope waters of our study area and elsewhere in the CCS (Croll et al. 2005, NOAA 2004; Pyle and Gilbert 1996). These whales feed mainly on zooplankton and are present during the period when the fledglings of locally-breeding seabirds are first beginning to forage and breeders are attempting to recover body condition. Especially with prey reduced from historical levels owing to climate factors (noted above), trophic competition from the whales could well be involved in survival and the population trajectories of locally breeding seabird species in the study area.

Decreases were also evident in the Ashy Storm-petrel and Western Gull. Decrease in the gull's population, consistent with a long-term decrease in their reproductive output (Sydeman et al. 2001), might well be related to the declining prey availability mentioned above. This could be so for the storm-petrel as well, but see below.

Other factors involved in trends.

Factors other than prey availability certainly also played a role in driving the patterns we detected for some species.

Important to the Ashy Storm-petrel, and perhaps the main factor in population trends, has been changes in breeding habitat at its main breeding site, SEFI. Sydeman et al. (2001) detected a decline in this species' productivity but only beginning in the later 1990s, well after the decline seen in at-sea numbers. This timing argues against oceanographic factors involved, or at least the ones that we investigated.

The breeding habitat of this small (40 g), non-aggressive species has changed dramatically during the past few decades. Ashy Storm-petrel does not dig burrows but nests in crevices and cavities of bare, talus slopes like other storm-petrels of southern California and Mexico (Ainley 1995, 2005). In the mid-1970s, European hares (*Oryctolagus cuniculus*) were removed from the Farallones, having been present since the 1700s, with one result

being a spectacular blooming of vegetation not seen for >200 years (Ainley and Lewis 1974; Ainley, pers. obs.). While larger-bodied, cavity-nesting species benefited from reduced competition with hares for breeding sites (e.g., Scott et al. 1974, Ainley and Boekelheide 1990), storm-petrels did not. Included in the renewed vegetative growth were species of grasses transported to the islands in the feed of pack animals formerly used in the operations of the light station (beginning in the late 1850s). As these grasses spread, thickened and grew to full height among the slopes, access to cavities by the storm-petrels became more difficult (Ainley, pers. obs.). Moreover, the re-invigorated vegetation likely led to more seeds and, thus, to a larger, more seasonally persistent population of the house mouse (*Mus musculus jenski*), also present since the early years of human occupation (in this case, a mouse brought by Russian sealers; P. Pyle pers. comm.). In turn, this may have allowed Burrowing Owls (*Athene cunicularia*), once just an 'uncommon' autumn visitor (DeSante and Ainley 1980) to remain on the island more consistently into the next storm-petrel nesting season, thus increasing storm-petrel vulnerability to predation (Ainley and Boekelheide 1990, Ainley 1995; P. Pyle pers. comm.). Difficulty in penetrating cavities, owing to vegetation, would exacerbate predation. Future plans to remove the mouse (http://www.fws.gov/sfbayrefuges/Farallon/Comment.htm) may well bring unintended surprises without vegetation management.

Another species that was less abundant later than earlier in the study period is the California Gull. Like the Sooty Shearwater, the lack of a statistical significance to the pattern might be due in part to confidence intervals that were too broad early in the period. However, this species' variation was not explainable by any of the oceanographic factors we considered. This outcome is perhaps not surprising, given that the pattern could have been related to continental rather than marine factors, since this species nests inland in North America (see Winkler and Shuford 1988, Wredge et al. 2006).

The remaining species exhibited a more complex relationship in both the patterns of their abundance during our study, as well as to the factors that likely affected them. Leach's Storm-petrel, Brown Pelican, Brandt's Cormorant and Common Murre were more abundant during ENSO (a higher PC1 score), likely because fewer individuals were occupied with breeding under such conditions (Ainley and Boekelheide 1990), and thus spent less time in breeding colonies and more time on the water. The Red Phalarope and Northern Fulmar had the opposite relationship to PC1, indicating that their populations spent less time in the study area during ENSO. The murre and fulmar prevalence were affected as well 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 strong. None of these species exhibited any overall decreasing or increasing trend in numbers at sea, although the numbers of murres at Southeast Farallon, the main colony, have been slowly declining (Lee et al. 2008). Unlike many of the other breeding species considered herein decline at the Farallones could have been compensated by increases at colonies along the mainland coast.

Not only are there factors that directly affect a seabird species' overall abundance, but there are factors, too, that may affect their dispersion and thus detectability. In the case of the latter, our study area may have been an inappropriate size to properly quantify the true prevalence or trends in some of these species in the study region, for instance phalaropes, Sabine's Gull and Leach's Storm-petrel.

Final Thoughts.

Overall, our study points to the complexity of marine species' responses, particularly far-ranging seabirds, to variation in attributes of their habitat, which are in turn affected by remote and local climatic forcing at multiple temporal scales. We addressed seabird distributions during spring, a critical period of seasonal migrations and reproduction for locally-breeding species. Other studies involving multi-seasonal sampling of the northern CCS over multiple decades have documented long-term changes in water column structure, nutrient availability, and plankton and fish biomass (e.g., Batchelder et al. 2005, Peterson and Schwing 2003, Brodeur et al. 2007). Therefore, it is critical to consider this study within this broader historical context of changing ecosystem productivity and structure. On the other hand, we've suggested that biological factors in addition to changes in productivity, and namely interspecific competition for food, could well be involved in affecting certain species' population trends. Certainly, this requires more work to better understand. 'Shifting baselines' in marine systems, recently identified as a problem in the interpretation of present with past conditions, must be kept in mind especially as major, ecologically key species such as whales recover from earlier decimation (see, e.g., Pauly 1995, Schrope 2006).

Understanding the degree to which environmental conditions during the non-breeding season, which we considered for species such as the Sooty and Pink-footed shearwaters, influence the timing and success of seabird reproduction, and the survivorship of young and adults are critical to interpret and the population-level effects of environmental variability on marine resources, including seabirds and their prey. Given the hemispheric difference in the breeding and non-breeding grounds of the latter species, makes accomplishing this task a large challenge. Likely more tractable is working with breeding CCS species, which tend to be present in the vicinity of nesting colonies year round (Ainley and Boekelheide 1990), but a year-round census program is required. Of the breeding species that we considered, for instance auklets and murres, the importance of various PC variables confirmed the importance the pre- or between-breeding season factors. Increasingly increasing our grasp of this part of the annual cycle of the CCS is crucial to anticipate future change in complicated marine ecosystems, impacted by synergistic climate changes, short-term oceanographic variability, and anthropogenic impacts.

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Figure Captions

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

Fig. 2. Time series of large-scale oceanographic forcing over 23 years (October 1984 – September 2007): (A) the Pacific Decadal Oscillation (PDO) and (B) the Multi-variate El Niño Index (MEI). The black squares indicate the timing of the yearly surveys.

Fig. 3. Sea surface temperature (SST) conditions (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. 4. Cross-correlations of four monthly environmental variables over a range of temporal lags from 1 – 12 mo. The horizontal lines indicate two levels of statistical significance defined by alpha = 0.001 (solid line) and 0.0001 (dashed line).

Fig. 5. Time series of abundance of 18 focal seabird species during spring-time cruises off central California during the early 1985-1994) and the late 1997-2006) periods analyzed, showing the long-term mean (solid line) ± 1 SD (dashed lines). Years when the species were not sighted are highlighted with an asterisk (*). Only those "common" species sighted in at least 50% of the annual cruises were analyzed using a multiple regression. The significant variables are listed for each species.

Fig. 6. Generalized additive model (GAM) results relating seabird density (number km $^{-2}$) to the survey year 1985 – 2006). For each variable, the best-fit loess function (thick line), the 95 % confidence intervals (fine lines), and the distribution of surveys (vertical ticks) are shown. Only those species which occurred in > 75% of annual cruises are shown: (A) Three species with highly significant ($p < 0.003$) trends (Cassin's Auklet AKCA, Western Gull GUWE, Black-footed Albatross ALBF); (B) three species with significant ($p < 0.05$) trends (Rhinoceros Auklet AKRH, Ashy Storm-petrel STAS, Pigeon Guillemot GUPI).

Fig. 7. Generalized additive model (GAM) results relating seabird density (number km $^{-2}$) to PC1 scores. For each variable, the best-fit loess function (thick line), the 95 % confidence intervals (fine lines), and the distribution of surveys (vertical ticks) are shown. Only those species with significant responses ($p < 0.05$) which occurred in > 75% of annual cruises are shown: Brandt's Cormorant COBR, Pigeon Guillemot GUPI, Common Murre MUCO, Brown Pelican PELB.

Fig. 8. The number of Humpback Whales (*Megaptera novaeangliae*) seen per day on the cruises reported on herein 1985-2006.

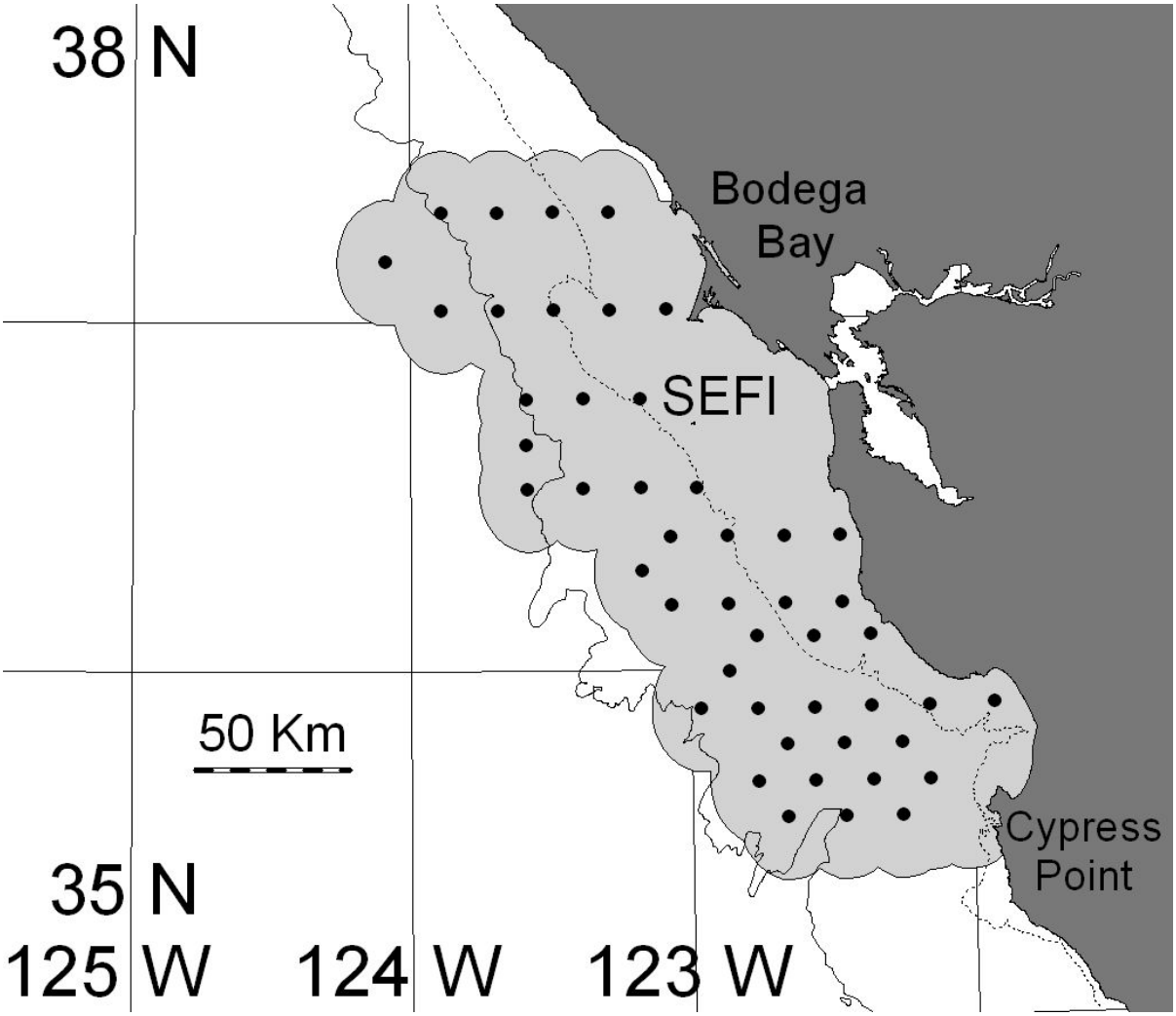
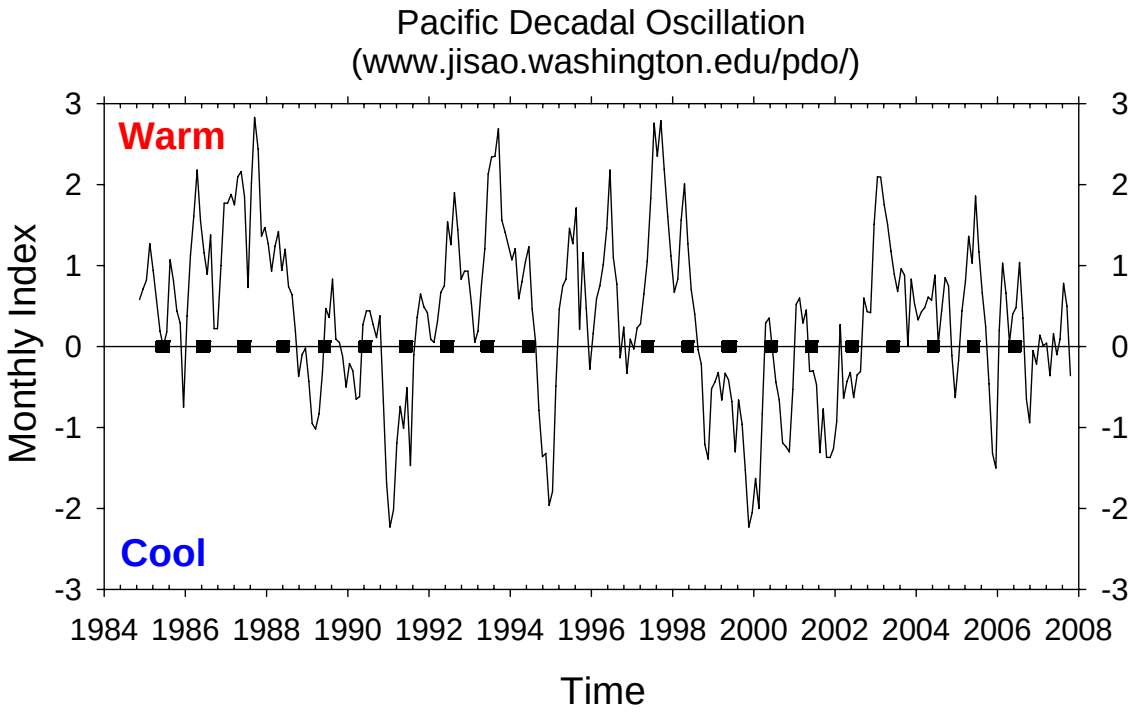


Figure 1


Pacific Decadal Oscillation
(www.jisao.washington.edu/pdo/)
Warm
Cool
Monthly Index
Time
3
2
1
0
-1
-2
-3
1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008

-

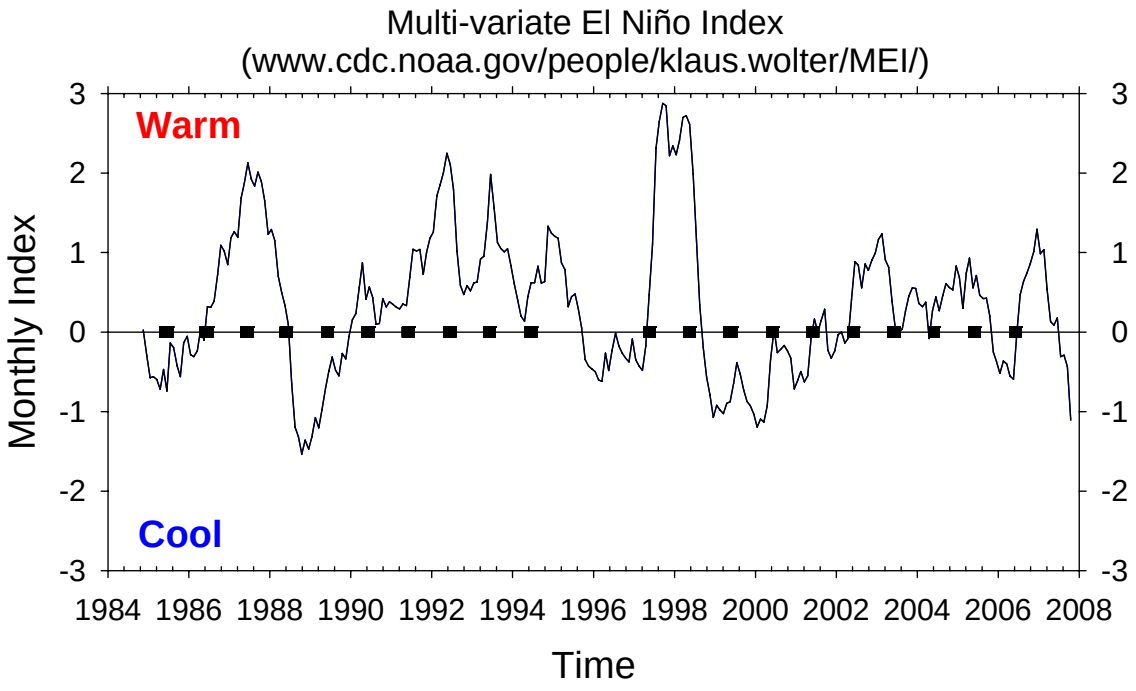

Multi-variate El Niño Index
(www.cdc.noaa.gov/people/klaus.wolter/MEI/)
Warm
Cool
Monthly Index
Time
3
2
1
0
-1
-2
-3
1984 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008

Figure 2.

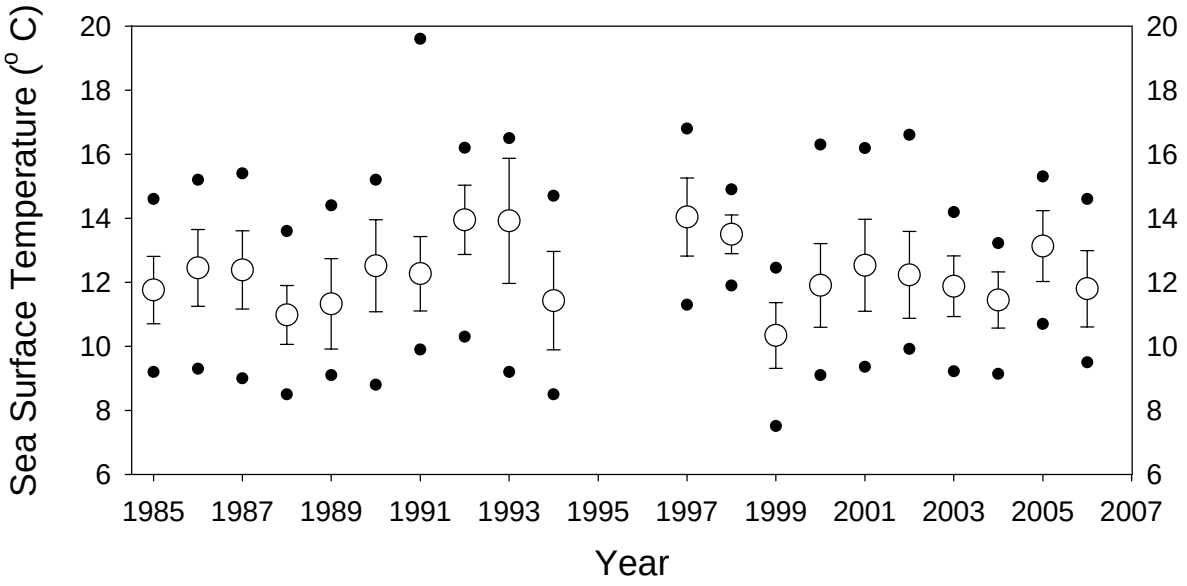

Sea Surface Temperature (° C)
20
18
16
14
12
10
8
6
1985
1987
1989
1991
1993
1995
1997
1999
2001
2003
2005
2007
Year

Figure 3.

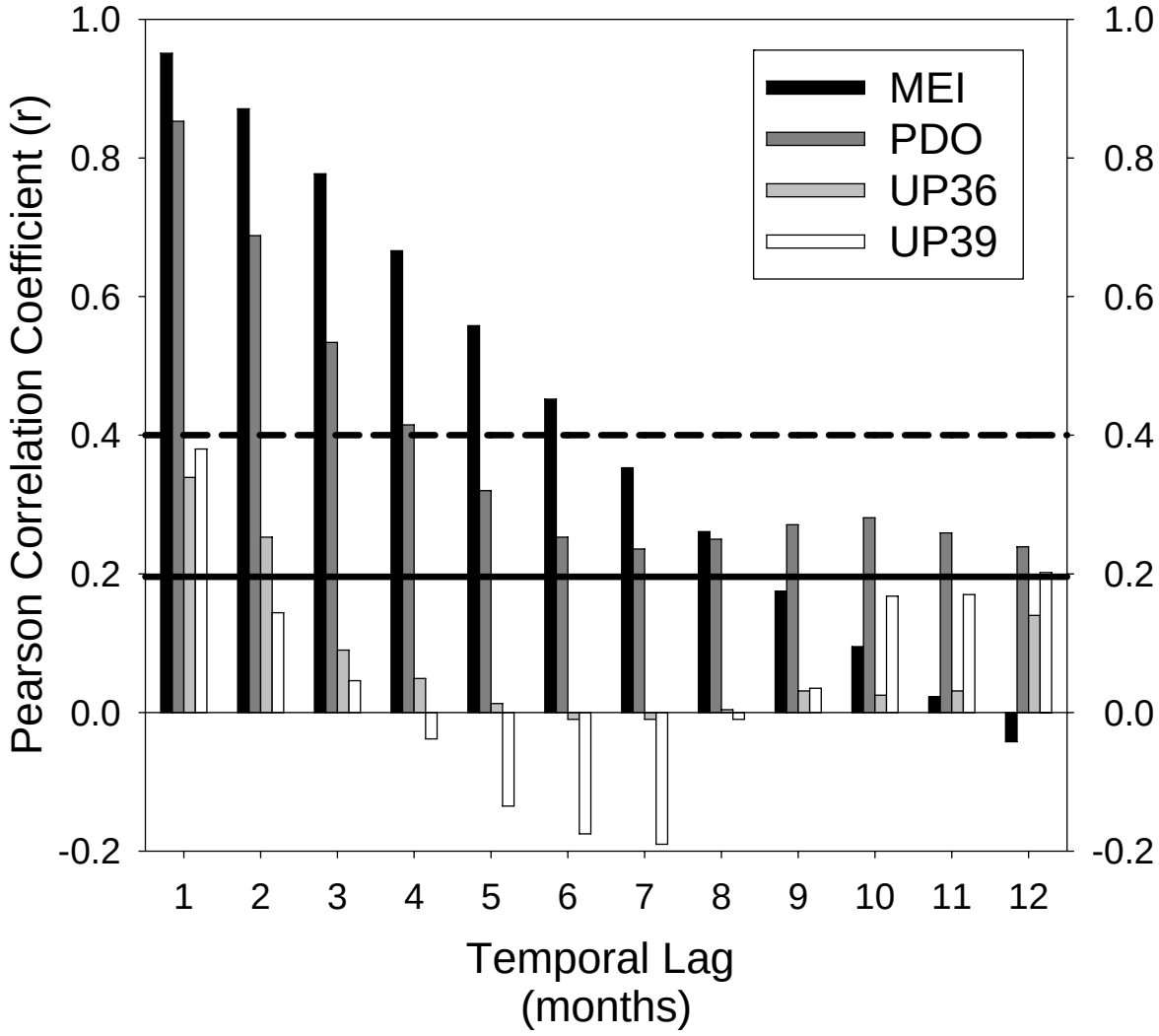
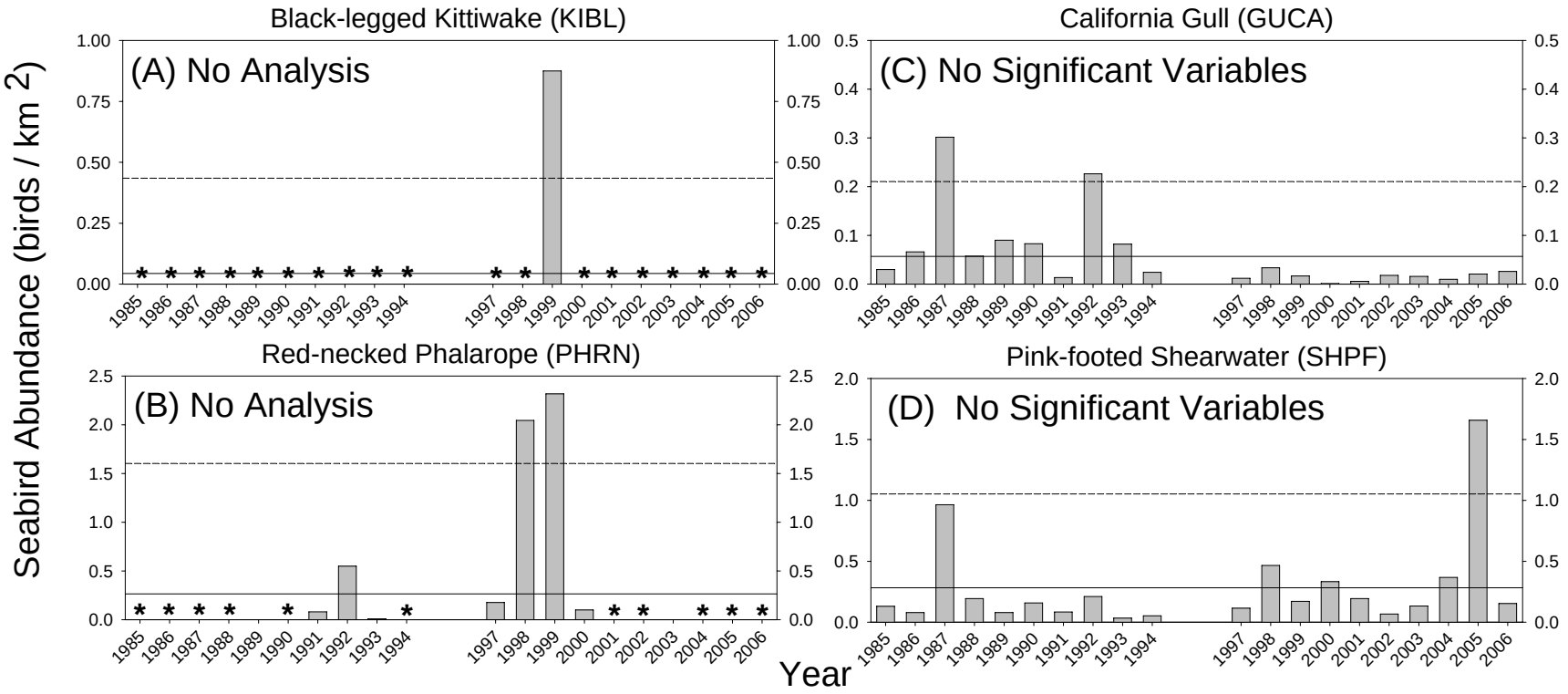
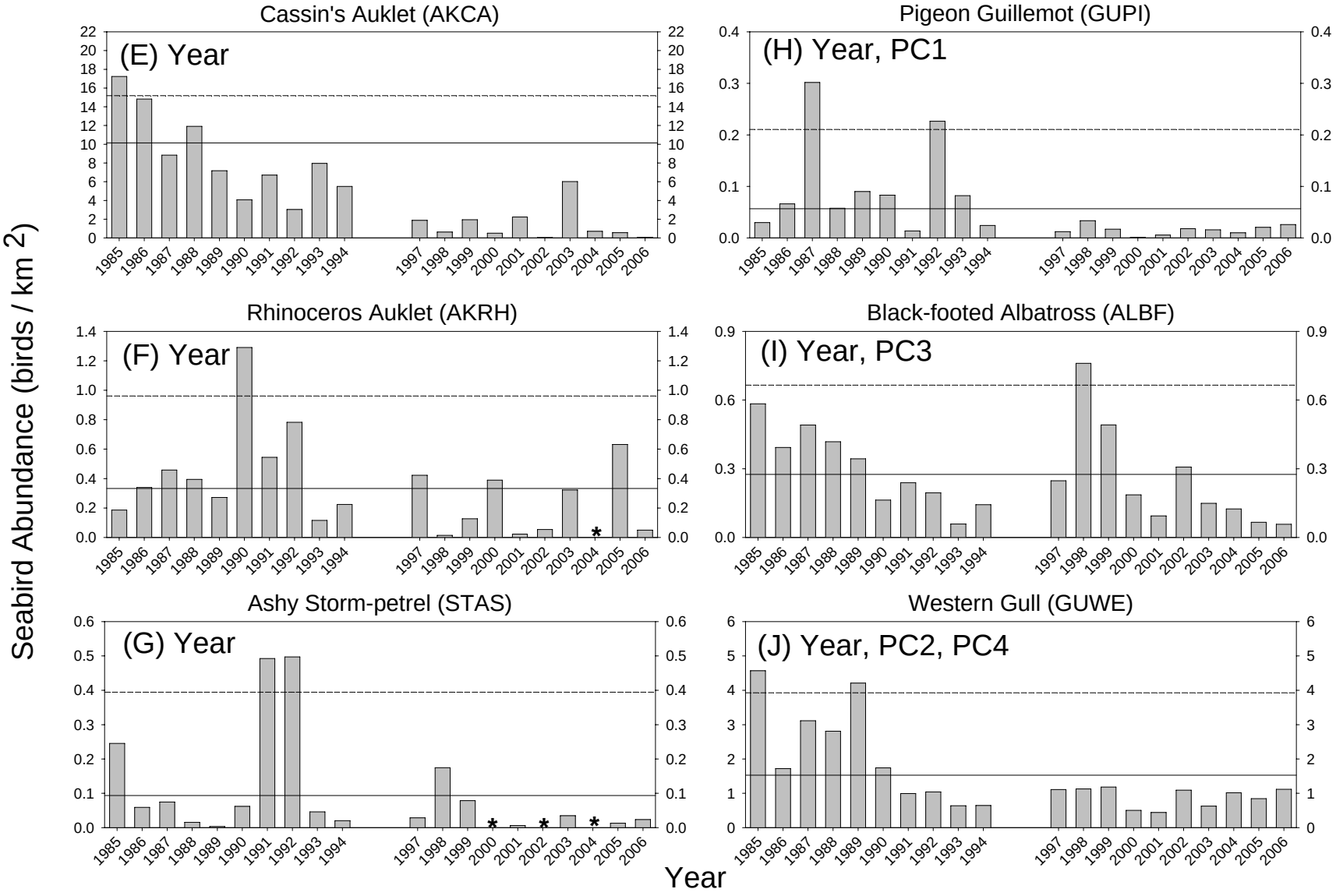
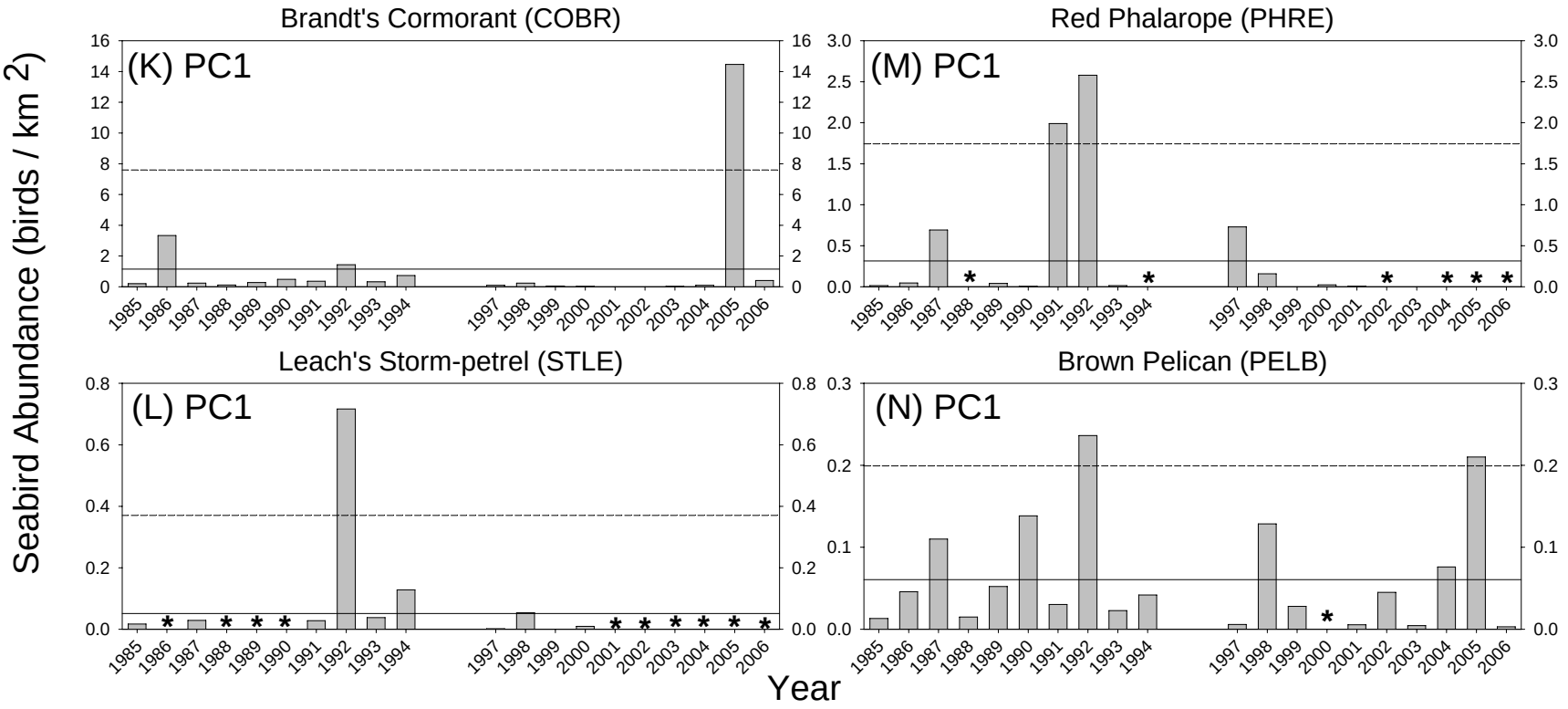
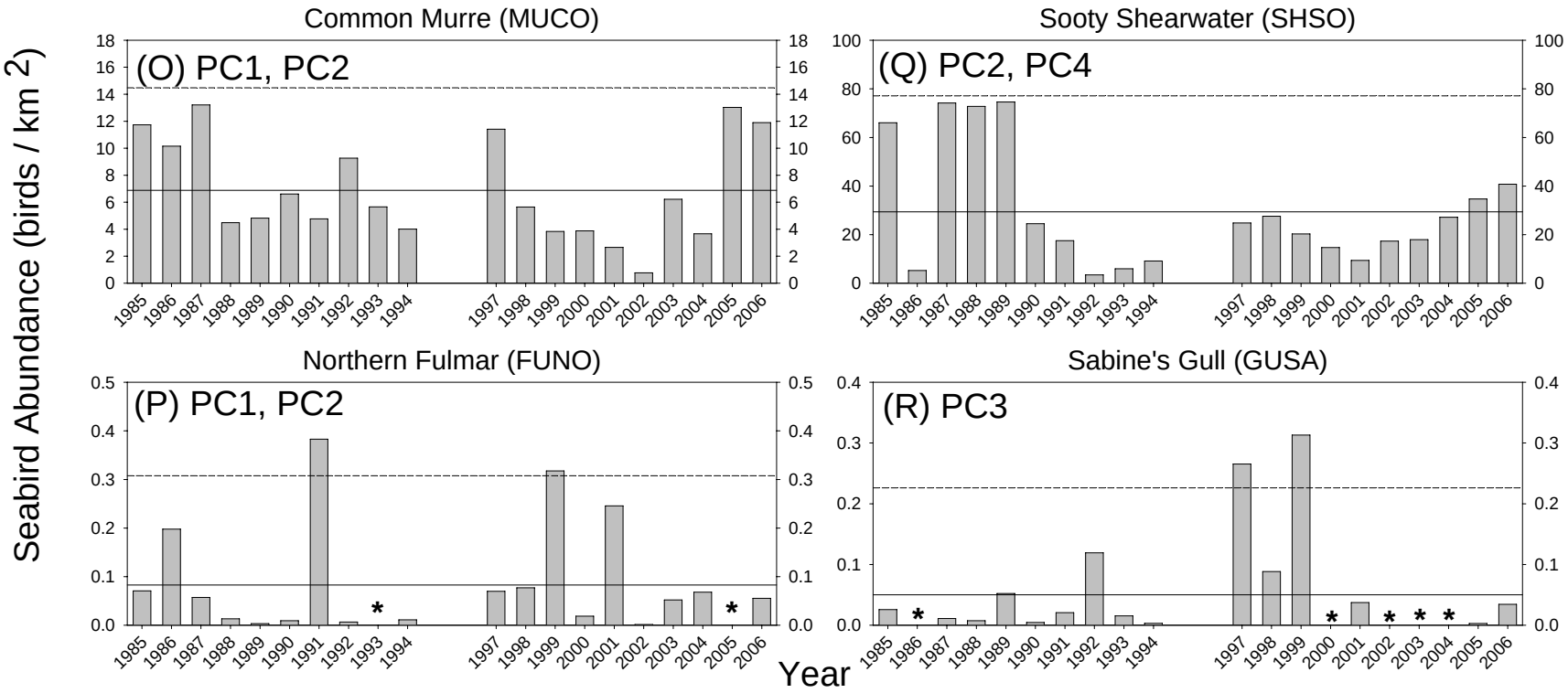

1.0
0.8
0.6
0.4
0.2
0.0
-0.2
Pearson Correlation Coefficient (r)
MEI
PDO
UP36
UP39
1
2
3
4
5
6
7
8
9
10
11
12
Temporal Lag
(months)

Figure 4.


Black-legged Kittiwake (KIBL)
(A) No Analysis
California Gull (GUCA)
(C) No Significant Variables
Red-necked Phalarope (PHRN)
(B) No Analysis
Pink-footed Shearwater (SHPF)
(D) No Significant Variables
Seabird Abundance (birds / km 2)
Year


Cassin's Auklet (AKCA)
(E) Year
Pigeon Guillemot (GUPI)
(H) Year, PC1
Rhinoceros Auklet (AKRH)
(F) Year
Black-footed Albatross (ALBF)
(I) Year, PC3
Ashy Storm-petrel (STAS)
(G) Year
Western Gull (GUWE)
(J) Year, PC2, PC4
Seabird Abundance (birds / km 2)
Year


Brandt's Cormorant (COBR)
(K) PC1
Red Phalarope (PHRE)
(M) PC1
Leach's Storm-petrel (STLE)
(L) PC1
Brown Pelican (PELB)
(N) PC1
Seabird Abundance (birds / km 2)
Year


Common Murre (MUCO)
(O) PC1, PC2
Sooty Shearwater (SHSO)
(Q) PC2, PC4
Northern Fulmar (FUNO)
(P) PC1, PC2
Sabine's Gull (GUSA)
(R) PC3
Seabird Abundance (birds / km 2)
Year

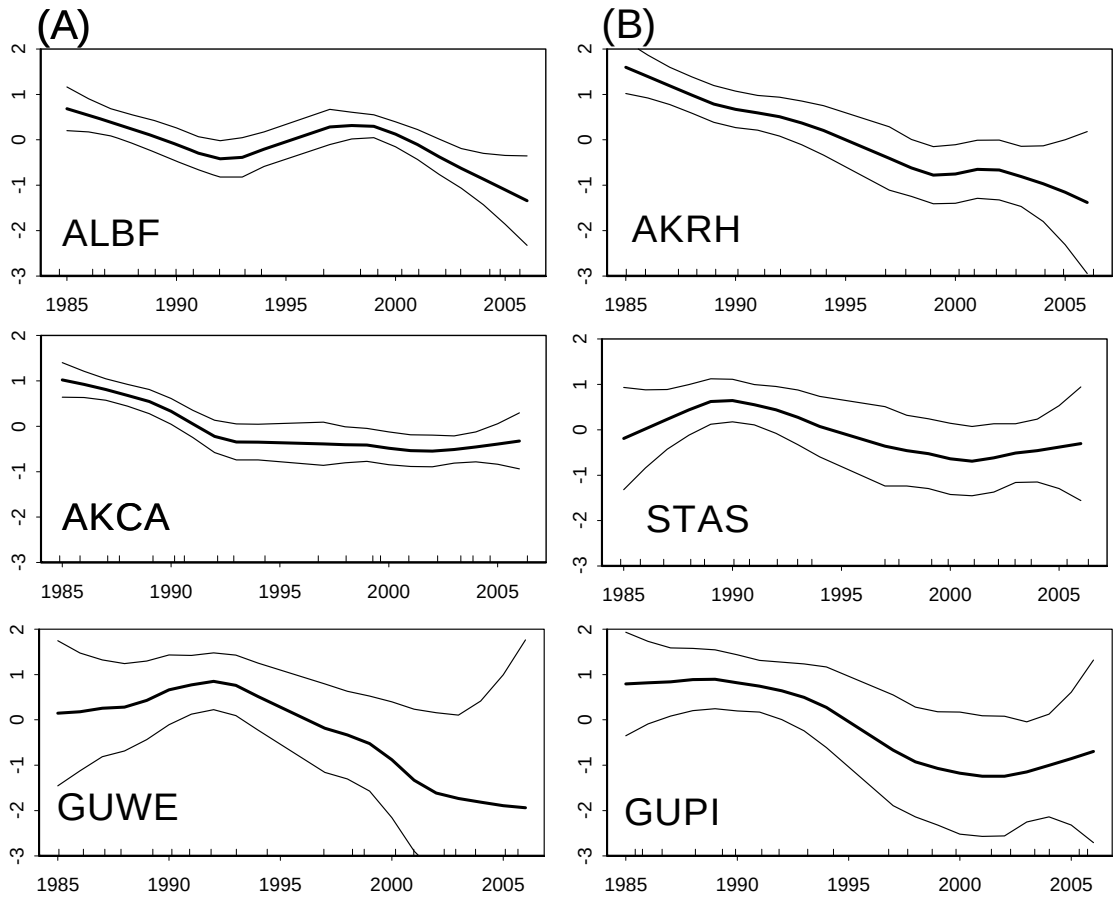

(A)
(B)
ALBF
AKRH
AKCA
STAS
GUWE
GUPI
2
1
0
-1
-2
-3
1985
1990
1995
2000
2005

Figure 6

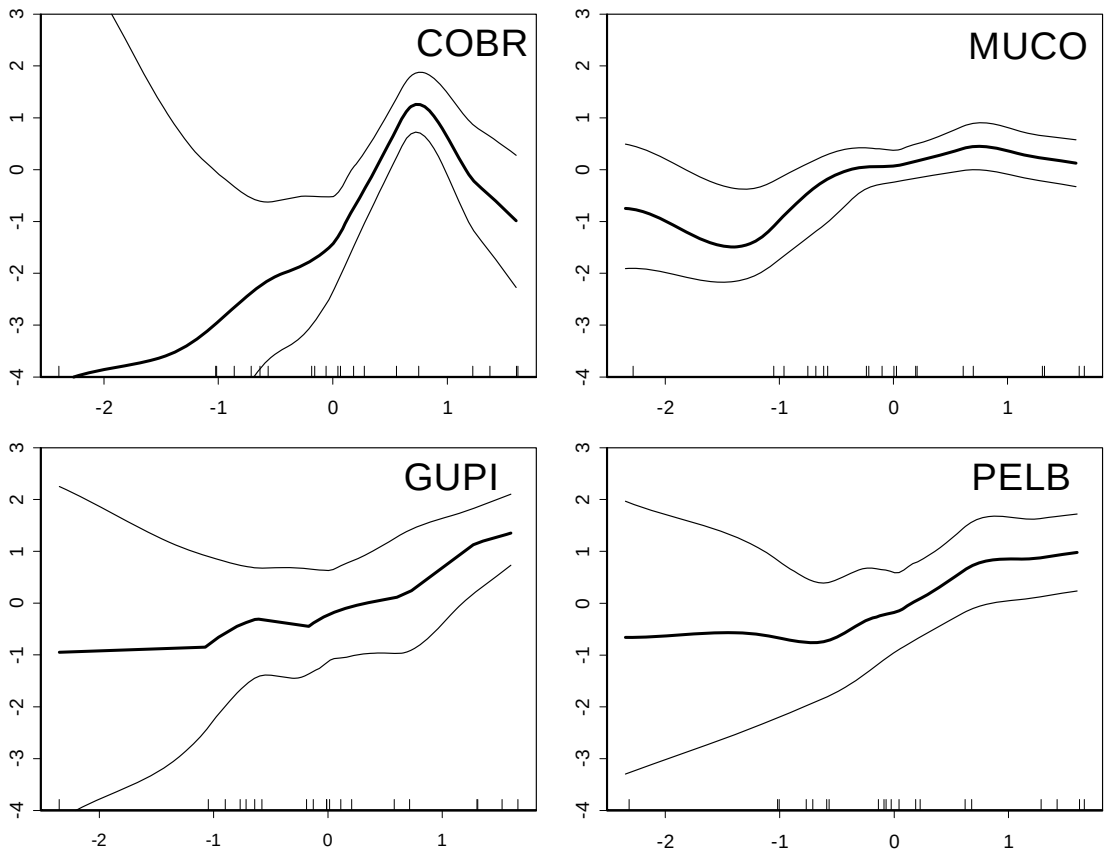


Figure 7.

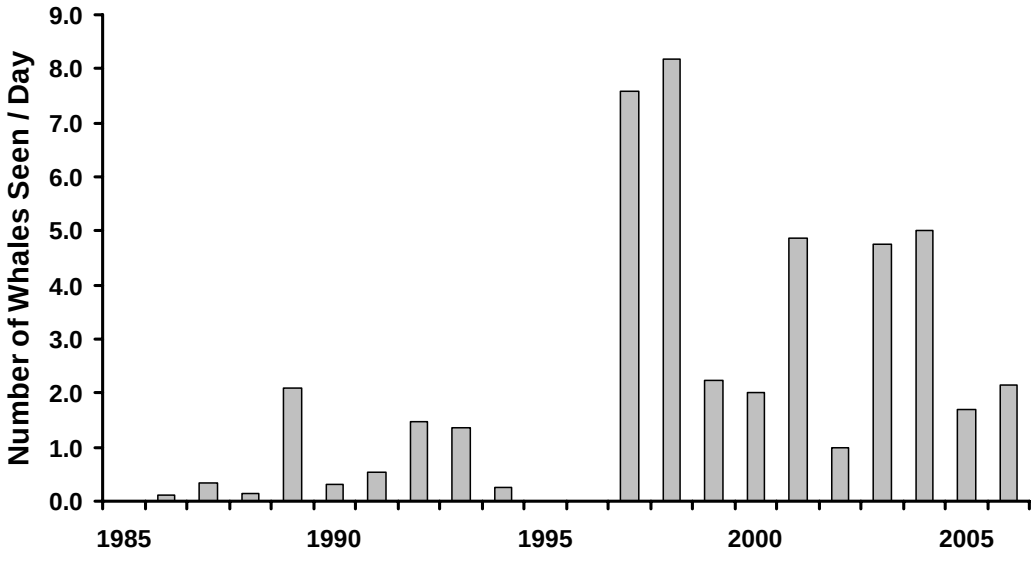


Figure 8

TABLE 1. Seabird survey effort during the early 1985-1994) and late periods 1997-2006), showing the number of survey days, 15-min survey bins, and area surveyed each year.

	Survey Dates		Survey Effort		
Year	Start	End	days	bins	km^2
1985	5/31	6/22	22	164	194.3
1986	5/30	6/19	20	426	586.0
1987	6/2	6/19	17	360	454.2
1988	5/23	5/31	8	217	277.7
1989	5/31	6/11	11	273	324.7
1990	5/29	6/11	13	395	447.8
1991	5/28	6/11	14	541	684.5
1992	6/3	6/18	15	460	597.3
1993	6/3	6/12	9	346	411.8
1994	6/11	6/18	7	268	326.1
1997	5/14	5/19	6	216	272.3
1998	5/14	5/20	5	199	276.9
1999	5/10	6/3	24	422	500.3
2000	5/30	6/6	7	226	272.0
2001	5/30	6/6	7	180	214.3
2002	5/29	6/3	5	144	167.0
2003	5/30	6/6	7	262	300.6
2004	5/30	6/2	3	69	85.1
2005	5/25	5/31	6	181	216.4
2006	5/29	6/9	11	172	231.8
Early Period 1985 - 1994)			136	3450	4304.3
Late Period 1997 - 2006)			81	2071	2536.7
Total			217	5521	6841.0

TABLE 2. 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 of sightings and individuals of each species. The bold font denotes the "common" focal species considered in this study.

	Occurrence	Sightings		Individuals	
Species	(% cruises)	(number)	(proportion)	(number)	(proportion)
Sooty Shearwater *Puffinus griseus* (SHSO)	100	14042	29.42	256963	60.97
Common Murre *Uria aalge* (MUCO)	100	10773	22.57	70075	16.63
Cassin's Auklet *Ptychoramphus aleuticus* (AKCA)	100	4163	8.72	43744	10.38
Western Gull *Larus occidentalis* (GUWE)	100	6506	13.63	14428	3.42
Brandt's Cormorant *Phalacrocorax penicillatus* (BRCO)	100	1274	2.67	9308	2.21
Red Phalarope *Phalaropus fulicarius* (PHRE)	70	733	1.54	4904	1.16
Red-necked Phalarope *Phalaropus lobatus* (PHRN)	45	368	0.77	3421	0.81
Rhinoceros Auklet *Cerorhinca monocerata* (AKRH)	95	1637	3.43	2872	0.68
California Gull *Larus californicus* (GUCA)	70	542	1.14	2686	0.64
Black-footed Albatross *Phoebastria nigripenis* (ALBF)	100	1763	3.69	2556	0.61
Pink-footed Shearwater *Puffinus creatopus* (SHPF)	100	1040	2.18	2135	0.51
Ashy Storm-petrel *Oceanodroma homochroa* (STAS)	85	646	1.35	977	0.23
Northern Fulmar *Fulmarus glacialis* (FUNO)	90	808	1.69	962	0.23
Brown Pelican *Pelecanus occidentalis* (PELB)	95	376	0.79	770	0.18
Pigeon Guillemot *Cepphus columba* (GUPI)	100	364	0.76	648	0.15
Sabine's Gull *Xema sabini* (GUSA)	75	217	0.45	548	0.13
Black-legged Kittiwake *Rissa tridactyla* (KIBL)	5	209	0.44	546	0.13
Leach's Storm-petrel *Oceanodroma leucorhoa* (STLE)	50	433	0.91	511	0.12
Total		45894	96.14	418054	99.19

TABLE 3. Pearson linear correlation coefficients (r) among environmental variables; n = 276 monthly values during 23 years (October 1984 – September 2007).

		P-Value			
		MEI	PDO	UP-36	UP-39
Pearson Correlation	MEI	-	**+0.492**	-0.150	-0.139
	PDO	<0.001	-	**-0.266**	**-0.234**
	UP-36	0.002 - 0.005	<0.001	-	**+0.593**
	UP-39	0.02 - 0.05	<0.001	<0.001	-

TABLE 4. Results of principal component analysis showing the loadings of the different components of the four dominant resulting 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	PC 1	PC 2	PC 3	PC 4
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	$UP\text{-}39_1$	-0.396	-0.444	**+0.619**	+0.153
Upwelling North - early spring	$UP\text{-}39_2$	**-0.609**	**+0.572**	+0.164	+0.216
Upwelling North - late spring	$UP\text{-}39_3$	**-0.704**	**+0.513**	-0.078	+0.059
Upwelling South - winter	$UP\text{-}36_1$	-0.471	-0.166	**+0.643**	+0.288
Upwelling South - early spring	$UP\text{-}36_2$	-0.466	**+0.651**	+0.425	+0.011
Upwelling South - late spring	$UP\text{-}36_3$	**-0.785**	+0.373	-0.113	+0.146
Sea Surface Temperature - late spring	SST	**+0.685**	+0.236	+0.476	-0.356

TABLE 5. Abundance of focal species, showing the coefficient of variation (CV) in density across years and results of the test of residuals from the best-fit multiple regression (Kolmogorov-Smirnov test, $n = 20$).

Breeding	Species	Density (number / km^2)			Residuals		
Status	Name	Mean	(Min - Max)	CV (%)	STD	Max_Diff	*P*-value
Locally	MUCO	6.88	0.77 - 13.20	55.12	0.234	0.120	0.901
breeding	AKCA	5.09	0.04 - 17.23	99.08	0.274	0.107	0.957
	GUWE	1.53	0.45 - 4.57	78.51	0.170	0.160	0.631
	COBR	1.14	0.01 - 14.46	281.93	0.602	0.201	0.345
	AKRH	0.33	0.00 - 1.29	94.67	0.478	0.124	0.880
	STAS	0.09	0.00 - 0.50	160.14	0.464	0.128	0.860
	GUPI	0.06	0.01 - 0.30	135.61	0.229	0.153	0.680
	STLE	0.05	0.00 – 0.71	312.27	0.429	0.147	0.724
Non-	SHSO	29.38	3.37 - 74.58	81.25	0.325	0.196	0.374
resident	GUCA	0.35	0.00 - 2.90	220.22	0.746	0.095	0.985
	PHRE	0.32	0.00 - 2.58	226.32	0.417	0.180	0.483
	SHPF	0.28	0.03 - 1.66	136.43	0.341	0.158	0.646
	ALBF	0.28	0.06 - 0.76	70.62	0.237	0.123	0.885
	FUNO	0.08	0.00 - 0.38	135.73	0.432	0.263	0.104
	PELB	0.06	0.00 - 0.24	114.45	0.372	0.121	0.896
	GUSA	0.05	0.00 - 0.31	175.99	0.423	0.169	0.561

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 by the best-fit model are shown, alongside the sign of the coefficient and the associated *p*-value for each of the five independent variables considered. The sign (positive / negative) of the coefficients are shown for marginally significant variables having at least alpha = 0.10. Significant ($p < 0.05$) variables are shown in bold font. Highly significant variables, adjusted for multiple comparisons (alpha = 0.05 / 16 = 0.003), are underlined.

Species	Number	% Variance	PC1		PC2		PC3		PC4		Year	
Name	Variables	(adjusted r^2)	Sign	*P*	Sign	*P*	Sign	*P*	Sign	*P*	Sign	*P*
MUCO	2	29.8	+	**0.018**	-	0.090		0.248		0.197		0.580
AKCA	1	62.1		0.895		0.675		0.575		0.224	**-**	**<u><0.001</u>**
GUWE	3	58.2		0.453	-	**0.040**		0.735	+	0.091	**-**	**<u>0.001</u>**
COBR	1	23.1	+	**0.018**		0.161		0.970		0.703		0.490
AKRH	1	20.4		0.799		0.492		0.411		0.520	-	**0.026**
STAS	1	19.0		0.335		0.106		0.843		0.428	-	**0.031**
GUPI	2	58.8	+	**0.005**		0.437		0.939		0.949	-	**0.030**
STLE	1	21.9	+	**0.021**		0.306		0.786		0.100		0.362
SHSO	2	22.5		0.375	-	0.052		0.612	+	0.095		0.971
GUCA	0	0		0.218		0.867		0.798		0.344		0.621
PHRE	1	25.7	-	**0.013**		0.329		0.729		0.954		0.120
SHPF	0	0		0.174		0.792		0.558		0.529		0.223
ALBF	2	37.3		0.224		0.224	+	0.056		0.264	**-**	**<u>0.003</u>**
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

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 (PC) quantifies the magnitude of the shift in mean density across periods. The bold font highlights those species with significant long-term changes in abundance.

Breeding Status	Species Name	Early Mean (± SD)	Late Mean (± SD)	PC Change (%)	*t*-test (*P*-value)
Locally breeding	MUCO	7.47 ± 3.35	6.30 ± 4.29	-16	1.149 (0.266)
	AKCA	**8.72 ± 4.61**	**1.46 ± 1.79**	**-83**	**4.805 (< 0.001)**
	GUWE	**2.15 ± 1.45**	**0.91 ± 0.28**	**-58**	**2.661 (0.016)**
	COBR	0.74 ± 0.99	1.54 ± 4.54	+107	1.888 (0.075)
	AKRH	**0.46 ± 0.35**	**0.20 ± 0.22**	**-56**	**2.594 (0.018)**
	STAS	**0.15 ± 0.19**	**0.03 ± 0.05**	**-76**	**2.143 (0.046)**
	GUPI	**0.10 ± 0.09**	**0.02 ± 0.01**	**-84**	**4.183 (0.001)**
	STLE	0.09 ± 0.22	0.01 ± 0.01	-93	1.960 (0.066)
Non-resident	SHSO	35.32 ± 32.16	23.44 ± 9.49	-34	0.176 (0.862)
	GUCA	0.35 ± 0.91	0.34 ± 0.63	-2	1.366 (0.189)
	PHRE	0.54 ± 0.95	0.09 ± 0.23	-83	1.386 (0.183)
	SHPF	0.20 ± 0.27	0.37 ± 0.47	+84	1.551 (0.138)
	ALBF	0.30 ± 0.17	0.25 ± 0.22	-18	0.968 (0.346)
	FUNO	0.07 ± 0.12	0.09 ± 0.10	+20	0.789 (0.440)
	PELB	0.07 ± 0.07	0.05 ± 0.07	-28	1.278 (0.217)
	GUSA	0.03 ± 0.04	0.07 ± 0.12	+186	0.536 (0.599)