

SEABIRDS AND CLIMATE IN THE CALIFORNIA CURRENT—A SYNTHESIS OF CHANGE

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ABSTRACT

We investigated changes in ocean climate and ecosystems by reviewing select case histories for seabirds in the California Current ecosystem (CCE) and the transition zone between the CCE and the Gulf of Alaska large marine ecosystems using data from the early 1970s to the present. We used information spanning the entire CCE, from the south (California Cooperative Oceanic Fisheries Investigation [CalCOFI]) to the north (Ocean Station Papa/Line P surveys) and colonies sites in between, to make this assessment. Seabird timing of breeding, productivity, and abundance at sea have changed in ways consistent with predictions under an ocean-warming scenario, but we cannot dismiss the hypothesis that low-frequency variability explains some of these patterns. In contrast, recent reproductive failures of auklets and other species cannot be explained by El Niño–Southern Oscillation (ENSO) or low-frequency variability. Declining trends in the productivity of murre and auklet “trophic chains,” including the relative abundance of mesozooplankton (krill) and forage fish (juvenile *Sebastes*) cannot be explained by low- or high- (ENSO-scale) frequency climate variability. Changes in relative abundance at sea in the CalCOFI and Line P study areas, however, could be related to change points related to regime shifts in the North Pacific Ocean. Contrasting trends in life history (timing), demographic (productivity), and population (density) patterns by species highlight the need to consider spatial ecology and habitat quality (food web attributes) in order to develop a deeper understanding of how climate change or ecosystem change is affecting seabirds in the CCE and adjacent North Pacific regions.

INTRODUCTION

Ocean warming is evident in the global ocean (Levitus et al. 2000), but the ecological consequences have been poorly documented, specifically in International Panel on Climate Change (IPCC) assessment reports (Richard-

son and Poloczanska 2008). Relative to many of the world’s oceans, the California Current ecosystem (CCE) has been well-studied for a long period of time, and has been identified as a system with strongly coupled environmental and ecosystem variability. This variability occurs on multiple time scales from seasons to centuries (Hickey 1979; Bograd and Lynn 2003; Chavez et al. 2003; Field et al. 2006a, b).

The CCE is a complex ecosystem. In the south, the ecosystem is composed mostly of species with sub-tropical zoogeographical affinities, whereas sub-arctic species dominate in the north. There is substantial intra-annual variability in ecosystem dynamics, with seasonal pulses in productivity along a latitudinal gradient from south to north (generally earlier in the south, later in the north). Productivity is related to upwelling and other oceanographic processes that mix the water column and bring nutrients to surface waters to stimulate primary productivity (Hickey 1979). As a productive marine ecosystem, there are both well-developed commercial fishery and ecotourism (whale and seabird-watching) industries in all regions, resulting in significant public support for a healthy and robust ecosystem. Understanding current and future effects of climate variability and climate change on the CCE is therefore of great interest to the people of western North America.

The CCE responds to interannual climate variability, exemplified by El Niño–Southern Oscillation (ENSO) events (Lenarz et al. 1995), and long-term (interdecadal) variability exemplified by the Pacific Decadal Oscillation (PDO, Mantua et al. 1997) and North Pacific Gyre Oscillation (NPGO, Di Lorenzo et al. 2008). Some secular trends in oceanographic processes have also been described (Rykaczewski and Checkley 2008). While the periodicity of ENSO events is relatively well-known, every three to seven years, the periodicity of the PDO/NPGO is poorly understood with only a few cycles evident in the longest available observational or mod-

eled datasets. There is evidence that the periodicity and amplitude of various modes of climate variability is changing. For example, warm-water ENSO events in the North Pacific Ocean appear to have increased, with concomitant changes in marine ecosystem structure and functions (Hayward 1997; McGowan et al. 1998; Gergis and Fowler 2009). These changes are poorly understood mechanistically, both in the physical and biological realms. The lack of understanding of the interactions and relationships between various scales of temporal environmental variability, from seasonal to interannual to interdecadal, presents major complications for understanding the effect of long-term climate change on the CCE and related North Pacific large marine ecosystems. Specifically, change in the periodicity of interannual and/or interdecadal climate variability makes it difficult to assign effects of secular (unidirectional) climate change vs. natural (cyclical) variation to ecosystem dynamics. Natural variability may exacerbate or dampen signals of secular climate change depending on whether the natural variability is leading to warmer or cooler alternative stable states.

The complexity of the issue may be better understood by considering how key biological communities have changed and are changing in marine ecosystems. Plankton and seabirds have been put forth as reliable indicators of change in marine ecosystems (Cairns 1987; Beaugrand 2005; McGowan et al. 1996; Piatt et al. 2007; Lavaniegos and Ohman 2007). Both zooplankton and seabirds are well-known in the CCE, with documented changes in species composition, abundance, ecology, and distributions. Relative to ocean climate, zooplankton are: (1) ectothermic, making their physiology directly sensitive to changes in ocean temperature and ocean chemistry, (2) lower in the trophic web, suggesting a more direct link to primary production and effects on growth and reproduction, and (3) passive drifters in the ocean realm, such that changes in distribution must reflect changes in currents and/or water mass distributions. Some have argued that zooplankton are the most reliable indicators of system state (Richardson 2008). On the other hand, seabirds are endothermic, have a higher trophic level, and move rapidly from place to place on scales of hours and tens of kms in search of favorable habitat and prey fields. Such characteristics would appear to make them less reliable indicators of ecosystem change, but seabirds are arguably the most conspicuous of all marine organisms, and as upper-trophic level species, may “amplify” changes in physical oceanographic attributes and difficult-to-study mid-trophic level species, thereby providing meaningful signals of change (Sydeman et al. 2001; Taylor et al. 2002; Abraham and Sydeman 2004; Sydeman et al. 2006; Piatt et al. 2007). Seabirds congregate at colonies and at pelagic or nearshore ocean

productivity “hotspots” where they can be studied in large numbers, providing for robust sample sizes.

In this paper, we examine oceanographic climate and ecosystem change by considering select case histories for seabirds in the CCE and the transition zone between the CCE and Gulf of Alaska (GoA) large marine ecosystems (from $\sim 30^{\circ}$ – 52° N). We investigate how seabird population parameters (e.g., productivity), food habits, and community composition have changed over time, particularly from the early 1970s through 2007, where possible. This is the extent of the longest time series available for consideration, and untangling climate-predator-prey relationships is still a challenge. Specifically, we consider whether the observed changes in seabird parameters mostly reflect natural climate variability or a response to secular climate change, which we call “cyclic or episodic variability” or “trends,” respectively. We also examine the hypothesis that change in seabird parameters can be related to changes in their forage base, a “bottom-up” perspective (Ware and Thompson 2005). To accomplish this goal for some time series, we examine relationships between seabird population parameters, oceanographic indices, and indices of prey abundance. Finally, because they are indicator species (Piatt et al. 2007), understanding seabird responses to climate variability and climate change may be important to understanding climate-forced ecosystem dynamics and predator-prey relationships for other upper-trophic level predators in the CCE which are inherently more difficult to study (e.g., fish), yet are of considerable economic and societal value. We surmise that as seabirds and some fish and marine mammals exist on similar trophic levels and consume similar prey, we can learn something about these more difficult-to-study organisms by developing a better understanding of climate-ecosystem-seabird interactions (Roth et al. 2007; Sydeman et al. 2008).

METHODS

The observational data we review and present herein have been collected over the past 40 years as part of long-term fisheries oceanography and seabird monitoring programs designed to inform management of CCE living marine resources (fig. 1). Information on seabird distribution and abundance at sea off southern California has been collected since May 1987 as part of the California Cooperative Oceanic Fisheries Investigation (CalCOFI; <http://www.calcofi.net>). This seabird program, initiated by R. R. Veit and J. A. McGowan, with funding from the National Science Foundation, has resulted in counts and density (no. birds/km²) estimates of ~ 60 species of seabirds over the period (Veit et al. 1996; Hyrenbach and Veit 2003; Yen et al. 2006). Briefly, on CalCOFI surveys seabirds are counted using the 300 m strip transect method of Tasker et al. 1984. Details of observational

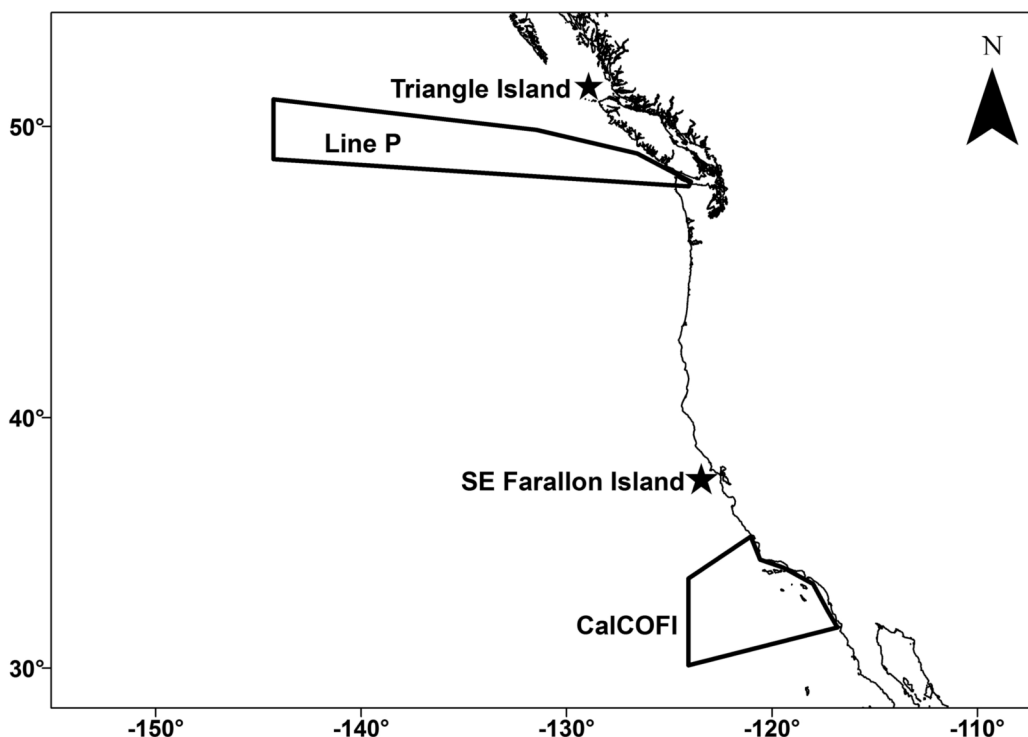


Figure 1. Map of the California Current Ecosystem (CCE) showing the locations of study areas referenced in this paper. The areal extent of the CalCOFI and Line P surveys are shown as polygons. Stars mark the locations of the Southeast Farallon Island and Triangle Island seabird colonies.

methods are available in the above papers. In this paper, we analyzed changes in the relative abundance of the overall seabird community as well as changes in two species/groups, “dark” shearwaters (mostly reflecting sooty shearwater, *Puffinus griseus*) and Cassin’s auklet (*Ptychoramphus aleuticus*). We selected these species and those listed below from colonies because they are some of the most abundant seabird species in the system (Briggs et al. 1987), and they have been the subject of many previous studies.

The Canadian Department of Fisheries and Oceans (DFO), Station Papa Line P survey (http://www-sci.pac.dfo-mpo.gc.ca/osap/projects/linepdata/default_e.htm) is situated in the transition zone between the CCE and the Gulf of Alaska ecosystem. The Line P transect is located in the CCE when the North Pacific Current traverses the North Pacific Ocean in a more northerly position, and is partly in the CCE and GoA when the current is distributed further south (Batten and Freeland 2007). Information collected on seabird distribution and abundance at sea in the GoA has been obtained since May 1996. This program, initiated by K. H. Morgan with funding from Environment Canada/Canadian Wildlife Service, has resulted in density (no. birds/km²) estimates of ~40 species of seabirds over the period. Observational and analytical methods for this data set are available from Yen et al. 2005 and O’Hara et al. 2006. Given the rela-

tively short length of this time series, there have been no previous attempts at trend analyses. In this paper, we examine overall changes in seabird abundance and diversity from 1996 through 2006, stratified by the season of observation (winter = February, summer = June, or fall = September).

Seabirds have been studied on numerous colonies in the CCE. Herein, we focus on results obtained at two, Southeast Farallon Island (SEFI) and Triangle Islands (TRI). SEFI is located in central-northern California (37°42’N, 123°00’W) in the heart of the Gulf of the Farallones National Marine Sanctuary and in a region downstream from one of the most dynamic upwelling cells (the Point Arena-Point Reyes cell) along the West Coast (Hickey 1979). SEFI is part of the Farallon National Wildlife Refuge operated by U.S. Fish and Wildlife Service. Monitoring of seabird populations on SEFI is conducted under a cooperative agreement with PRBO Conservation Science (formerly Point Reyes Bird Observatory). Overall design of the program may be attributed to D. G. Ainley who initiated many of the protocols still used today starting in 1971. Information collected for the Refuge includes estimates of population size, demographic and life history (e.g., timing of breeding) attributes, and food habits. Field and various analytical methods may be found in Ainley et al. 1995, Sydeman et al. 2001, and many of the references cited

below. Previous trend analyses relative to long-term climate-ecosystem change include Sydeman et al. 2001, and relative to short-term climate anomalies include Sydeman et al. 2006 and Jahncke et al. 2008. In this paper, we examine estimates of annual breeding success and timing of breeding for trends.

TRI, like Line P, is located in the transition domain between the CCE and GoA. In general, unlike the role of upwelling in central-northern California, the mechanisms driving ocean productivity in this region are not well known. TRI is protected as the Anne Vallée Triangle Island Ecological Reserve (http://www.env.gov.bc.ca/bcparks/eco_reserve/anne_er.html). Monitoring of seabird populations there is conducted by Environment Canada-Canadian Wildlife Service and Simon Fraser University under a permit from the province of British Columbia. Overall design of the program may be attributed to K. Vermeer, who initiated studies on TRI in the mid 1970s, and I. Jones, who reinitiated the program in the early 1990s. Basic information collected includes indices of population size, demographic attributes, and food habits. Field and various analytical methods may be found in Bertram et al. 2001 and Hedd et al. 2006. We examine this data for trends in breeding success and relationships to oceanographic conditions.

**Data Treatment and Statistical Analyses—
 Seabirds at Sea**

For CalCOFI data, bird counts were summarized into “bins,” generally 3 km in length. Survey densities were calculated by averaging the densities for all birds, “dark” shearwaters, and Cassin’s auklets in all bins. For Line P data, bird counts were summarized per day, and then divided by the total area surveyed each day. Daily density estimates were averaged to produce survey estimates. Owing to the migratory nature of seabirds in the CCE and variation in the seasonal cycle of ocean productivity, we examined seasonal surveys separately (using Spearman rank correlation), or using a GLM approach (i.e., ANCOVA) that included “season” as a term, with “year” treated as a linear co-variate (i.e., $df = 1$) to test for trends. To approximate normality, survey-specific den-

sity estimates were log-transformed prior to all analyses. Surveys in the winter (January–February), summer (June–July), and fall (September–November) were used to examine trends and contrast patterns of change between CalCOFI and Line P for total bird density and species richness (fig. 2). There were no springtime (March–April) Line P surveys, hence the CalCOFI spring survey data were used only for investigating trends in shearwater and auklet densities and their relationships to ocean temperature (fig. 3). For illustrations, seasonal densities were expressed as anomaly statistics. To calculate anomalies in density, replicate surveys conducted in each season were averaged to produce a grand seasonal mean for each series (CalCOFI: 1987–2004; Line P: 1996–2006). Seasonal deviations (or anomalies) from the grand mean were calculated by subtracting the seasonal value for each year from the seasonal grand mean. To examine changes in dark shearwater and Cassin’s auklet abundances relative to ocean temperature, we used CTD measurements at 100 m from line 80 in the CalCOFI grid (fig. 1); this line is located in the center of the CalCOFI study area; shearwaters were found over the entire study area (Yen et al. 2006) and for this species at least, line 80 provides a reasonable central location to investigate temperature relationships. Cassin’s auklets were found mostly in the northern sector of the grid. Information from 1987 through 2004 is provided in this update. A more comprehensive analysis of species-specific trends, but for a more limited time period (1987–97) is available in Hyrenbach and Veit 2003.

**Data Treatment and Statistical Analyses—
 Seabirds on Colonies**

Data on timing of breeding, reproductive success and food habits (take of juvenile rockfish by murre) was analyzed using Spearman rank correlation to test for trends. For illustration, anomalies were calculated by subtracting annual means from a grand mean established for the entire time series for each species and parameter. Anomalies for seabird density, species richness, reproductive success, timing of egg-laying, and food habits are shown as histograms, with the 0-line reflecting the grand

TABLE 1
 Trends in seabird species richness and density stratified by season for CalCOFI and Line P surveys.
 Spearman rank correlations, sample size and *p*-values for the above datasets.

| Dataset | Winter | | | Summer | | | Fall | | |
|------------------|----------|--------------|-----------------------|----------|--------------|-----------------------|----------|--------------|-----------------------|
| | <i>N</i> | Spearman rho | <i>p</i> < <i>t</i> | <i>N</i> | Spearman rho | <i>p</i> < <i>t</i> | <i>N</i> | Spearman rho | <i>p</i> < <i>t</i> |
| CalCOFI Density | 13 | -0.3571 | 0.2309 | 15 | -0.5143 | 0.0498 | 18 | -0.4448 | 0.0644 |
| CalCOFI Richness | 13 | -0.4635 | 0.1107 | 15 | -0.4816 | 0.0691 | 18 | -0.6211 | 0.0059 |
| Line P Density | 10 | 0.0667 | 0.8548 | 10 | 0.4182 | 0.2291 | 8 | 0.7143 | 0.0465 |
| Line P Richness | 10 | 0.6342 | 0.0489 | 10 | -0.0675 | 0.853 | 8 | 0.8982 | 0.0024 |

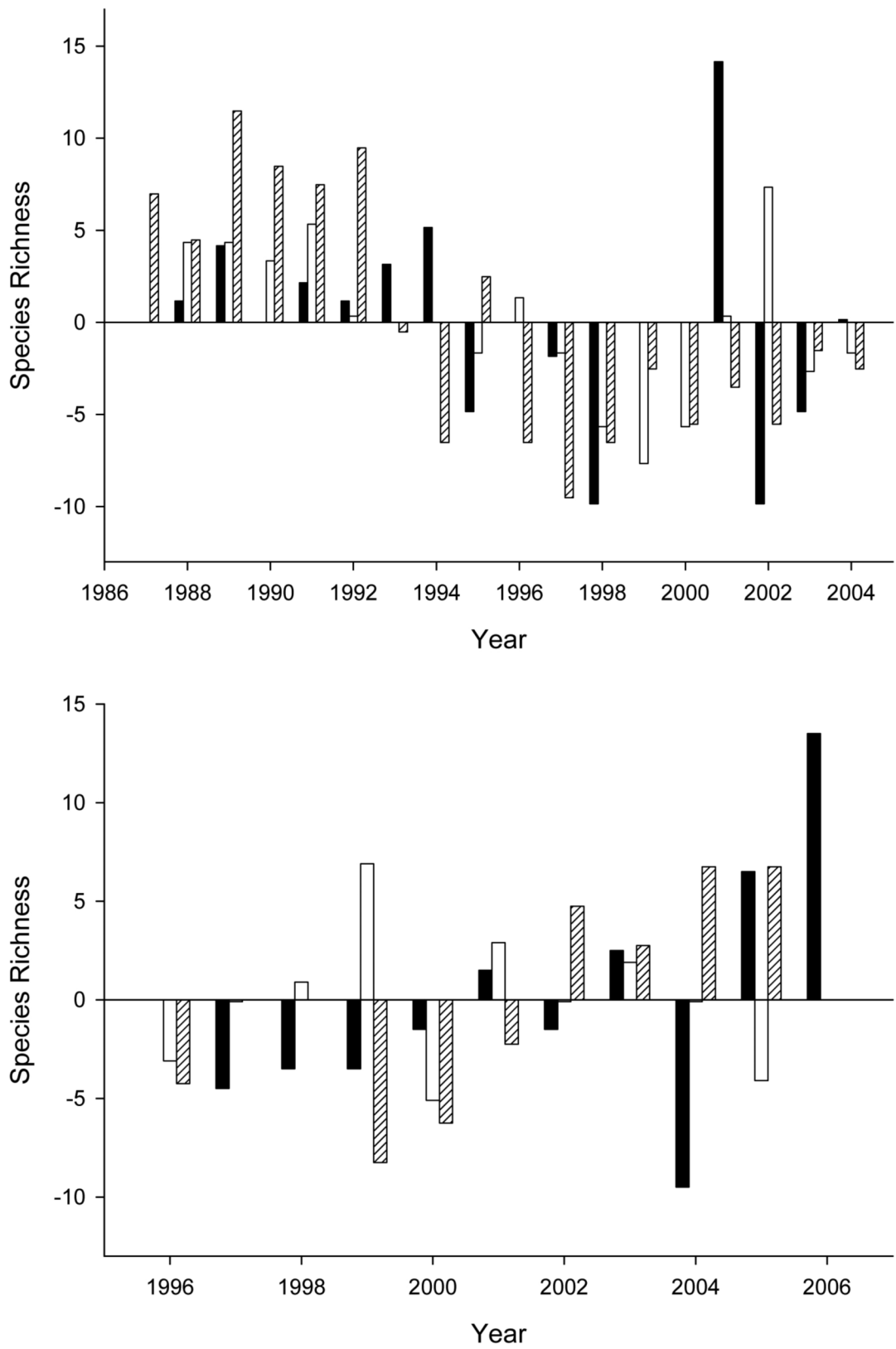


Figure 2. Trends in seabird species richness (seasonal anomalies, see text for details of calculations) and total seabird density (birds/km²) from winter, summer, and fall long-term surveys in the southern and northern portions of the California Current Ecosystem. (A) CalCOFI species richness, (B) Line P species richness, (C) CalCOFI density, (D) Line P density. Black bar = winter; open bars = summer, cross-hatched bars = fall.

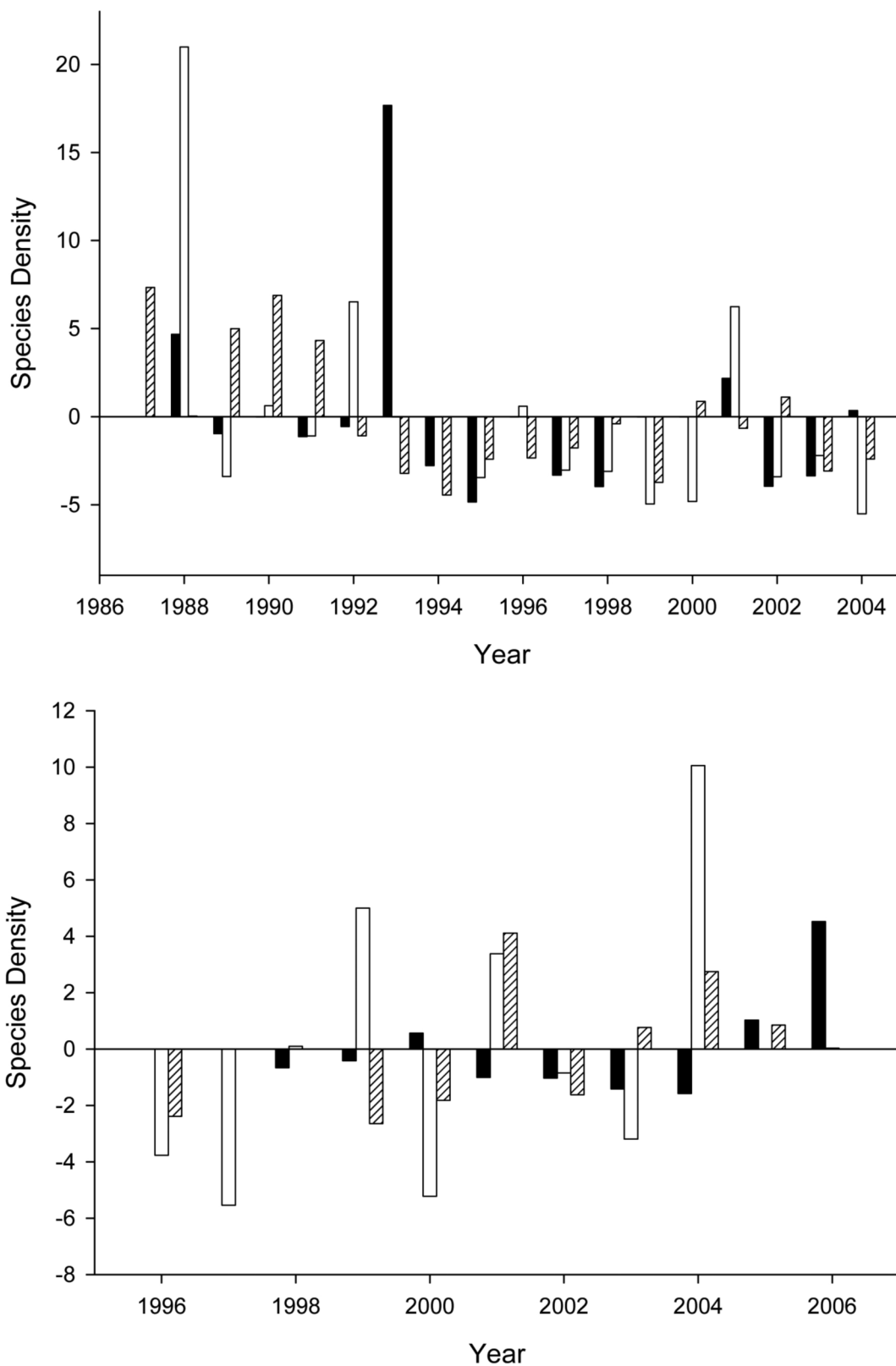


Figure 2. (continued) Trends in seabird species richness (seasonal anomalies, see text for details of calculations) and total seabird density (birds/km²) from winter, summer, and fall long-term surveys in the southern and northern portions of the California Current Ecosystem. (A) CalCOFI species richness, (B) Line P species richness, (C) CalCOFI density, (D) Line P density. Black bar = winter; open bars = summer, cross-hatched bars = fall.

seasonal (for densities) or annual (for other parameters) means. To illustrate years or season of substantial variation, we calculated the standard deviation of the anomalies; dashed lines above and below the 0-line in figures show 1 s.d. from the grand mean for each parameter.

RESULTS – CASE HISTORIES

Trends in Seabird Species Richness and Overall Abundance

Southern Trends from CalCOFI Analysis of species richness (i.e., the number of individual species recorded on each survey), which provides a simple measure of community diversity, from winter, summer and fall CalCOFI surveys, reveals a general decline through time (tab. 1; fig. 2A), and with increasing temperature (ANCOVA: $\ln(\text{species richness})$: overall $F = 8.82$, $p < 0.0001$, $R^2 = 0.4276$; season: $F = 2.62$, $p = 0.0594$; year: coefficient = -0.020 , $F_{1,59} = 24.13$, $p < 0.0001$; temperature @ 100m on line 80: coefficient = -0.087 , $F_{1,59} = 15.15$, $p = 0.0003$). Overall seabird density in the CalCOFI region also declined over time (Table 1; Figure 2c), and with increasing temperature (ANCOVA: $\ln(\text{density})$: overall $F = 6.58$, $p = 0.0001$, $R^2 = 0.358$; season: $F = 1.36$, $p = 0.2651$; year: coefficient = -0.071 , $F_{1,59} = 22.81$, $p < 0.0001$; temperature @ 100m on line 80: coefficient = -0.254 , $F_{1,59} = 9.32$, $p = 0.0034$).

Northern Trends from Line P. In contrast to the CalCOFI data set, species richness on Line P increased through time (tab. 1; fig. 2B), though the time series (1996–2006) was considerably shorter. Analysis of change in species richness reveals seasonal variability and an increase in richness through time (ANCOVA: $\ln(\text{species richness})$: overall $F = 3.33$, $p = 0.0364$, $R^2 = 0.2940$; season: $F_{2,24} = 2.49$, $p = 0.1036$; year: coefficient = 0.029 , $F_{1,24} = 4.81$, $p = 0.0383$). The opposite pattern between CalCOFI and Line P is evident for seabird density as well. Analysis of density reveals seasonal variability and an increase through time (fig. 2D) (ANCOVA: $\ln(\text{density})$: overall $F = 7.00$, $p = 0.0015$, $R^2 = 0.4667$; season: $F_{2,24} = 8.94$, $p = 0.0013$; year: coefficient = 0.103 , $F_{1,24} = 5.32$, $P = 0.0300$).

Trends in Density, Timing and Productivity for Select Species

(1) Dark (Sooty) Shearwaters

Dark shearwaters are the most abundant species observed during CalCOFI surveys, particularly in the spring and summer (Hyrenbach and Veit 2003). Analysis of change in density reveals a decline through time, seasonal variability, but no effect of temperature (fig. 3A, C; ANCOVA: $\ln(\text{density})$: $F_{6,58} = 14.02$, $p < 0.0001$, $R^2 = 0.543$; season: $F_{3,58} = 19.76$, $p < 0.0001$; year: coefficient = -0.045 , $F_{1,58} = 14.01$, $p = 0.0004$; temperature @

100m on line 80: coefficient = -0.037 , $F_{1,58} = 0.30$, $p = 0.587$). While the decline in shearwater density previously reported (Veit et al. 1996; Hyrenbach and Veit 2003) is confirmed by this updated analysis, we were unable to distinguish whether the rate of decline has accelerated or leveled-off; in GLM, we fit different transformations of year, but none were any better than the linear model of decline (unpubl. data). Nonetheless, from the data alone it appears that the decline has leveled-off in recent years (fig. 3A).

(2) Cassin's Auklet

Analysis of change in CalCOFI auklet density reveals a decline through time, seasonal variability, but no effect of temperature during the survey period (fig. 3B, D; ANCOVA: $\ln(\text{density})$: $F = 6.36$, $p = 0.0001$, $R^2 = 0.3503$; season: $F = 8.38$, $p = 0.0001$; year: coefficient = -0.015 , $F_{1,59} = 6.22$, $p = 0.0155$; temperature @ 100m on line 80: coefficient = -0.041 , $F_{1,59} = 1.53$, $p = 0.2211$).

The timing of breeding and productivity of Cassin's auklet has been monitored on Southeast Farallon Island (SEFI) since 1972 (timing: mean egg-laying date) and 1971 (productivity: mean number of young fledged/pair/year), respectively. On the interannual scale, there is substantial variability in mean egg-laying dates (fig. 4A), with notable delays of 40–60 days in average timing during ENSO events that affected wintertime conditions (1983, 1992, 1998; see also Schroeder et al., in press). Recent auklet productivity failures in 2005–07 do not correspond to ENSO events (fig. 4B). While there are no significant trends in the mean values of either parameter, both timing and productivity have become significantly more variable through time (tab. 2). Moreover, despite a period of generally later breeding in the 1990s and earlier breeding thereafter, there is no significant

TABLE 2
Trends in means and variance in seabird timing of breeding and reproductive success (average number of offspring fledged/pair) over the past 35 years.

| | N | Spearman rho | $p < t $ |
|---|----|--------------|-----------|
| Means | | | |
| Cassin's Auklet Mean Egg Laying Date | 35 | 0.2614 | 0.1293 |
| Common Murre Mean Egg Laying Date | 35 | -0.3263 | 0.0557 |
| Cassin's Auklet Reproductive Success | 37 | -0.0937 | 0.5810 |
| Common Murre Reproductive Success | 36 | -0.2910 | 0.0851 |
| Brandt's Cormorant Reproductive Success | 37 | 0.4692 | 0.0034 |
| Interdecadal Variance | | | |
| Cassin's Auklet Mean Egg Laying Date | 4 | 0.4 | 0.6 |
| Common Murre Mean Egg Laying Date | 4 | 0.2 | 0.8 |
| Cassin's Auklet Reproductive Success | 4 | 1 | 0 |
| Common Murre Reproductive Success | 4 | 0.4 | 0.6 |
| Brandt's Cormorant Reproductive Success | 4 | -0.2 | 0.8 |
| PCA | | | |
| Community Productivity (PC1) | 36 | -0.0986 | 0.5673 |

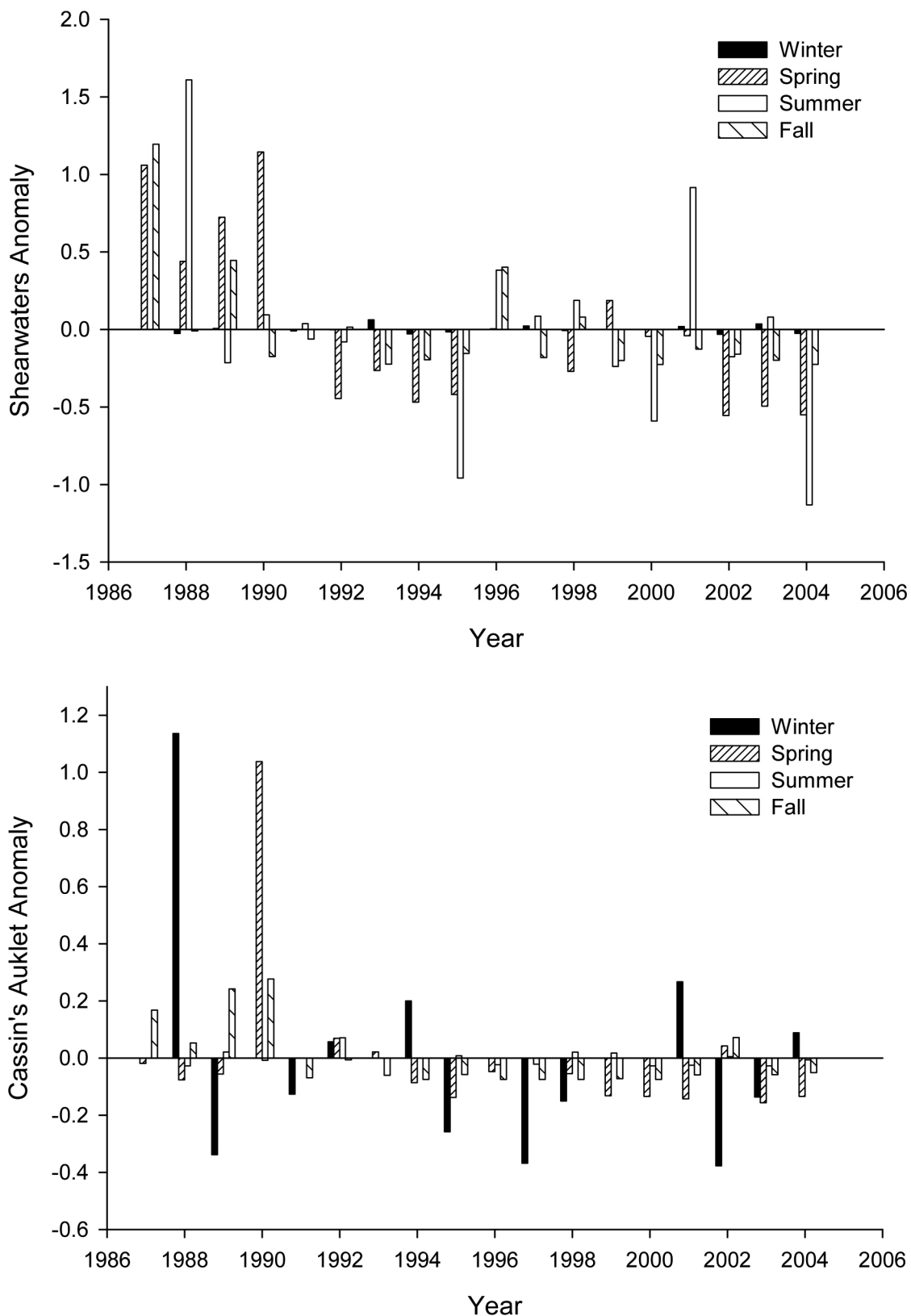


Figure 3. Trends in density (seasonal anomaly in birds/km²) of (A) dark shearwaters (assumed to be mostly sooty, *Puffinus griseus*) and (B) Cassin's auklet (*Ptychoramphus aleuticus*) from long-term CalCOFI surveys. Scatterplots of the relationships between (C) dark shearwater density, and (D) auklet density relative to ocean temperature (mean T @ 100m on line 80) for surveys between May 1987 and November 2004. See text for statistical analyses and explanation of anomaly calculations.

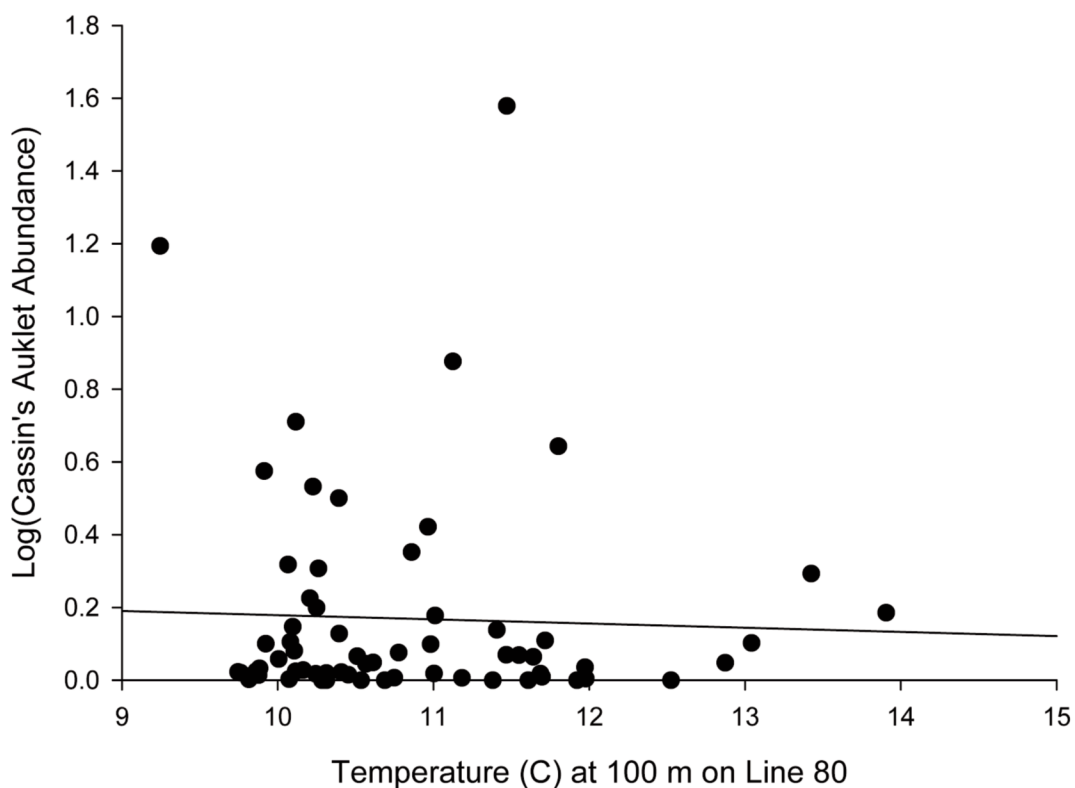
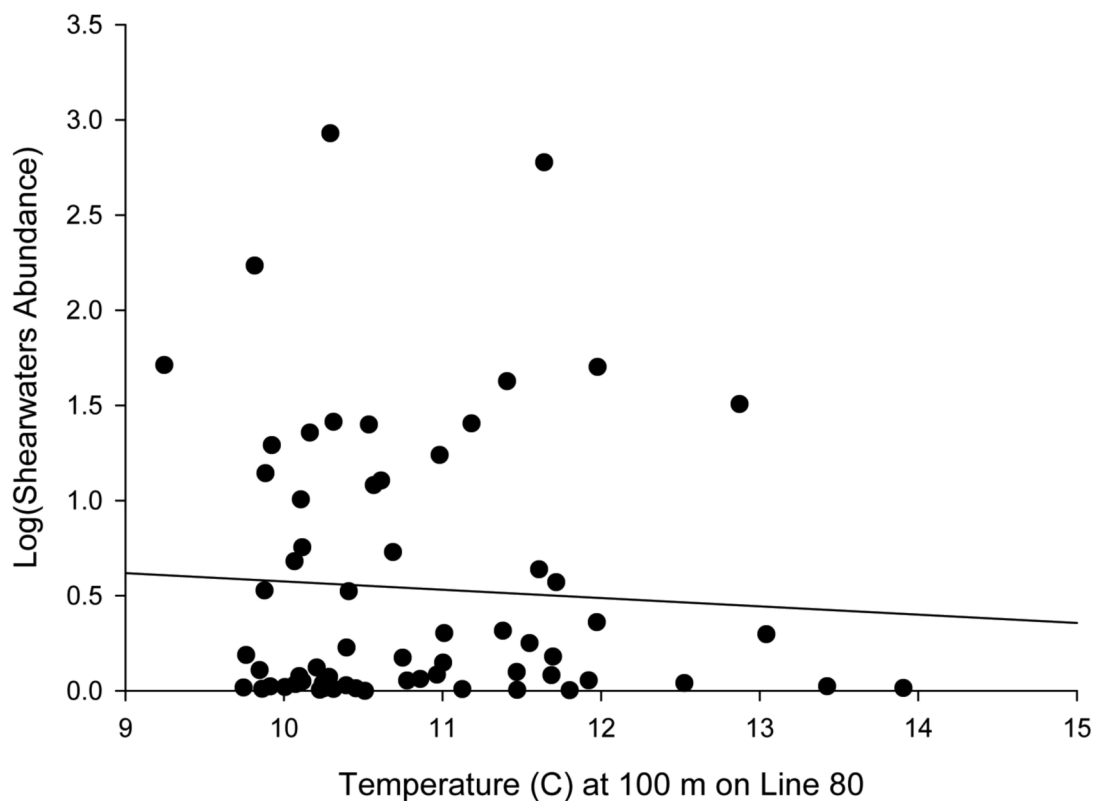


Figure 3. (continued) Trends in density (seasonal anomaly in birds/km²) of (A) dark shearwaters (assumed to be mostly sooty, *Puffinus griseus*) and (B) Cassin's auklet (*Ptychoramphus aleuticus*) from long-term CalCOFI surveys. Scatterplots of the relationships between (C) dark shearwater density, and (D) auklet density relative to ocean temperature (mean T @ 100m on line 80) for surveys between May 1987 and November 2004. See text for statistical analyses and explanation of anomaly calculations.

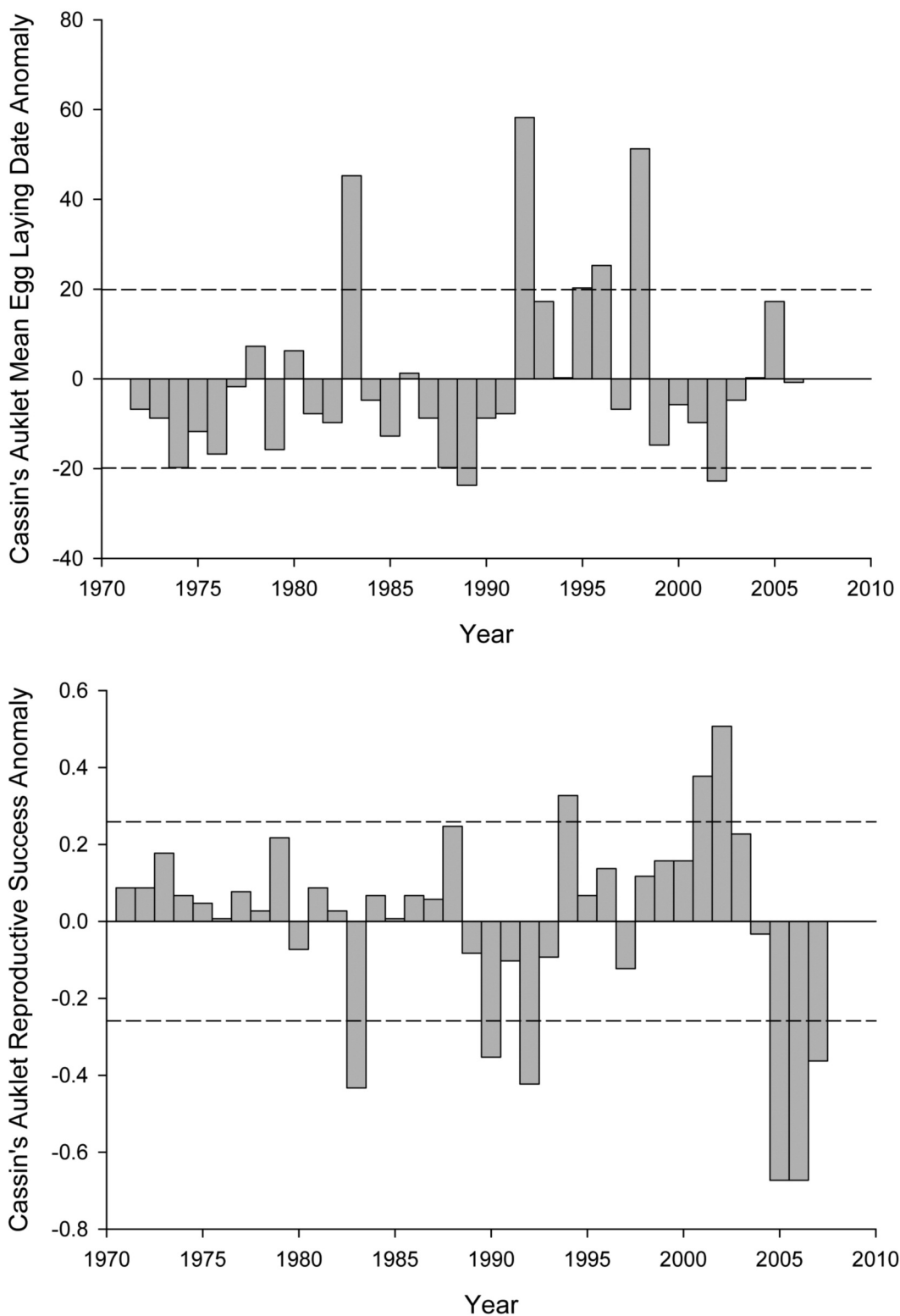


Figure 4. Interannual variability in phenology and productivity of seabirds breeding on the Farallon Islands, 1971–2007. Anomalies (see text for explanation) in dates of egg-laying and breeding success (no. young pair⁻¹) are presented. Dashed lines illustrate ± 1 s.d. of the mean. (A) Cassin's auklet (*Ptychoramphus aleuticus*) timing, (B) Cassin's auklet productivity, (C) common murre (*Uria aalge*) timing, (D) common murre productivity, (E) Brandt's cormorant (*Phalacrocorax penicillatus*) productivity, and (F) community productivity assessed as PC1 of western gull (*Larus occidentalis*), Brandt's cormorant, common murre, pigeon guillemot (*Cepphus columba*), pelagic cormorant (*Phalacrocorax pelagicus*), and Cassin's auklet productivity (1972–2007).

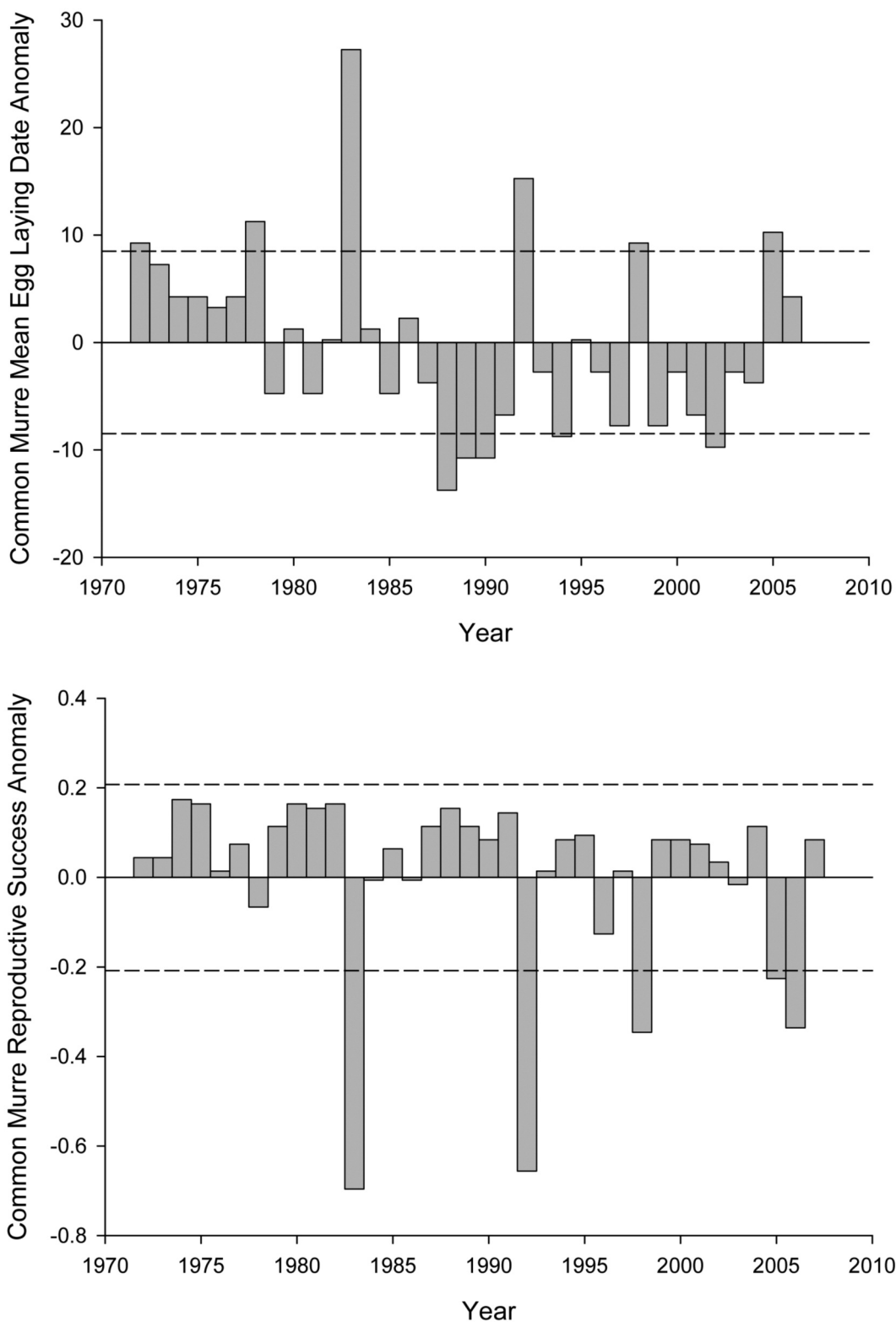


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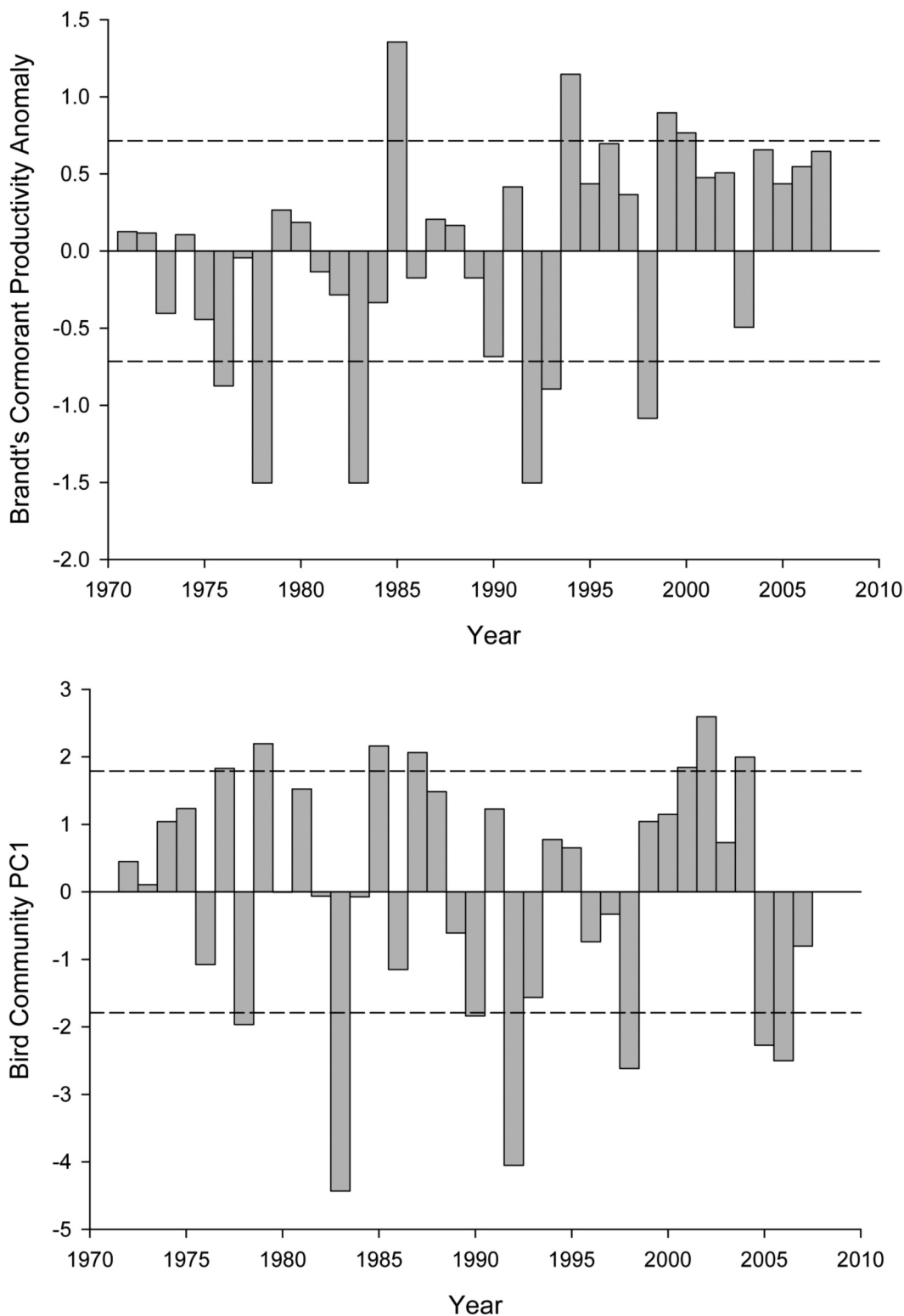


Figure 4. (continued) Interannual variability in phenology and productivity of seabirds breeding on the Farallon Islands, 1971–2007. Anomalies (see text for explanation) in dates of egg-laying and breeding success (no. young pair⁻¹) are presented. Dashed lines illustrate ± 1 s.d. of the mean. (A) Cassin's auklet (*Ptychoramphus aleuticus*) timing, (B) Cassin's auklet productivity, (C) common murre (*Uria aalge*) timing, (D) common murre productivity, (E) Brandt's cormorant (*Phalacrocorax penicillatus*) productivity, and (F) community productivity assessed as PC1 of western gull (*Larus occidentalis*), Brandt's cormorant, common murre, pigeon guillemot (*Cephus columba*), pelagic cormorant (*Phalacrocorax pelagicus*), and Cassin's auklet productivity (1972–2007).

TABLE 3
 Cross-correlations (Spearman rank) of Cassin’s auklet (*Ptychoramphus aleuticus*) reproductive success at the Farallon Islands, California (1971–2007), against monthly values for the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), Northern Oscillation Index (NOI), and Southern Oscillation Index (SOI). Bold, underlined indicates a significant correlation, $p < 0.05$. The auklet’s breeding season lasts from approximately March–September each year. Atmospheric and oceanographic conditions prior to egg-laying may be important determinants of breeding success (no. young produced/pair/year), hence are included here.

| Month | NPGO | | NOI | | SOI | | PDO | |
|-----------|----------------|---------------|---------------|---------------|--------------|-----------|--------------|-----------|
| | Spearman rho | $p < t $ | Spearman rho | $p < t $ | Spearman rho | $p < t $ | Spearman rho | $p < t $ |
| January | 0.1190 | 0.4828 | 0.2747 | 0.0999 | 0.0395 | 0.8164 | 0.1373 | 0.4176 |
| February | 0.0095 | 0.9555 | 0.2968 | 0.0745 | 0.1475 | 0.3836 | 0.2272 | 0.1763 |
| March | 0.0357 | 0.8338 | 0.3019 | 0.0694 | 0.1740 | 0.3031 | 0.1597 | 0.3451 |
| April | -0.0836 | 0.6230 | 0.2999 | 0.0714 | 0.2216 | 0.1874 | 0.1719 | 0.3091 |
| May | -0.2461 | 0.1420 | 0.3852 | 0.0186 | 0.0749 | 0.6596 | -0.0134 | 0.9372 |
| June | -0.3017 | 0.0696 | 0.3706 | 0.0239 | 0.1807 | 0.2844 | 0.1722 | 0.3081 |
| July | -0.4197 | 0.0097 | 0.3409 | 0.0389 | 0.1967 | 0.2431 | 0.2607 | 0.1191 |
| August | -0.3917 | 0.0165 | 0.3136 | 0.0587 | 0.1625 | 0.3367 | 0.1983 | 0.2395 |
| September | -0.3583 | 0.0295 | 0.3119 | 0.0602 | -0.1881 | 0.2649 | 0.2004 | 0.2343 |

non-linear trend in the auklet’s timing of breeding ($F_{2,32} = 1.35, p = 0.274$).

Over the entire time series, 1971–2007, cross-correlations of auklet productivity against monthly large-scale climate indices reveal significant relationships with monthly values of the NPGO in May–July, and PDO in July–September (tab. 3). Notably, unlike the other indices, all of the correlations with the NPGO were consistent in sign from January through September. We found no correlation with monthly values of the Northern Oscillation Index or Southern Oscillation Index. The most compelling correlations involve the NPGO as it overlaps most in time with the auklet’s breeding season.

In the northern CCE, the timing of breeding, reproductive success, mass of offspring at fledging (independence), and food habits of Cassin’s auklets and rhinoceros auklets (*Cerorhinca monocerata*) have been monitored continuously since 1996. Cassin’s auklets at Triangle Island are a significant indicator of the timing of annual mesozooplankton biomass peaks, but in this case a single calanoid copepod, *N. cristatus*, is the primary component of nestling diets and the key determinant of productivity (Bertram et al. 2001; Hipfner, in press). Wolf et al. 2009 compare the relationships between TRI and SEFI auklet timing of breeding and productivity with local and large-scale oceanographic variables during the years 2000–05, including SST, sea surface height (SSH), and upwelling indices in the auklet’s foraging habitat during the breeding season. At both TRI and SEFI, auklets bred later when local SSH was higher, which indicates greater heat content (fig. 5A). At both TRI and SEFI, auklets also produced fewer offspring in years of higher SSH (fig. 5B). Notably, although the diets of these populations are different (mostly euphausiids in California, mostly copepods in British Columbia), auklets from these populations, spaced ~1300 km apart, responded similarly

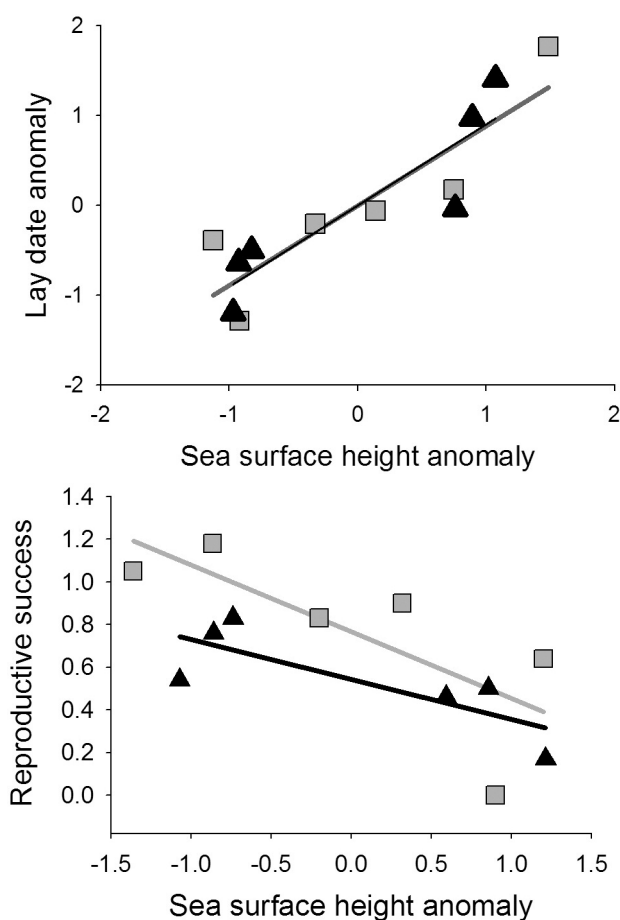


Figure 5. Relationships between (A) the annual mean lay date anomaly and sea surface height anomaly during the laying period and (B) productivity (chicks fledged per pair) and sea surface height anomaly (during the breeding period) for Cassin’s auklets (*Ptychoramphus aleuticus*), with Triangle Island depicted as black triangles and Farallon Island depicted as grey squares. Figure modified from Wolf et al. 2009. For laying date on Farallones: $\beta = 0.89, t = 3.83, p = 0.019, r^2 = 0.79$. For laying date on Triangle: $\beta = 0.90, t = 4.16, p = 0.014, r^2 = 0.81$. For breeding success on Farallones: $\beta = -0.31, t = -2.23, p = 0.09, r^2 = 0.55$. For breeding success on Triangle: $\beta = -0.18, t = -2.61, p = 0.06, r^2 = 0.63$.

to oceanographic climate, highlighting how ocean climate may affect different populations similarly through varying, yet similar “bottom-up” mechanisms. Understanding the mechanisms underlying parallel or divergent demographic responses of widely-spaced populations foraging on different species is clearly an important area for future research.

(3) Common Murre

The timing of breeding and productivity of the Common murre (*Uria aalge*) has been monitored on SEFI since 1973. Farallon murres are a significant indicator for the abundance of forage fish, particularly juvenile rockfish in the region (Mills et al. 2007). On an interannual scale, there is substantial variability in egg-laying dates with delays of 15–25 days in average timing during severe ENSO events (1983, 1992, 1998); there was also substantially late breeding (i.e., >1 s.d. of the mean) in 2005 (fig. 4C). There have also been nearly complete murre productivity failures in 1983 and 1992, and substantially reduced production in 1998 and 2005–06 (fig. 4D). There is a negative trend in murre productivity and timing (despite the delays in 2005 and 2006), but in both cases the trend was weakly significant ($0.10 > p > 0.05$; Table 2). There is also no significant change in the variance in these parameters.

(4) Brandt’s Cormorant

The productivity of Brandt’s cormorants (*Phalacrocorax penicillatus*) has been monitored on SEFI since 1971. Farallon cormorants are a significant indicator for the abundance of forage fish, particularly juvenile rockfish and anchovies in the region (Nur and Sydeman 1999). On an interannual scale, cormorants show the same pattern of failures as murres and auklets, with complete productivity collapses in El Niño years, 1983 and 1992, and substantially reduced production in 1998; however, unlike the other species their reproductive success was within normal bounds in 2005 and 2006 (fig. 4E). Moreover, there has been a significant linear increase in productivity (tab. 2), as first reported by Sydeman et al. 2001 for the same time series, but ending in 1997. Ten years later, the pattern remains the same. As opposed to murres (no change in variance) and auklets (increasing variance), there is a non-significant decrease in the variance of cormorant productivity over the nearly four decades of study.

(5) Rhinoceros Auklet

Triangle Island rhinoceros auklets appear to be a significant indicator for the abundance of forage fish, particularly sandlance (Hedd et al. 2006). This time series is short, but on an interannual scale, rhinoceros auklets show a similar pattern of variability to Farallon murres and Cassin’s auklets, with poor productivity in the late 1990s, reasonable success in 1999–2002, followed by a poor year in 2005 (fig. 6A). Fledgling mass follows the

TABLE 4
Trends in the reproductive success and fledging mass of rhinoceros auklets (*Cerorhinca monocerata*) on Triangle Island. Spearman rank correlations for the above graphs.

| | N | Spearman rho | p < t |
|----------------|----|--------------|--------|
| Productivity | 14 | 0.1364 | 0.6419 |
| Fledgling Mass | 14 | 0.1473 | 0.6154 |

TABLE 5
Trends in the take of rockfish by common murres (*Uria aalge*) and abundance in the environment.

| | N | Spearman rho | p < t |
|-------------------------------|----|--------------|--------|
| Juvenile Rockfish | 25 | -0.4546 | 0.0224 |
| Rockfish in Common Murre Diet | 32 | -0.581 | 0.0005 |

same interannual pattern of variability. There was no trend in this parameter through time (tab 4).

Trends in Community Metrics: Linking Seabird Productivity and Trophic Structure

(1) Multivariate Farallon Productivity Index

Sydeman et al. 2001 developed a multivariate index of seabird breeding success on the Farallones; Figure 4F is an update to the Sydeman et al. figure. The index is based on the three species discussed above, as well as the pelagic cormorant (*Phalacrocorax pelagicus*, PECO), pigeon guillemot (*Cepphus columba*, PIGU), and western gull (*Larus occidentalis*, WEGU). Productivity trends for these species indicate variability (PECO), a weak non-significant decline (PIGU) and a strong decline (WEGU; W. J. Sydeman, unpubl. data). When coupled, the six species reveal the same patterns of variability, with overall community failure in 1983, 1992, and 1998 (all below 1 s.d. of the mean), a period of reasonably high productivity from 1999–2003 (above 1 s.d. of the mean), and very poor productivity in 2005 and 2006 (below 1 s.d. of the mean). There is no trend in the mean or variance of community-wide productivity (tab. 2).

(2) The Importance of Juvenile Rockfish (*Sebastes* spp.)

The diets of Farallon common murre chicks have been monitored since 1973. The abundance of prey in the region, including juvenile rockfish, anchovies, and other forage fish, has been monitored since 1983 through NMFS trawl surveys (NMFS/S. Ralston, unpubl. data¹). On a long-term scale, murre chick diets and NMFS trawl surveys show the same temporal pattern of collapse in juvenile rockfish relative abundance starting in ~1989–90 (Mills et al. 2007, fig. 7A). Murre chick diets show a slight recovery in the take of juvenile rockfish in 2001–04, matched to a lesser extent by the trawl surveys in the

¹S. Ralston, NOAA/NMFS/SWFSC, 110 Shaffer Road, Santa Cruz, California, 95060.

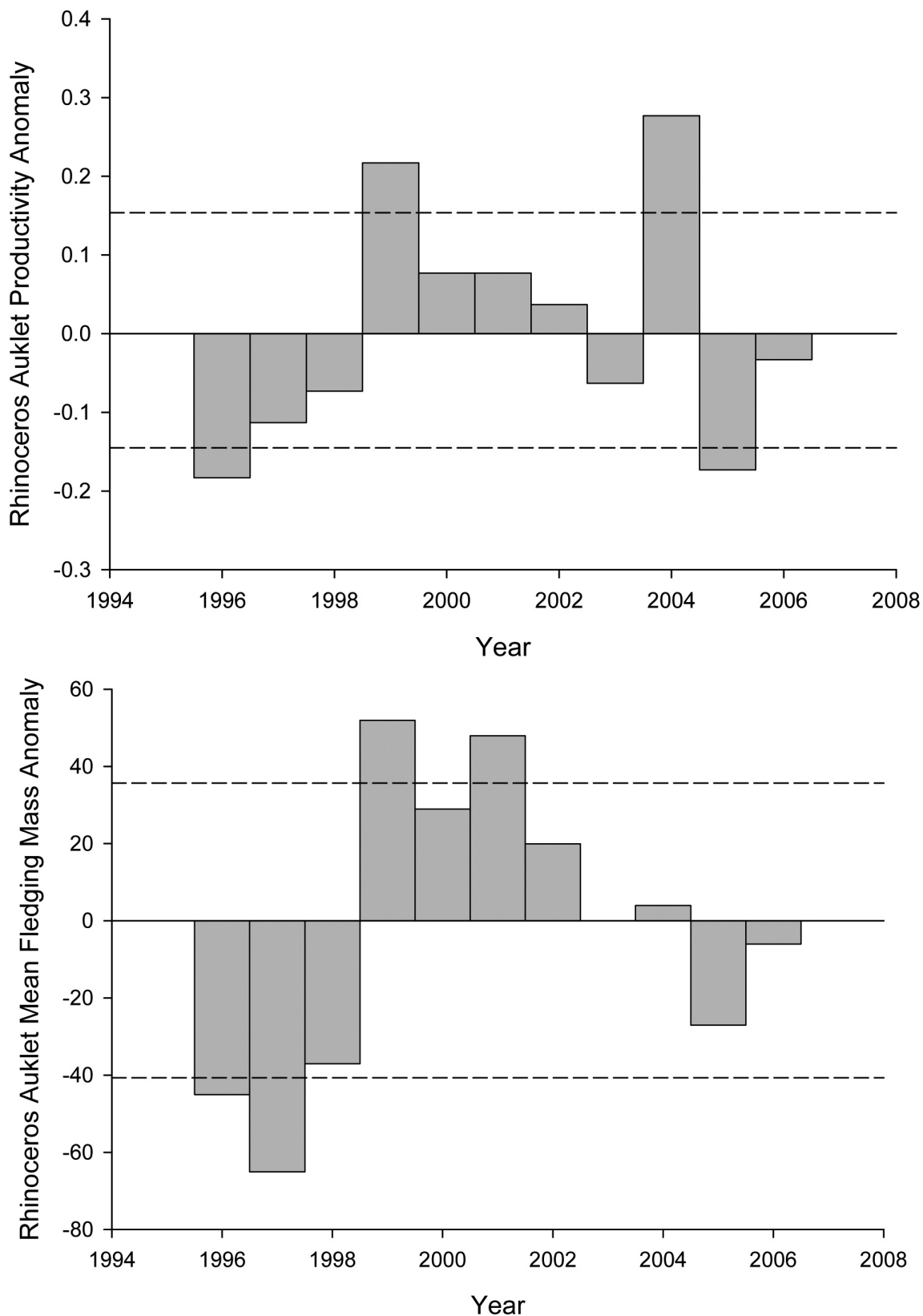


Figure 6. Interannual variability in (A) reproductive success and (B) mass of young at fledging for rhinoceros auklets (*Cerorhinca monocerata*) breeding on Triangle Island, British Columbia, 1996–2006. Anomalies (histogram) in productivity (no. young/pair) and fledging mass (g) are presented (see text for analytical details). Dashed lines illustrate ± 1 s.d. of the mean.

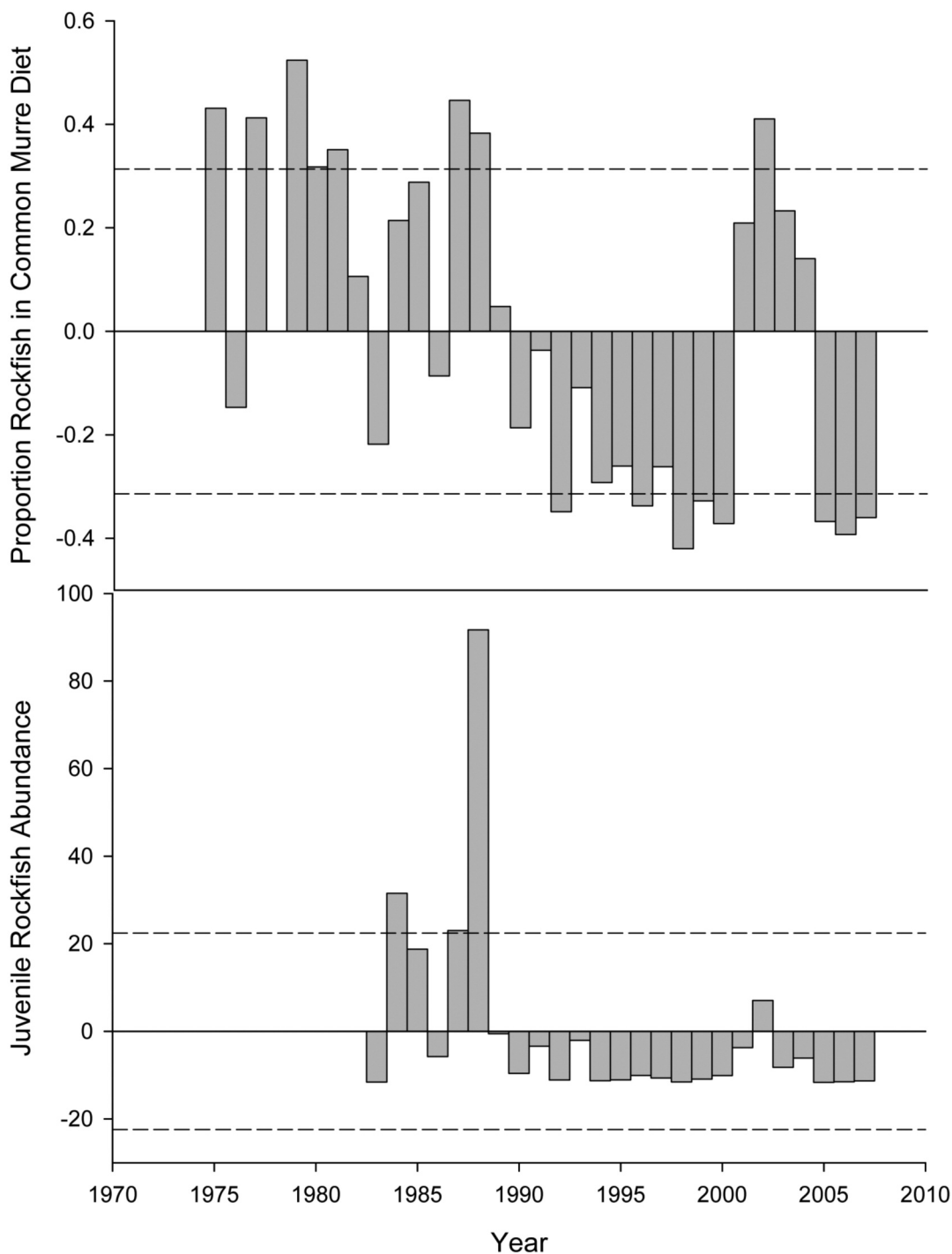


Figure 7. (a) Time series of interannual anomalies (see text for details of calculations) in the take of juvenile rockfish (*Sebastes* spp.) by common murre (*Uria aalge*) on the Farallon Islands (1975–2007) and the abundance of juvenile rockfish in the greater Gulf of the Farallones as measured by NOAA-NMFS (1983–2007; S. Ralston and J. Field, unpubl. Data¹). Dashed lines illustrate ± 1 s.d. of the long-term mean.

same years (fig. 7A), followed by three years of no rockfish in the diet or trawls in 2005–07. There is a significant linear decrease in both of these indices of juvenile rockfish abundance (tab. 5). The relationship between juvenile rockfish in the murre’s diet and relative abun-

dance in the environment follows an exponential plateau curve (fig. 7B). At low and high levels of rockfish abundance, there was little change in the murre diet composition, but at moderate levels of prey abundance, there was a linear change in the murre’s diet.

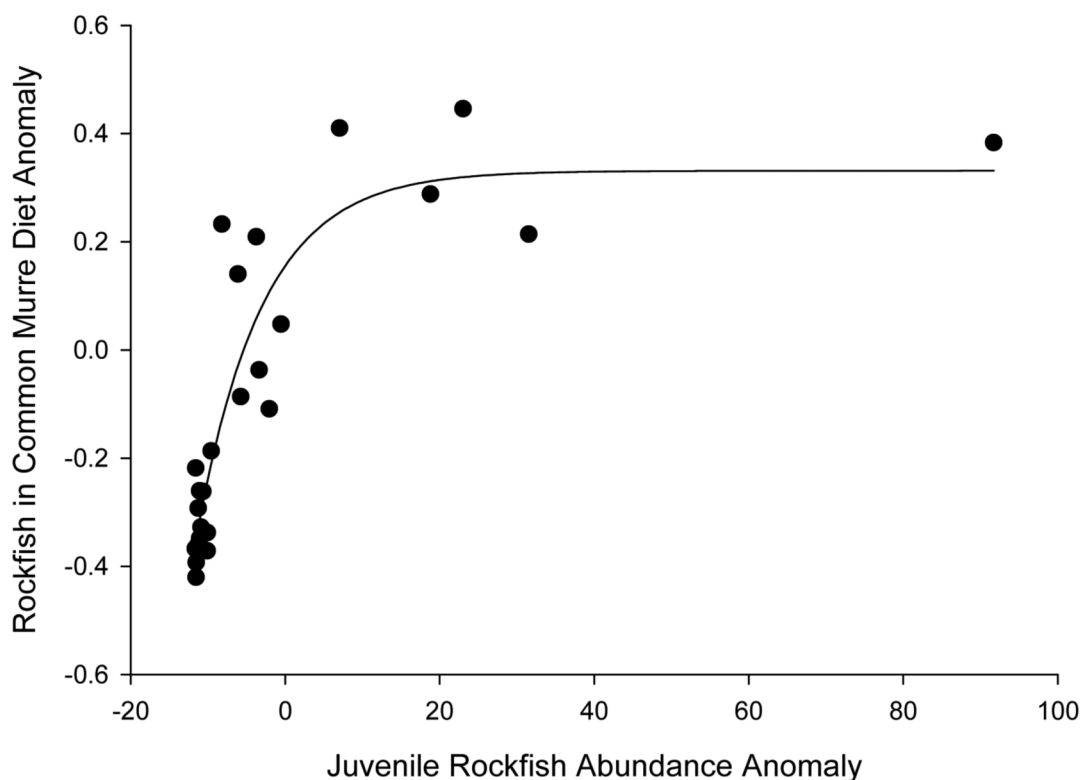


Figure 7. (continued) (b) The relationship between juvenile rockfish abundance in the environment as determined by NOAA-NMFS and take of juvenile rockfish by murre; fit is an exponential rise to maximum, 3 parameter GLM; $R^2 = 0.81$.

(3) Food Chains and Productivity

Wells et al. 2008 developed a multivariate index of murre and auklet food chains for the Gulf of the Farallones, combining seabird data with information on the abundance of prey from the NMFS juvenile rockfish survey, as well as mesozooplankton abundance from CalCOFI surveys. Using this multivariate index, we have determined that both the auklet trophic chain, comprised of mesozooplankton and auklets, and the murre trophic chain, comprised of mesozooplankton, juvenile rockfish, and murre, have become less productive through time. In both cases, there is a declining trend in productivity for these multivariate food web indicators (fig. 8A, B).

DISCUSSION

Parmesan 2006 reviewed the possibilities of ecological and evolutionary change in relation to climate change, focusing primarily on terrestrial biota, and suggested a few fundamental observations which may be evident in all ecosystems. These include: (i) change in the timing of biological events, (ii) change in the geographic range and/or relative abundance of species, (iii) change in the community structure, and (iv) change in population or “system” productivity. We found evidence for changes in seabird communities and population parameters in

the CCE that are consistent with the possible responses to climate change: (i) mean egg-laying dates for one species (murre) became earlier through time (i.e., changes in timing); (ii) species mostly found in colder waters (i.e., shearwaters and auklets) became less abundant in the southern CCE, corroborating previous reports on these species (Veit et al. 1996; Oedekoven et al. 2001; Hyrenbach and Veit 2003) (i.e., changes in geographic range and abundance); (iii) the seabird community in the southern CCE had become less abundant and less diverse, while that of the northern CCE had become more abundant and more diverse (i.e., changes in community structure); and (iv) productivity of some species declined, whereas for others it increased (i.e., changes in productivity). In relation to changes in productivity, we demonstrate that changes in productivity for two species—auklets and murre—were related to changes in the abundance/availability of their prey (zooplankton and forage fish), and that when coupled, multivariate indices of productivity, integrating zooplankton, fish and birds, also declined (Wells et al. 2008). Finally, although Parmesan 2006 did not make generalizations about change in parameter variability (or variance), we found increasing variance in the productivity for one species (Cassin’s auklet) at SEFI.

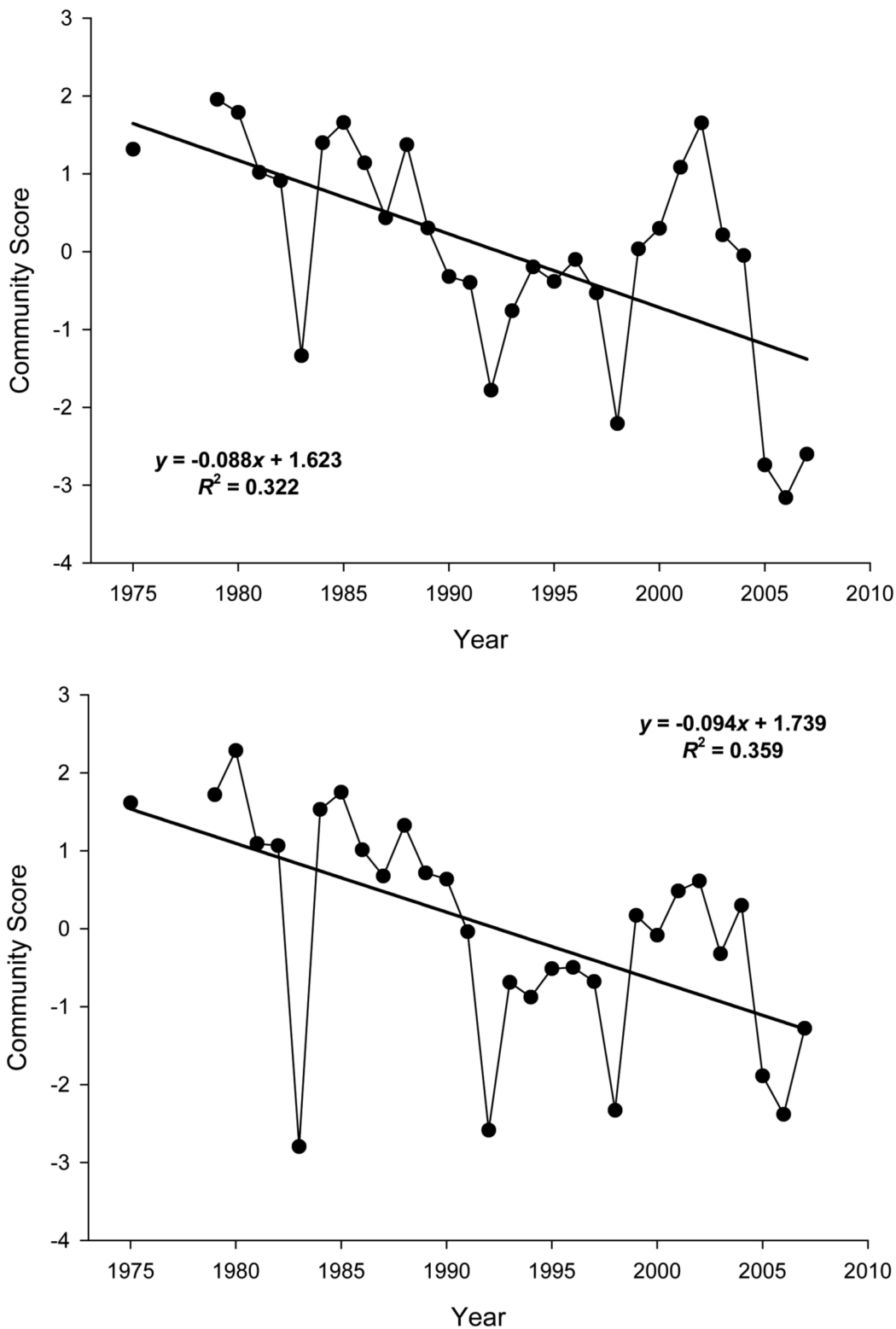


Figure 8. Trends in the multivariate "trophic chain" productivity for (A) Cassin's auklet (*Ptychoramphus aleuticus*) and (B) common murre (*Uria aalge*) in the Gulf of the Farallones, 1975, 1979–2008, as determined by Wells et al. 2008, updated to include 2007. Y axis reflects dimensionless units. Trophic chain for auklets includes measured and modeled "small zooplankton" from CalCOFI surveys in the region and auklet productivity. Trophic chain for murre includes measured and modeled "small zooplankton," estimated juvenile rockfish abundance from NMFS surveys in the region and murre productivity. See Wells et al. 2008 for statistical details. The model was updated for this paper, and now includes information for the year 2007.

Seabirds at Sea

We confirmed previous reports that in conjunction with ocean warming, seabirds with cold-water zoogeographic affinities have declined in the southern CCE (our fig. 2; Hyrenbach and Veit 2003). The decline in the numerically dominant shearwaters (fig. 3A), in particular, is associated with an overall decline in seabird community density in the southern CCE (fig. 2C). In contrast, seabird density along Line P increased, as did the richness of species encountered. While it is beyond the scope of this synthesis to review species-specific changes on Line P, it seems possible that there have been range expansions of some seabird species to the north. This is in keeping with the overall increase in seabird density observed along Line P, which is also consistent with predictions for response to climate change. Northward range expansions have also been observed for long-lived groundfish in the North Sea (Perry et al. 2005) and Bering Sea (Mueter and Litzow 2008).

Climate and Food

In this study, seabirds apparently responded to ocean climate change indirectly through spatial and temporal changes in prey base. We showed that in the central-northern region (SEFI), there was a simultaneous decline in juvenile *Sebastes* abundance and a non-linear take of juvenile *Sebastes* by murre (see also Sydeman et al. 2001; Mills et al. 2007). The decline in juvenile *Sebastes* compared to the birds may be related to range shifts or a reduction in productivity. Moreover, we have demonstrated a secular decline in the “trophic chains” of murre and auklet productivity, meaning that the productivity of the zooplankton (mostly krill) and forage fish (mostly juvenile *Sebastes*), leading to auklet and murre productivity, has also declined. Parsing out all the linkages between upwelling, advection, prey and predators is beyond the scope of this review, but it is clear from this and other work (Bertram et al. 2001; Mackas et al. 2007; Jahncke et al. 2008; Wells et al. 2008) that changes in basic oceanographic processes such as upwelling in the CCE could be driving changes in prey populations and distributions, which ultimately affect these seabirds. Seabirds require sufficient food resources prior to the breeding season for the production of eggs, and food relatively close to the colony when they are rearing offspring. Murres feed dependent offspring multiple times each day, and require food, in this case juvenile *Sebastes*, available close to the colony. Auklets forage for zooplanktonic prey with which to feed offspring at dusk and store multiple prey items in a throat-pouch, and then regurgitate prey for chicks when they return to the colony. Dependent offspring are typically fed once per night by each parent. While the auklets do not return to the breeding colony more than once per day, their foraging ambit is still restricted

(~60 km from the islands). Therefore, in 2005 and 2006 when krill were in low abundance, part of the problem seemed to be that no large krill patches were found in proximity to the Farallones (Santora et al.²).

Seabirds and Oceanographic Indices

The typical approach to understanding marine biota and ecosystem responses to climate change has been to develop simple, empirical correlations with environmental parameters. With this approach, seabirds of the CCE have provided numerous results, many of which are considered in this synthesis. However, it is important to consider that (i) correlations often break down over time (Myers 1998; see Miller and Sydeman 2004 for an example using murre and rockfish in the CCE), and (ii) no matter how solid the correlation, they provide little understanding of the actual mechanism of response. We have described several simple empirical correlations using temperature and sea surface height (SSH), and the covariance in these relationships for seabirds at sea and on colonies in the southern (CalCOFI), central-northern (SEFI), and northern (Line P, TRI) sectors of the CCE. In the case of SSH, auklets at both colonies responded similarly, with later breeding dates and decreases in productivity with increasing SSH (see also Wolf et al. 2009). SSH and SST are positively correlated, indicating that later breeding and reduced production would be expected under future ocean warming.

Changes in Variance

In addition to average state, variance is an important indicator of the impacts of change because increasing variance (or variability) of population parameters can lead to population declines even when average parameter values are stationary. Moreover, one of the predicted outcomes of global warming is greater variability in atmospheric and oceanographic conditions (IPCC 2007). With a relatively short 40-year time series, we found that variance in Cassin's auklet productivity increased significantly through time. Variance in murre productivity and auklet timing also tended to increase, while variance in cormorant productivity tended to decrease, but both of these changes were non-significant.

We found significant changes in the variance of auklet productivity, but not for murre or cormorants. Differences in diet and variability in diet may explain this observation. The productivity of Farallon auklets may be a significant indicator of the abundance of mesozooplankton, specifically euphausiid crustaceans (“krill;” *Euphasia pacifica* and *Thysanoessa spinifera*) that form the

²Santora, J. A., S. Ralston, and W. J. Sydeman. (In Review). Interannual indices of California Current krill spatial organization: an integrated approach. Can. J. Fish. Aquat. Sci. Contact address: J. A. Santora, Farallon Institute for Advanced Ecosystem Research, P.O. Box 750756, Petaluma, CA 94975.

majority of their diet (Ainley et al. 1996; Abraham and Sydeman 2004; 2006; Sydeman et al. 2006). Change in the variance structure of the auklet time series appears to reflect fluctuations in krill populations in the region. Based on net samples, mostly from the southern CCE, Brinton and Townsend 2003 indicate a range contraction for *T. spinifera*, but no change in the abundance of *E. pacifica* from ~1950–94; however, these authors did not test for a change in variance in this data set. Using the Brinton central California net-based time series, Sydeman et al. 2006 showed an apparent reduction in both *E. pacifica* and *T. spinifera* abundance in the region in 2005, but the gaps in these data preclude any assessments of changes in variance. Jahncke et al. 2008 found fewer krill in 2005 than 2004. But without context of a long time series with which to evaluate both of these years, we are uncertain of how to interpret these results. In combining both net and acoustically-derived estimates of abundance and spatial organization, Santora et al.¹ show major changes in krill from 2002–06, which clearly demonstrate low krill availability to breeding seabirds in 2005 and 2006. This series captures both the high and low points in the auklet productivity time series, and shows corresponding extremes in krill availability. In the productive years of 2002–03, krill were found in large patches near the Farallones, whereas in the unproductive years of 2005–06, no large patches were found in the region. With fewer large krill patches, auklets would have a reduced probability of encountering a productive food environment in these years. We surmise that changes in krill populations were responsible, in large part, for the increase in variance in the auklet's productivity over time, but acknowledge lack of sufficient information to make a full evaluation. Lavaniegos and Ohman 2007 show a euphausiid time series for spring surveys from central California for 1950–2004, but do not include an analysis of change in variance. From a visual inspection of their graph, it appears that the variance in euphausiid abundance has increased.

In contrast to auklets, murrens consume euphausiids, but also feed at higher trophic levels on juvenile rockfish and other forage fish much of the time (Roth et al. 2008). Cormorants do not consume zooplankton and are entirely piscivorous (Sydeman et al. 1997). Variance in productivity of murrens increased, and decreased for cormorants, suggesting that murrens may be tracking some of the same zooplankton fluctuations as the auklets. But, as they also feed on forage fish, their changes were not as substantial, so they fall between the variance trends of auklets and cormorants. For cormorants, variance in productivity decreased slightly, which suggests a more stable and consistent prey base through time, leading to more constant productivity. We know that juvenile rockfish populations have declined or changed distribution

(fig. 4), thus we surmise that other forage fish, probably northern anchovies (*Engraulis mordax*), have sustained murre and cormorant productivity at less variable levels over the study period. The majority of murrens' and rhinoceros auklets' diets consisted of anchovies in the 1990s and 2000s (Sydeman et al. 2001; Thayer and Sydeman 2007, respectively).

Troubling Trends or Meandering Variability?

Despite being some of the best time series data sets on seabirds globally, the relatively short duration of these studies make it difficult to parse out the relative effects of “climate change” (secular climate warming) versus “climate variability” (regime shifts/interdecadal variability). However, as we described above, trends in timing, abundance, and productivity for most parameters are consistent with predicted responses to climate change. Notably, the declines in auklet and murre “trophic chain” productivities suggest that climate change is responsible. Ocean warming may be acting to suppress food availability for some breeding and foraging seabirds. Anomalous ocean conditions in 2005 and 2006, with delayed and/or interrupted upwelling, resulted in reduced productivity for several seabird species (murrens and auklets). Moreover, increases in variance/variability coupled with declining productivity will have negative population consequences for the specific populations, such as the Farallon and Triangle Cassin's auklets. Indeed, the Farallon auklet population has declined severely (by ~80%) over the past 30 years (Lee et al. 2008) and future population declines are likely (Wolf et al.³).

These relatively short data sets are also confounded by low-frequency variability, particularly the “regime shifts” of 1977–78 (McGowan et al. 2003) and 1989–90 (Hare and Mantua 2000). The decline in CalCOFI seabird abundance seemingly corresponds to the 1989–90 regime shift (Hare and Mantua 2000), and the increase in seabird abundance along Line P corresponds with a possible regime shift in 1998–99 to cooler conditions. In addition, we provided a simple cross-correlation analysis for auklet productivity and found correlations with the PDO and NPGO (Di Lorenzo et al. 2008). This supports the idea that low-frequency variability is driving some of the observed changes in seabird communities and populations. In the North Pacific Ocean, quasi-interdecadal variation, characterized by the Pacific Decadal Oscillation and related phenomena (PDO: Mantua et al. 1997; Hare and Mantua 2000; Victoria pattern: Bond et al. 2003), are clearly related to plankton abundance and

³Wolf, S. G., M. A. Snyder, W. J. Sydeman, and D. A. Croll. Predicting population consequences of ocean climate change for an ecosystem sentinel, the seabird Cassin's auklet. *Glob. Change Biol.* (Submitted). Contact address: Shaye G. Wolf, Center for Biodiversity, 351 California St., Suite 600, San Francisco, CA 94014.

community dynamics (Peterson and Schwing 2003; Hooff and Peterson 2006), and it appears that some seabird parameters are following this mode of climate variability.

CONCLUSIONS

From the long-term seabird data presented, we attribute most of the changes described to long-term climate change, though there are certainly some patterns that could be attributed to climate variability, or most likely a combination of the two. There are also species-interactions (e.g., interspecific competition and predation) and human interactions (e.g., fisheries impacts) that have affected CCE food webs and the apparent seabird responses to climate change. From a “bottom-up” climate perspective, there are several physical oceanographic observations which support this attribution. First, as noted for the birds, observed physical changes in the CCE exhibit regional and/or onshore-offshore complexity. Second, McGowan et al. 1998, Mendelssohn et al. 2003, Di Lorenzo et al. 2005, and Field et al. 2006b found warming of the CCE at both inshore and offshore stations. However, Palacios et al. 2004 and Di Lorenzo et al. 2005 demonstrated inshore-offshore variation in changes in ocean stratification. For example, from 1950–93, the thermocline strengthened and deepened at inshore stations, but weakened and shoaled offshore (Palacios et al. 2004). Bakun 1990 hypothesized that global warming should lead to upwelling intensification, which could also have a cross-shelf signature. Indeed, for the southern CCE, Rykaczewski and Checkley 2008 showed that offshore curl-driven upwelling displayed an increasing trend over the past 50 years, whereas nearshore upwelling showed no trend. However, in the central-northern CCE, from approximately 35°–39°N, proxies of upwelling such as winds and SST have shown patterns of increase suggesting upwelling intensification in nearshore environments (Schwing and Mendelssohn 1997; Mendelssohn and Schwing 2002; Garcia-Reyes and Largier, in press). Notably, ocean warming and increased stratification may counteract increasing winds and upwelling; indeed, changes in the efficacy of upwelling, mixing, nutrient input, and corresponding biological productivity will depend on the relative strength of these opposing effects.

Some contrasting trends in productivity and variance of seabirds may reflect regional or cross-shelf changes in upwelling, physical oceanographic conditions and trophic ecology. For example, Brandt's cormorant showed increasing productivity and decreasing variance, at least

through 2007 (Sydeman et al. 2001; this paper), and population increases to the mid 2000s nearly equivalent to those seen in the early 1970s (Ainley and Lewis 1974; Warzybok and Bradley 2007⁴). Cassin's auklets have shown episodic declines in productivity and increasing variance. Why the auklets and cormorants are showing contrasting trends is not understood, but may relate to their foraging distributions and trophic ecology. Auklets feed on mesozooplankton (krill) of the outer continental shelf region, whereas cormorants feed on forage fish of the inner shelf and bay habitats. Therefore, possibly due to cross-shelf variation in upwelling intensification, the food web of the outer shelf may have declined, whereas that of the inner shelf may have improved. The decline in murre (and auklet) trophic chain productivity supports this hypothesis, as many of the juvenile rockfish, especially *Sebastes jordanii* which formed the basis for the murre's offspring diet in the 1970s and 1980s, once inhabited the outer shelf domain of the Gulf of the Farallones and have since declined substantially from that region (Field et al. 2007). Data from the southern CCE also support this hypothesis. Hsieh et al. 2009 demonstrated declining trends for many oceanic mid-water fish species. Obviously, there is still much to be learned to rectify patterns of change in inshore-offshore physical oceanography and zooplankton, forage fish, and seabird populations in the CCE. This is an area ripe for research, and highlights the need to integrate spatial ecology into time-series approaches towards understanding the impacts of climate change on marine biota and ecosystems of the North Pacific Ocean.

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