PERGAMON

Deep-Sea Research II 50 (2003) 2537–2565

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Ocean warming and seabird communities of the southern California Current System (1987–98): response at multiple temporal scales

K. David Hyrenbach[a,]*, Richard R. Veit[b]

[a] *Scripps Institution of Oceanography, University of California San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0208, USA*
[b] *Biology Department, The College of Staten Island, 2800 Victory Blvd., Staten Island, NY 10134, USA*

Received 1 March 2002; received in revised form 15 August 2002; accepted 1 November 2002

Abstract

Declines in ocean productivity and shifts in species assemblages along the West Coast of North America during the second half of the XXth century have been attributed to the concurrent warming of the California Current. This paper addresses changes in the avifauna off southern California between May 1987 and September 1998, in response to shifting water mass distributions over short (<1 year) and long (interannual) temporal scales. More specifically, our research focuses on the relative importance of distinct foraging guilds and species assemblages with an affinity for warm and cold water. Over the long term, the avifauna off southern California shifted from a 'high-productivity' community typical of eastern boundary upwelling systems, to a 'low-productivity' assemblage similar to those inhabiting the subtropical gyres. Overall seabird abundance decreased; the relative importance of cold-water seabirds that dive in pursuit of prey declined; and warm-water species that feed at the surface and plunge to capture prey became more numerous. These community-level changes are consistent with the northward shifts in species ranges and the declining ocean productivity anticipated as a result of global warming. However, the response of individual taxa with an affinity for warm-water and cold-water conditions has been more difficult to predict, due to differences in species-specific responses to ocean warming. The three cold-water species investigated (Sooty Shearwater *Puffinus griseus*, Cassin's Auklet *Ptychoramphus aleuticus*, and Rhinoceros Auklet *Cerorhinca monocerata*) decreased in abundance during this study. On the other hand, only one of the six warm-water species considered (Pink-footed Shearwater, *Puffinus creatopus*) increased significantly over the long term. Yet, the warm-water Leach's Storm-petrel (*Oceanodroma leucorhoa*) increased between 1987 and 1993, and then declined between 1994 and 1998. Moreover, cross-correlations between seasonally adjusted anomalies of bird abundance and ocean temperature revealed that seabirds responded differently to ocean warming over intermediate (1–8 years), and long (8–12 years) time scales. We hypothesize that this nonlinear behavior of seabird populations in response to ocean warming is caused by the juxtaposition of distinct behavioral and demographic responses operating at different temporal scales.

1. Introduction

Large-scale physical forcing influences the productivity and structure of marine ecosystems

---

*Corresponding author. Duke University Marine Laboratory, 135 Duke Marine Laboratory Road, Beaufort, NC 28516, USA. Tel.: +1-252-504-7576; fax: +1-252-504-7648.

E-mail address: khyrenba@duke.edu (K.D. Hyrenbach).

0967-0645/$ - see front matter © 2003 Elsevier Ltd. All rights reserved.
doi:10.1016/S0967-0645(03)00123-1

(Dickson et al., 1975; Aebischer et al., 1990; Brodeur et al., 1996; McGowan et al., 1998). In the late 1970s, a major climatic shift perturbed the atmospheric forcing, the ocean circulation, and the productivity of five large marine ecosystems in the Pacific Ocean: the subtropical North Pacific Gyre, the subarctic North Pacific, the Kuroshio-Oyashio Current off Japan, the Peru Current, and the California Current System (CCS) (Venrick et al., 1987; Miller et al., 1994; Polovina et al., 1994; Hayward, 1997). This change in oceanic climate was particularly evident in the CCS (Roemmich, 1992; Roemmich and McGowan, 1995a, b; Veit et al., 1996).

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has monitored the physical, chemical, and biological properties of the southern CCS for over five decades (Reid et al., 1958). These time series revealed a 1.2–1.6°C increase in the temperature of the upper 100 m of the water column between the 1950s and the 1990s (Roemmich, 1992; Roemmich and McGowan, 1995a). More recent surveys suggest that this warming trend has continued through the late 1990s (Hayward et al., 1996; Schwing et al., 1997; Lynn et al., 1998; Levitus et al., 2000).

Declines in the standing stocks of macro-algae (Tegner et al., 1996), macrozooplankton biomass (Roemmich and McGowan, 1995a, b), juvenile rockfish (*Sebastes* spp.) (Lynn et al., 1998), reef fishes (Holbrook et al., 1997), and seabirds (Veit et al., 1996) suggest that the productivity of the CCS has decreased in response to the warming trend described above. Nearshore, the abundance of the giant kelp *Macrocystis pyrifera* declined by approximately 2/3 between the 1950s and the 1990s (Tegner et al., 1996). Offshore, the amount of sinking particulate organic carbon (POC) reaching the sea floor decreased by approximately 50% between 1989 and 1996 (Smith and Kaufmann, 1999). In addition to declining ocean productivity, concurrent increases in southern, warm-water species and declines of northern, cold-water taxa are suggestive of shifting species ranges in response to ocean warming. In coastal areas, changes in reef fish assemblages in the southern California Bight (Holbrook et al., 1997) and intertidal communities off central California (Sagarin et al., 1999) have been ascribed to increasing ocean temperatures along the west coast of North America. Similar shifts have been described in pelagic assemblages, where the composition of euphausiid (*Euphausia* spp., *Nyctiphanes* spp., *Thysanoessa* spp.), juvenile rockfish (*Sebastes* spp.), and larval fish assemblages have changed in response to the northward expansion of species ranges (Brinton, 1996; Horne and Smith, 1997; Lynn et al., 1998; Smith and Moser, 2000). These fluctuations correspond to the expected latitudinal migration of water masses and oceanographic domains in response to global warming (Fulton and LeBrasseur, 1985; Fields et al., 1993; Lubchenco et al., 1993; Peterson et al., 1993).

In this study we focus on the avifauna of the CCS because marine birds are indicators of large-scale changes in water mass distributions, ocean productivity, and prey resources (Montevecchi and Myers, 1995; Veit et al., 1996; Furness and Camphuysen, 1997; Sydeman et al., 2001). Studies of marine bird communities over macro-mega scales (1000s km) have revealed that species with different foraging methods, wing morphologies, and diving capabilities preferentially inhabit specific regions of the world's oceans (Ashmole, 1971; Wahl et al., 1989; Gould and Piatt, 1993; Ballance et al., 1997). These distribution patterns suggest that distinct seabird assemblages are adapted to exploit specific marine environments and prey types associated with particular water masses (Ainley, 1977; Abrams and Griffiths, 1981; Griffiths et al., 1982; Spear and Ainley, 1998). In the North Pacific Ocean, diving species preferentially inhabit highly productive areas of cool ocean temperature and elevated chlorophyll concentration. Conversely, low-productivity areas sustain impoverished seabird communities dominated by species that feed at the surface and plunge in pursuit of prey (Ainley, 1977; Wahl et al., 1989; Gould and Piatt, 1993; Ballance et al., 1997; Table 1).

This paper documents long-term changes in the abundance and the composition of marine bird communities off southern California between May 1987 and September 1998, a period of continued ocean warming and declining ocean productivity. First, we expand and reanalyze the time series

Table 1
Indicators of ocean productivity off southern and Baja California. Summer and winter values are monthly averages for July and January respectively

Variable	Southern California (California current) (30–35°N, 117–125°W)	Baja California (subtropical water) (25–30°N, 113–125°W)	References
Near-surface temperature (10 m depth) (°C)	Summer: 16.79 Winter: 14.67	Summer: 17.35 Winter: 17.43	Antonov et al. (1998)
Thermocline temperature (100 m depth) (°C)	Summer: 10.98 Winter: 11.32	Summer: 14.15 Winter: 14.14	Antonov et al. (1998)
Primary production (mg C/m^2/0.5 day)	Summer: 604	Summer: 240	Haury et al. (1993)
Zooplankton biomass (0–210 m) (ml/1000 m^3) (day/night)	Summer: 335/474	Summer: 117/149	Haury et al. (1993)
Prevalent seabird feeding methods (% breeding species)	Diving (50%) Surface feeding (40%) Plunging (10%)	Plunging (38%) Surface feeding (37%) Diving (25%)	Ainley (1977)

The temperature data are monthly climatologies for 1945–96 compiled in the 1998 World Ocean Database.

previously studied by Veit and coworkers (1996) to determine whether there are concurrent trends in ocean temperature and seabird abundance. More specifically, we test for changes in the abundance of warm-water and cold-water indicator species in response to short- (<1 year) and longer-term (interannual) fluctuations in the temperature of the CCS.

Because marine birds inhabit specific oceanic habitats (Ainley, 1976, 1977; Wahl et al., 1989; Veit et al., 1996), large-scale alterations of water mass distributions off the West Coast of North America should cause range shifts that are consistent with the changing oceanography. In other words, we anticipate that warm-water and cold-water species should increase and decrease respectively in response to the warming of the California Current. Furthermore, if these numerical responses are solely driven by population redistributions, they should be consistent whether we are considering short (<1 year) or longer (interannual) temporal scales. In other words, positive temperature anomalies should be followed by increases in the abundance of subtropical species that shift their distributions north during warm-water episodes. Conversely, disparate numerical responses to temperature fluctuations over short and long temporal scales would suggest that seabird populations respond to climatic variability via several distinct mechanisms operating over different temporal scales. For instance, cold-water species that initially vacate the area in response to the northward incursion of the subtropical water mass eventually may be impacted demographically by depressed ocean productivity. Similarly, warm-water species that initially become more numerous in response to the warming of the California Current, may also decline during the ensuing prolonged period of low ocean productivity due to a decline in their reproductive success. These temporal patterns would suggest that the statistical associations between bird abundance and ocean temperature may eventually break down when the long-term demographic response (e.g., reproductive success) is superimposed on the initial, short-term behavioral response (e.g., redistribution).

Previous research has addressed the response of individual bird species to changes in ocean temperature off southern California (Ainley, 1976; Briggs et al., 1987; Veit et al., 1996). This paper complements the existing studies by placing the responses of individual species within a broader context of community-level changes. We hypothesize that seabird communities should change in response to ocean warming and declining ocean productivity (Roemmich and McGowan, 1995a, b; Veit et al., 1996; Lynn et al., 1998). In particular, we test whether the relative

Table 2
Comparison of the seabird assemblages inhabiting the North Pacific Central water mass (Subtropical Gyre) and the Upwelling Domain waters off California during summer (July) and winter (January)

Variable	Upwelling domain		North Pacific Central water		References
Mean bird density (Birds/km^2)	Summer 23	Winter 11	Summer <2	Winter <1	Wahl et al. (1989) Tyler et al. (1993)
Prevalent feeding method (% Total Birds)	Divers (80%) Surface feeders (20%)		Plungers (55%) Surface feeders (45%)		Wahl et al. (1989)
Numerically dominant species (Feeding Method)	Summer	Winter	Summer	Winter	Wahl et al. (1989)
	SOSH (D) PFSH (S) WEGU (S)	CAGU (S) NOFU (S) RHAU (D)	BRNO (P) WTSH (S) SOTE (P)	BFAL (S) BWPT (S) RTTR (P)	Tyler et al. (1993)

Three general feeding methods are considered: surface-feeding (S), diving (D), and plunging (P).
BFAL: Black-footed Albatross (*Phoebastria nigripes*); BRNO: Brown Noddy (*Anous stolidus*); BWPT: Black-winged Petrel (*Pterodroma nigripennis*); CAGU: California Gull (*Larus californicus*); NOFU: Northern Fulmar (*Fulmarus glacialis*); PFSH: Pink-footed Shearwater (*Puffinus creatopus*); RHAU: Rhinoceros Auklet (*Cerorhinca monocerata*); RTTR: Red-tailed Tropicbird (*Phaeton rubricauda*); SOSH: Sooty Shearwater (*Puffinus griseus*); SOTE: Sooty Tern (*Sterna fuscata*); WEGU: Western Gull (*Larus occidentalis*); WTSH: Wedge-tailed Shearwater (*Puffinus pacificus*).

abundance of seabirds with different temperature affinities and foraging methods has changed in response to the long-term warming of the California Current. More specifically, we predict: (1) a decline in overall seabird abundance; (2) a decrease in the importance of cold-water taxa and species that dive in pursuit of their prey; and (3) an increase in the relative abundance of warm-water taxa, as well as surface-feeding and plunging species. Ultimately, the avifauna off southern California, should shift from a 'high-productivity' assemblage typical of eastern boundary upwelling systems like the Peru and Benguela Currents, to a 'low-productivity' community similar to the one inhabiting the North Pacific Subtropical Gyre (Murphy, 1936; Abrams and Griffiths, 1981; Wahl et al., 1989; Gould and Piatt, 1993; Tables 1 and 2).

2. Methods

2.1. Study area

Seasonal California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises survey six parallel transects, ranging in length from 470 (northernmost) to 700 (southernmost) km. Overall, the study site encompasses over $3 \times 10^5\,\mathrm{km}^2$ of the Pacific Ocean, extending from 30° to 35°N and from the southern California coast to 124°W (Fig. 1). The CalCOFI grid is an ideal setting for the study of climate change because it samples the northern edge of the broad transition zone between the cool California Current and warmer, subtropical waters to the south. This ecotone delimits the latitudinal ranges of subarctic and subtropical marine bird, fish, and zooplankton species (Hunt et al., 1981; Haury et al., 1993; Moser and Smith, 1993; McGowan et al., 1996). Moreover, the location of this dynamic faunal boundary undergoes substantial seasonal and interannual variability, and has likely shifted in response to the long-term warming of the California Current (Brinton, 1981; Norton and Crooke, 1994; Veit et al., 1996; Smith and Moser, 2000).

2.2. Seabird surveys

Trained observers employed standardized population censusing techniques (Tasker et al., 1984) to survey the distribution and abundance of

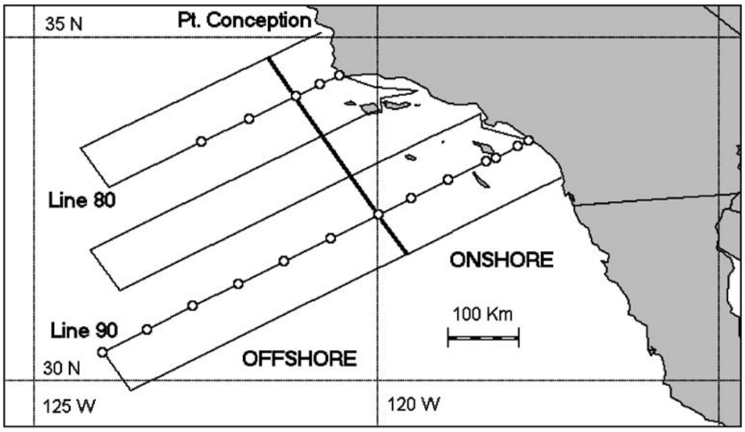

Fig. 1. The study area off southern California, showing the regularly surveyed cruise track and hydrographic stations used to calculate the average water temperature along line 80 and line 90.

marine birds within the CalCOFI grid during 45 seasonal cruises between May 1987 and September 1998. Observers censused birds continuously during all daylight hours while the vessel was underway at speeds of 5 knots (9 km h^{-1}) or greater, and surveyed an average of 1600 km per cruise. A range-finder was used to estimate the width of the survey transect (Heinemann, 1981), and only those birds sighted within a 300 m arc from the bow (directly ahead) to 90° off the side with best visibility (e.g., least glare) were logged into a field computer. Ship-following birds were recorded the first time they were detected and were ignored thereafter. Overall, this data set comprises over 159,000 birds and 70,000 km of survey effort collected during 11.4 years. The bird abundance data were tabulated as a relative encounter rate (birds sighted per 100 km surveyed).

Distinct marine bird assemblages inhabit the coastal and pelagic regions of the CalCOFI grid, and overall seabird abundance is highest over the continental shelf and the slope (Briggs et al., 1987; Hyrenbach, 2001). Therefore, we stratified the study area into two physically and biologically distinct onshore (shelf-slope) and offshore (pelagic) regions delineated by the 2000 m isobath (Briggs et al., 1987; Fargion et al., 1993; Hayward and Venrick, 1998). We estimated seabird relative abundance (birds 100 km^{-1}) within each domain separately by dividing the number of birds sighted by the distance surveyed. We then calculated the overall bird abundance within the entire study area by combining the separate onshore and offshore estimates, weighted by the proportional areal extent of each domain (onshore: 100,000 km^2, offshore: 200,000 km^2) (Buckland et al., 1993). We also computed the overall bird biomass (kgs 100 km^{-1}) by multiplying the numerical abundance of each species by their body mass (Appendix A; Dunning, 1993).

2.3. Water temperature

The temperature of the ocean can be used to define distinct water masses (Sverdrup et al., 1942; Norton and Crooke, 1994), and as a proxy for ocean productivity off southern California (Roemmich and McGowan, 1995a; Hayward and Venrick, 1998). Near-surface (10 m) temperature is indicative of advection and upwelling, two processes known to influence the productivity of the CCS (Chelton et al., 1982; Lynn et al., 1998; Bograd et al., 2000). Subsurface temperature anomalies (50–150 m) are indicative of the depth of the thermocline, which also has important implications for ocean productivity off California (McGowan, 1985; Fiedler et al., 1992; Lynn et al., 1995; Chavez, 1996).

We used the data from conductivity-temperature-depth (CTD) casts along CalCOFI line 90 (13 stations) and line 80 (5 stations) to characterize the temperature of the study area (Roemmich and

McGowan, 1995a; Veit et al., 1996). We compared CTD measurements from both lines to determine whether the warming trend was restricted to the southern part of the study area (line 90), or had also affected the northern region in the vicinity of the Point Conception upwelling center (line 80) (Fig. 1).

2.4. Time series analysis

Ocean temperature, marine productivity, and bird abundance are markedly seasonal off southern California (Lynn et al., 1982; Briggs et al., 1987; Hayward and Venrick, 1998; Hyrenbach, 2001). In particular, most of the bird species that inhabit the southern CCS migrate into the area during one or two seasons of the year (Ainley, 1976; Briggs et al., 1987). Therefore, we calculated seasonal anomalies designed to highlight the long-term trends that may be otherwise obscured by the seasonal variability (Veit et al., 1996, 1997). First, we computed seasonal climatologies (Winter: January–February; Spring: March–May; Summer: July–August; Fall: September–November) of ocean temperature and bird abundance, using data collected between May 1987–September 1998. Next, we calculated how each individual cruise from the time series deviated from these mean seasonal conditions. For instance, we computed the average springtime temperature by averaging the observations during all spring cruises in the time series as follows:

$$T_{\mathrm{Spring}} = [\Sigma(T_{\mathrm{i}})/n],$$

where n is the number of springtime cruises, T_{i} is the temperature for each individual spring cruise, and T_{Spring} is the average springtime temperature. Then, we calculated 'seasonal anomalies' by subtracting the seasonal mean from the observations during each spring cruise ($\mathrm{Anomaly}_{\mathrm{i}} = T_{\mathrm{i}} - T_{\mathrm{Spring}}$). We repeated this procedure for the four seasonal temperature and bird data sets.

We determined if there were long-term trends in the temporal distribution of the seasonal anomalies between May 1987 and September 1998 using regression analysis (Zar, 1984). The climate of the North Pacific is characterized by long-term (20–30 year) oscillations interspersed by step-like 'regime shifts' (Miller et al., 1994; Mantua et al., 1997). Since the period of these inter-decadal oscillations is longer than the duration of this study, 11.4 years, the time series analyzed here could have captured a period of progressive change, an abrupt reversal in ocean conditions, or neither. Therefore, we used linear and quadratic regressions to assess two different models of ocean warming: a 'linear' trend ($y = a + bx$) or part of a 'cyclical' oscillation with an inflexion point ($y = a + bx + cx^2$) (Zar, 1984).

Because the seasonal anomalies of water temperature and seabird abundance were not normally distributed, we determined the significance of these regressions using randomization tests (Manly, 1991; Veit et al., 1996, 1997). For the linear formulation, the null hypothesis stated that the slope of the best-fit line was indistinguishable from zero. First, we calculated an 'observed slope' using the real sequence of seasonal anomalies. Then, we randomly arranged each time series 1000 times, and calculated a distribution of the 'randomized' slopes. We estimated the statistical significance of the 'observed' trends by calculating the proportion of the 'randomized' slopes that were larger in absolute value than the slope obtained from the original time series. For instance, if 50 randomizations using the shuffled data yielded a slope with a larger absolute value than the 'observed' slope, the p value for that test was 0.05 (50/1000). We repeated the same analysis for the quadratic model, but this time the null hypothesis stated that the time series had no inflexion point, and the quadratic term of the best-fit curve was indistinguishable from zero (Zar, 1984).

In some instances, both the linear and the quadratic regressions yielded significant trends. Because a linear and a quadratic trend entail very different responses to climatic change, we determined which model provided a more accurate description of the observed time series. However, since the two models have a different number of parameters, the sums of squares cannot be compared directly. The quadratic model will likely fit the time series better because it relies on three parameters (a, b, c), while the linear formulation uses only two (a, b). Therefore, for each time series, we contrasted the performance of the linear and the quadratic models using the *Cp* information criterion described below:

$$Cp = \mathrm{SSQ}/(n - 2p),$$

where n is the sample size, p is the number of parameters in each model, and SSQ is the sum of the residual squared deviations for each model. In *Cp*, above, the numerator quantifies the model fit to the data, while the denominator represents the penalty for increasing the number of parameters. The model with the smallest *Cp* value is the most desirable formulation since it provides the best fit to the data, normalized by the number of parameters employed (Efron and Tibshirani, 1993; Hilborn and Mangel, 1997).

To further explore the changes in the physical and biological properties of the CCS over the long-term, we partitioned the 11.4-year data set into three temporal bins. We calculated the mean conditions during an early (1987–90), a middle (1991–94), and a late (1995–98) part of the time series by averaging the observations from 12 cruises (3 years × 4 seasons) during each time period. Furthermore, we quantified the change in ocean temperature and bird abundance over the long-term using the proportional change (PC) in conditions between the beginning and the end of the time series (the early and late bins):

$$\mathrm{PC} = \frac{(\text{Late Mean} - \text{Early Mean})}{(\text{Early Mean})} 100\%.$$

2.5. *Composition of the avifauna*

Once we had documented the long-term warming of the study area and the decline of overall bird abundance and biomass, we tested whether the composition of the avifauna had changed between the beginning (1987–90) and the end (1995–98) of the time series. More specifically, our goal was to assess whether differences in foraging methods and temperature affinities influenced the response of the avifauna to ocean warming. Even though the habitats, feeding ecology, and distributions of seabird species are intimately related to each other (Ainley, 1977; Birt-Friesen et al., 1989; Costa, 1991; Spear and Ainley, 1998), we considered foraging guilds and species assemblages with warm-water and cold-water affinities separately.

We assigned bird species to one of three distinct feeding guilds: (1) surface-feeders including albatrosses, phalaropes, gulls, fulmars, gadfly petrels (*Pterodroma* spp.) and some shearwaters capture prey at the surface using a variety of methods such as dipping, surface seizing, and pattering; (2) divers and pursuit plungers such as alcids, cormorants, and most shearwaters pursue prey underwater using their feet or wings for propulsion; (3) and surface plungers including tropicbirds, pelicans, boobies, and terns enter the water using the momentum of a fall (Appendix A). We did not include piracy in this analysis because the four jaeger species (Stercorariidae) that occur off southern California accounted for less than 0.5% of the total seabird numbers and biomass recorded during this study. Kleptoparasitic species constitute a minor part of the avifauna of the North Pacific, and their distributions show no obvious relationship to large-scale water temperature and ocean productivity patterns (Ainley, 1977; Wahl et al., 1989). We also classified seabirds as warm-water or cold-water indicators on the basis of published short-term (<1 year) numerical responses to temperature anomalies off southern California (Ainley, 1976; Briggs et al., 1987; Veit et al., 1996). Taxa that did not show a response to short-term changes in ocean temperature were classified as having no water temperature preference (Appendix A).

We calculated the mean relative abundance (birds $100\,\mathrm{km}^{-1}$) and biomass (kgs $100\,\mathrm{km}^{-1}$) of bird assemblages and feeding guilds by averaging data from 12 cruises (3 years × 4 seasons) during the early (1987–90), and late (1995–98) parts of the time series. To assess the significance of the changes in seabird community composition, we contrasted the relative contribution of different temperature assemblages and feeding guilds using G tests (Zar, 1984).

2.6. *Responses of indicator species*

We tested for short-term (<1 year) and longer-term (>1 year) changes in the abundance of warm-water and cold-water ‘indicator’ species in response to ocean temperature fluctuations. We restricted these analyses to nine seabird species that had been previously shown to respond to temperature fluctuations off southern California over short time periods (<1 year) (Ainley, 1976; Veit et al., 1996). The objective of this analysis was to determine to what extent individual species responses reflected the documented long-term changes at the community level.

First, we analyzed the short-term response of bird abundance using cross-correlation analysis. We compared the temporal distribution of the seasonal anomalies of bird abundance and near-surface (10 m) and thermocline (100 m) ocean temperature during two periods of contrasting oceanographic conditions: (1) the initial warming period between 1987–94 discussed by Veit and coworkers (1996); and (2) the entire time series (1987–98), including a transient cold-water period (1995–96) and the 1997–98 El Niño event. Instead of breaking the time series into an initial (first 29 cruises between 1987 and 1994) and a latter (last 16 cruises between 1994 and 1998) part, we followed a more conservative approach and compared the first 29 cruises against the entire time series of 45 surveys. To make these results comparable with previous research by Veit and coworkers (1996), we restricted the analyses to temperature measurements taken exclusively along CalCOFI line 90.

We performed these cross-correlations for a variety of temporal lags ranging from three months (one cruise) when temperature lagged behind birds (lag of –3), to 12 months (four cruises) when birds lagged behind temperature (lag of +12). For each lag, we randomly arranged the time series of bird abundance relative to those of water temperature 1000 times, and assessed the significance of the correlation as the proportion of the comparisons that yielded a Pearson correlation coefficient (r) larger in absolute value than the one obtained from the original data set (Manly, 1991; Veit et al., 1996).

We also used linear and quadratic regression to analyze changes in the numerical abundance of the warm-water and cold-water indicator species over the long-term (1987–98). We performed analyses analogous to those used to characterize the trends of ocean temperature and overall bird abundance and biomass.

2.7. Type I error rate

We used additional randomization tests to estimate the probability of committing a type I error when performing the cross-correlation and the regression analyses (Schneider and Duffy, 1985; Schneider and Piatt, 1986). We shuffled each time series and analyzed the randomized data in the same way we did the real data sets. Because the data had been shuffled prior to performing the randomization tests, we did not expect there would be any underlying trends or associations. Therefore, any significant result we detected would have arisen purely by chance. We repeated this procedure 1000 times and determined the probability of committing a type I error as the proportion of these comparisons that yielded a significant trend. That is, the number of tests where the slope, quadratic term, or Pearson correlation coefficient were different from zero. We estimated the type I error rate for probability levels of alpha = 0.01, 0.05, and 0.10.

3. Results

3.1. Ocean temperature

Near-surface (10 m) and thermocline (100 m) water temperature increased significantly off southern California between May 1987 and September 1998 (Figs. 2 and 3). This warming trend was spatially coherent across the study area (Table 3), though the magnitude of the increase was larger off Point Conception (line 80) than along the southern part of the study area (line 90) (Fig. 1). Between the early (1987–90) and the late (1995–98) parts of the time series, average 100 m ocean temperature increased by 0.99°C (line 80) and by 0.91°C (line 90) respectively. Near-surface (10 m) temperature increased slightly along the southern part of the study area (0.49°C) and more strongly off Point Conception (1.16°C) during the same period (Table 4). The randomization tests also

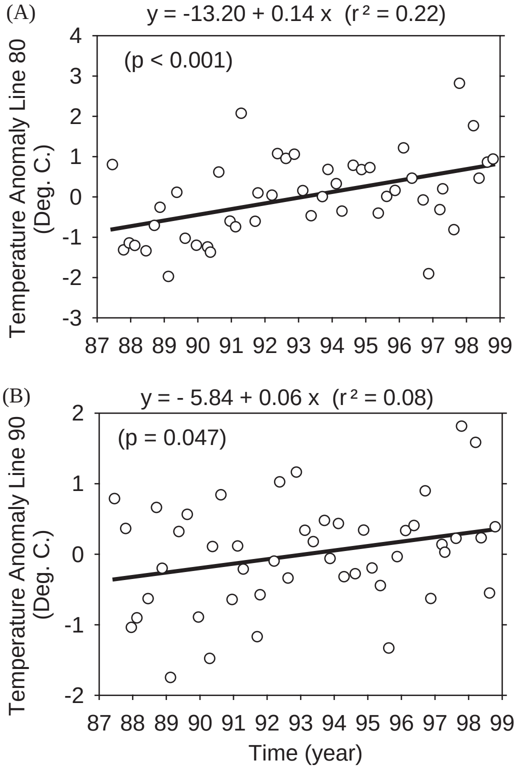

Fig. 2. Long-term increase in near-surface (10 m) ocean temperature off southern California between May 1987 and September 1998. Time series of seasonally adjusted anomalies of near-surface temperature along line 80 (A) and line 90 (B). Anomalies were obtained by subtracting the average temperature for each cruise from the long-term seasonal mean (1987–1998). Positive anomalies indicate warmer conditions and negative anomalies indicate cooler conditions respectively. Significance was determined using randomization tests.

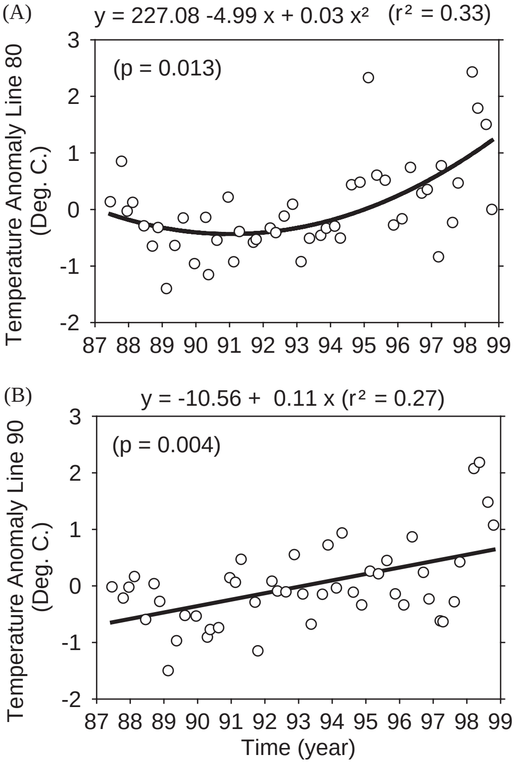

Fig. 3. Long-term increase in thermocline (100 m) ocean temperature off southern California between May 1987 and September 1998. Time series of seasonally adjusted anomalies of thermocline temperature along line 80 (A) and line 90 (B). Anomalies were obtained by subtracting the average temperature for each cruise from the long-term seasonal mean (1987–1998). Positive anomalies indicate warmer conditions and negative anomalies indicate cooler conditions respectively. Significance was determined using randomization tests.

Table 3
Coherence between seasonal anomalies of near-surface (10 m) and thermocline (100 m) water temperature along CalCOFI lines 80 and 90 (May 1987–September 1998)

Depth (m)	Simple linear regression			One sample Kolmogorov–Smirnov test		
	df	*F*-ratio	*p*-value	*n*	Max_Diff	*p*-value
10 (Near-surface)	1, 45	22.087	<**0.0001**	47	0.117	0.535
100 (Thermocline)	1, 45	35.059	<**0.0001**	47	0.119	0.513

One-sample Kolmogorov–Smirnov tests were used to assess the normality of the regression residuals (Zar, 1984).
Bold font denotes significant results.

revealed that 0.12% (10/8000), 1.26% (101/8000), and 1.26% (101/8000) of the regressions yielded significant results merely by chance at alpha = 0.01, 0.05, and 0.10 significance levels. Since we performed eight regressions and used a significance level of 0.05, the overall

Table 4
Increase in near-surface (10 m) and thermocline (100 m) ocean temperature off southern California between May 1987 and September 1998, illustrated by comparing mean conditions during the beginning and the end of this study

Hydrographic stations	Depth (m)	Early Mean (87–90) (°C)	Late Mean (95–98) (°C)	Percent change (%)
Line 80	10	14.22	15.38	+8.11
Line 80	100	10.10	11.09	+9.79
Line 90	10	16.79	17.28	+2.84
Line 90	100	11.53	12.44	+7.82

Twelve cruises (3 years × 4 seasons) were averaged during each time period. A positive percent change indicates that the water temperature increased during the long-term (May 1987–September 1998).

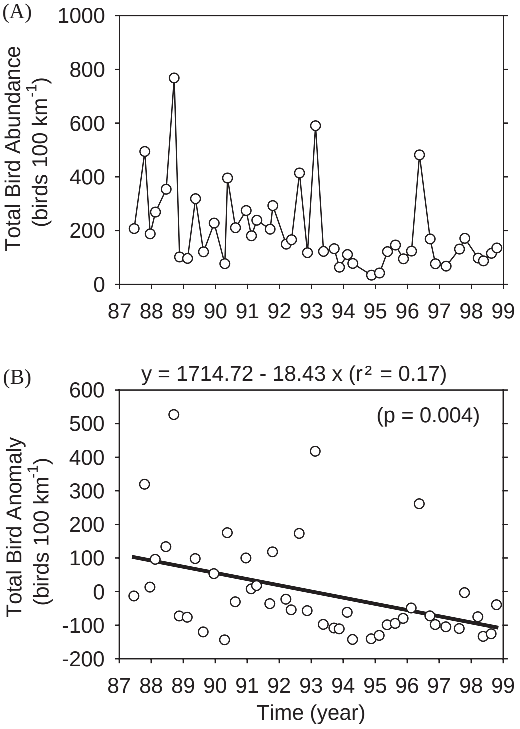

Fig. 4. Long-term decline in overall seabird relative abundance (all species combined) within the CalCOFI region. Time series of raw (A) and seasonal anomalies (B) of bird abundance between May 1987 and September 1998. Anomalies were obtained by subtracting the average value for each cruise from the long-term seasonal mean. Significance determined using randomization tests.

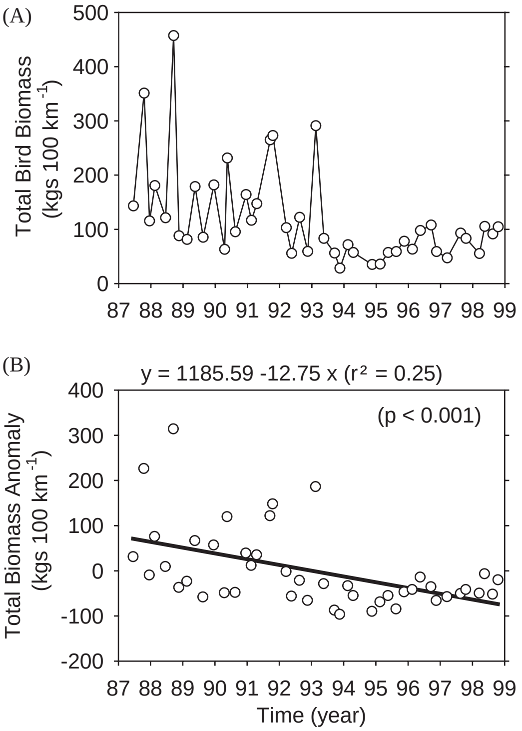

Fig. 5. Long-term decline in overall bird biomass (all species combined) within the CalCOFI region. Time series of raw (A) and seasonal anomalies (B) of bird biomass between May 1987 and September 1998. Anomalies were obtained by subtracting the average value for each cruise from the long-term seasonal mean. Significance determined using randomization tests.

probability of committing a type I error was approximately 0.10.

3.2. Overall bird abundance and biomass

Total bird numbers were highly variable between May 1987 and September 1998, with four large positive anomalies of abundance during the fall cruises of 1987 and 1988, the winter of 1993, and the spring of 1996. Otherwise, seasonal anomalies of overall bird abundance remained negative after the winter of 1993 (Fig. 4). The time series of overall bird biomass resembled that of total bird abundance, though the seasonal

Table 5
Decline in overall marine bird abundance off southern California between May 1987 and September 1998, illustrated by comparing mean conditions during the beginning and the end of this study

Variable	Early mean (87–90)	Late mean (95–98)	Percent change (%)
Total bird abundance (birds 100 km^{-1})	278.72	147.76	−46.99
Total bird biomass (kgs 100 km^{-1})	173.36	80.39	−53.63

Twelve cruises (3 years × 4 seasons) were averaged during each time period. A positive percent change indicates that bird abundance or biomass increased during the long-term (May 1987–September 1998).

Table 6
Change in the relative importance of distinct marine bird species assemblages and feeding guilds between May 1987 and September 1998, illustrated by comparing mean conditions during the beginning and the end of this study

Species group	Abundance (birds 100 km^{-1})			Biomass (kgs 100 km^{-1})		
	Early mean (87–90)	Late mean (95–98)	Percent change (%)	Early mean (87–90)	Late mean (95–98)	Percent change (%)
Cold-water	47.9	22.7	−52.6	56.0	29.3	−47.6
Warm-water	30.8	47.9	55.5	3.3	8.0	+142.0
Divers	44.3	29.1	−34.2	58.6	42.7	−27.1
Plungers	5.0	10.6	111.4	15.7	22.6	+43.5
Surface feeders	50.3	59.7	18.7	25.2	34.1	+34.9

Twelve cruises (3 years × 4 seasons) were averaged during each time period. A positive percent change indicates that the abundance or biomass of these species increased during the long-term (May 1987–September 1998).

anomalies of bird biomass were consistently negative after the winter of 1993 (Fig. 5). Overall bird numbers (birds 100 km^{-1}) and biomass (kgs 100 km^{-1}) declined significantly off southern California during this study (Figs. 4 and 5, Table 5).

3.3. Composition of the avifauna

In addition to the overall decline in bird abundance and biomass, we described changes in the importance of warm-water and cold-water assemblages and different feeding guilds (Tables 6 and 7). Warm-water species increased whereas cold-water taxa declined between the beginning (1987–90) and the end (1995–98) of the time series. Diving species declined, while the relative abundance and biomass of taxa that feed at the surface and plunge in pursuit of prey increased.

To illustrate the disparity in the response of seabird abundance and biomass, we contrasted the seasonal anomalies of overall bird abundance and biomass during the early (1987–90) and the late (1995–98) parts of the time series (Table 8). During the beginning of the time series, seasonal anomalies of biomass and abundance were significantly correlated. During the latter part of the time series, positive anomalies of bird abundance were not necessarily matched by increases in bird biomass (Figs. 4 and 5).

3.4. Short-term response of indicator species

Before we could interpret the results of the temperature/bird cross-correlations, we evaluated the probability of committing a type I error. Randomization tests revealed that the probability of finding a significant correlation merely by chance was 0.95% (1026/108000), 5.09% (5497/108000), and 11.34% (12247/108000), at significance levels of alpha = 0.01, 0.05, and 0.10, respectively. Because we performed 108 (9 species × 2 temperature depths × 6 lags) cross-correlations, we would expect one, five and twelve statistical tests to yield erroneous results at significance levels of 0.01, 0.05 and 0.10, respectively. We found seven significant

Table 7
Long-term changes in the composition of marine bird assemblages and feeding guilds off southern California between May 1987 and September 1998

Variable	Species guilds	df	*G* critical	*G*	*p*-value	Trend
Abundance (birds 100 km^{-1})	Temperature affinity	2	5.991	14.253	$\mathbf{p<0.001}$	Warm-water taxa increase Cold-water species decline
	Feeding method	2	5.991	11.812	$\mathbf{0.001<p<0.005}$	Divers decline Plungers increase Surface-feeders increase
Biomass (kgs 100 km^{-1})	Temperature affinity	2	5.991	15.157	$\mathbf{p<0.001}$	Warm-water taxa increase Cold-water species decline
	Feeding method	2	5.991	11.094	$\mathbf{0.001<p<0.005}$	Divers decline Plungers increase Surface-feeders increase

The importance of distinct seabird assemblages and guilds was calculated by averaging the relative abundance and biomass from 12 cruises (3 years × 4 seasons) during the 'early' (1987–90) and the 'late' (1995–98) part of the time series.
Bold font denotes significant results.

Table 8
Comparison of seasonal anomalies of total bird abundance (birds 100 km^{-1}) and total bird biomass (kgs 100 km^{-1}) during the beginning and the end of the time series

Time period	Simple linear regression			One sample Kolmogorov–Smirnov test		
	df	*F*-ratio	*p*-value	*n*	Max_diff	*p*-value
Early (1987–90)	1, 10	83.203	$<$**0.0001**	12	0.246	0.395
Late (1995–98)	1, 10	1.759	0.214	12	0.186	0.737

One-sample Kolmogorov–Smirnov tests were used to assess the normality of the regression residuals (Zar, 1984).
Bold font denotes significant results.

correlations involving five species at the alpha = 0.05 level, and three correlations involving two species at the alpha = 0.01 level (Fig. 6).

Two bird species were strongly ($p \leqslant 0.01$) correlated to temperature anomalies over short temporal scales (<1 year). The Sooty Shearwater increased significantly in abundance six months after near-surface (10 m) waters became anomalously cold (Fig. 6B), while peaks in Pink-footed Shearwater (*P. creatopus*) numbers preceded positive anomalies in near-surface (10 m) temperature by three months, and followed positive subsurface (100 m) temperature anomalies by nine months (Fig. 6C). The Pink-footed Shearwater also became more numerous 9–12 months after and three months before near-surface (10 m) and subsurface (100 m) positive temperature anomalies had been recorded off southern California, though these correlations were only marginally significant ($0.01 < p \leqslant 0.05$).

Four additional bird species were marginally ($0.01 < p \leqslant 0.05$) correlated with short-term (<1 year) temperature fluctuations. Three subtropical birds became more numerous in response to warm-water anomalies, especially during El Niño events. The Black-vented Shearwater (*Puffinus opisthomelas*) increased in abundance three months after positive near-surface (10 m) temperature anomalies were recorded off southern California (Fig. 6A). The abundance of this species peaked during the fall cruises of 1990 and 1997, and the winter of 1993 (Fig. 7A). The Black (*Oceanodroma melania*) and Least (*O. microsoma*) Storm-petrels became most numerous three months before positive

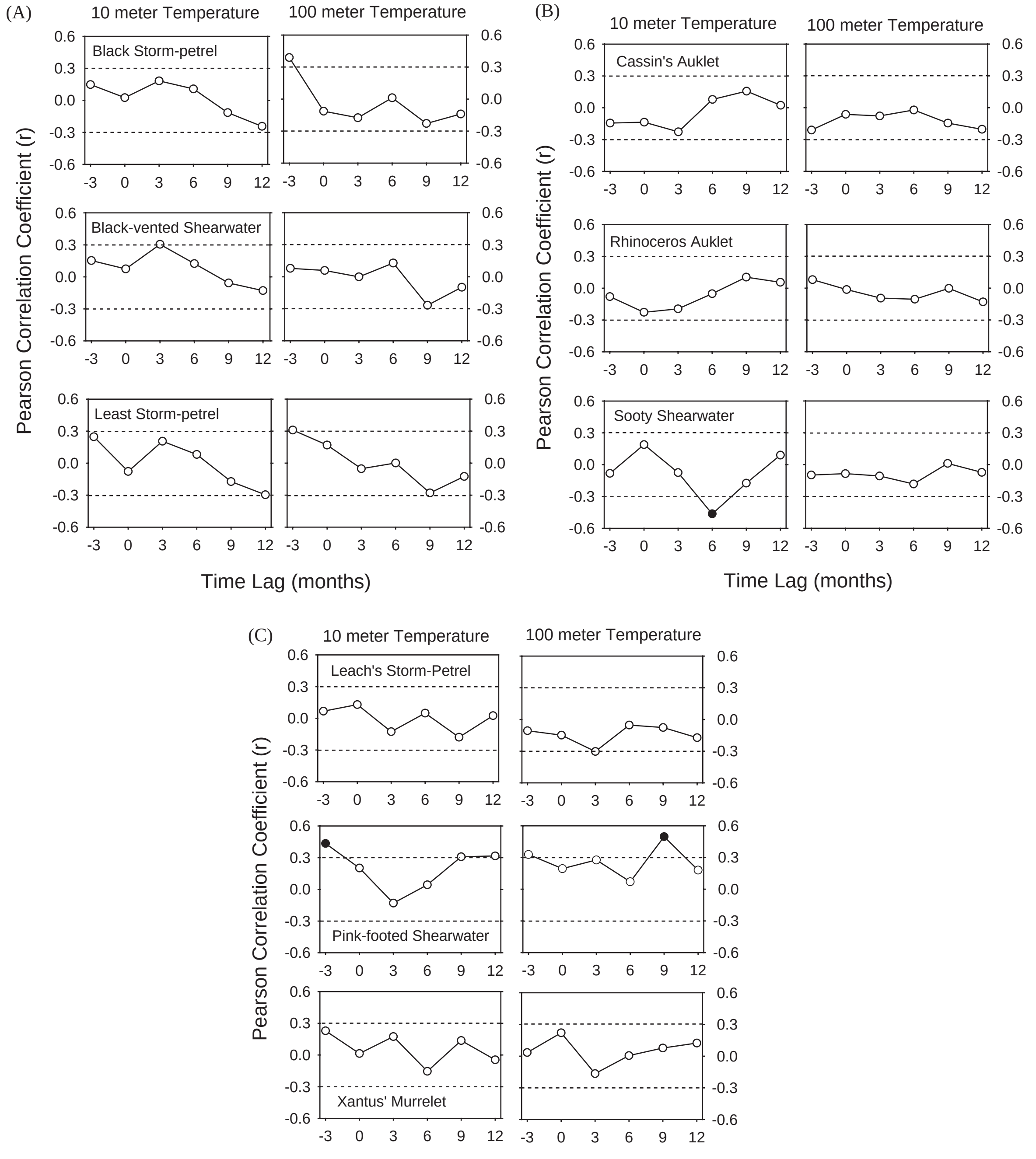

Fig. 6. Cross-correlations between seasonal anomalies of bird abundance (birds 100 km^{-1}) and near-surface (10 m) and thermocline (100 m) temperature for El Niño visitors (A), species with an affinity for cold-water (B), and warm-water taxa (C). Positive lags indicate that temperature fluctuations preceded changes in bird abundance, and negative lags that the temperature observations follow the bird data. Significance levels are shown by the hatched lines ($p \leqslant 0.05$) and the filled circles ($p \leqslant 0.01$).

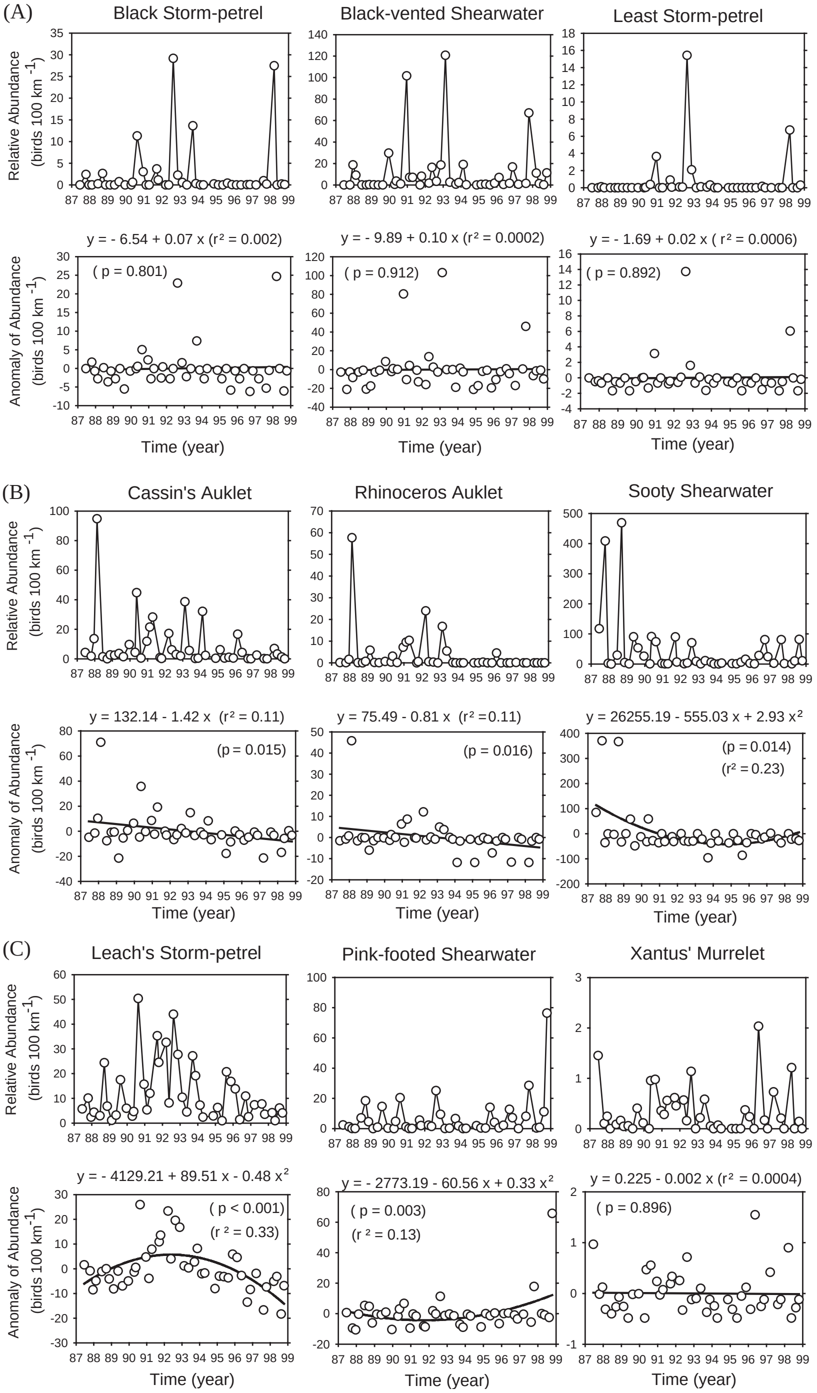

Fig. 7. Time series of seabird abundance off southern California (May 1987–September 1998) for El Niño visitors (A), species with an affinity for cold-water (B), and warm-water taxa (C). For each species, the raw abundance data and the seasonal anomalies of abundance are shown. The significance of the regressions was estimated using randomization tests.

thermocline (100 m) temperature anomalies became evident along CalCOFI line 90 (Fig. 6A). Least Storm-petrel abundance peaked during the fall of 1990, the summer of 1992, and the winter of 1998. Black Storm-petrel numbers were most numerous during the summers of 1990 and 1992, and in the winter of 1998 (Fig. 7A). Additionally, the Leach's Storm-petrel declined three months after positive 100 m temperature anomalies were recorded off southern California (Fig. 7C). Finally, three alcids (Cassin's and Rhinoceros Auklets *Cerorhinca monocerata*, and Xantus' Murrelet *Synthliboramphus hypoleucus*) showed no significant response to temperature anomalies over the short-term (<1 year) (Fig. 6B and C).

3.5. Long-term response of indicator species

The abundance of five indicator species changed significantly over the long-term. The three cold-water taxa considered in this analysis (Sooty Shearwater, Cassin's Auklet, and Rhinoceros Auklet) declined by 74%, 75%, and 93%, respectively, between 1987–90 and 1995–98 (Fig. 7B; Table 9). Additionally, the Leach's Storm-petrel, a cosmopolitan offshore species (Briggs et al., 1987; Veit et al., 1996) increased between 1987 and 1993, and then decreased thereafter (Fig. 7C). Overall, this storm-petrel, declined by 54% between the beginning (1987–90) and the end (1995–98) of the time series (Table 9). Finally, the Pink-footed Shearwater, a Transition Zone species with an affinity for warm water (Ainley, 1976; Gould and Piatt, 1993), more than doubled in abundance over the long term (Table 9). However, this trend must be interpreted with caution because it is heavily influenced by the peak in abundance during the last cruise of the time series, in the fall of 1998 (Fig. 7C).

Conversely, three subtropical birds that occur in the CalCOFI study area during warm-water periods (Black Storm-petrel, Least Storm-petrel, and Black-vented Shearwater, Fig. 7A), and an endemic California Current species (Xantus' Murrelet, Fig. 7C) showed no long-term trends in abundance during this study. The three subtropical visitors were more abundant during the middle part of the time series (1991–94, Table 9), possibly in response to the prolonged warming of near-surface waters during the 1992–94 El Niño event (Fig. 2; Lynn et al., 1995). However, these species did not increase significantly over the long term (Fig. 7).

Randomization tests revealed that the probability of committing a type I error when performing the regression analyses was 0.87% (157/18000), 5.50% (991/18000), and 17.22%

Table 9
Changes in the abundance of warm-water (+) and cold-water (–) indicator species during the beginning, the middle, and the end of the time series

Species	Water temperature affinity	Abundance (birds 100 km^{-1})			
		Early (87–90)	Middle (91–94)	Late (95–98)	Percent change (%) (87–90/95–98)
Black Storm-petrel	+	0.81	3.85	2.64	+226
Black-vented Shearwater	+	3.92	15.53	10.79	+175
Leach's Storm-petrel	+	11.48	18.46	5.29	–54
Least Storm-petrel	+	0.03	1.59	0.60	+1900
Pink-footed Shearwater	+	5.82	4.55	12.35	+112
Xantus' Murrelet	+	0.31	0.28	0.37	+19
Cassin's Auklet	–	12.01	9.02	2.97	–75
Rhinoceros Auklet	–	6.23	3.92	0.42	–93
Sooty Shearwater	–	106.16	9.32	27.31	–74

The average abundances during each time period are based on observations from 12 cruises (3 years × 4 seasons).
Positive percent changes indicate that the species increased during the long-term (May 1987–September 1998).

(3099/18000), at the 0.01, 0.05, and 0.10 probability levels. Since we performed 18 randomization tests, we would expect that on average less than one of these comparisons would have yielded a significant result merely by chance at the alpha = 0.05 significance level. Overall, nine regressions yielded significant results.

4. Discussion

The temperature of the California Current has increased in the last decades, concurrent with large-scale changes in the climate of the Pacific Ocean (Roemmich, 1992; Miller et al., 1994; Roemmich and McGowan, 1995a, b; Levitus et al., 2000). Previously, Veit and coworkers (1996) described the warming of near-surface (10 m) ocean temperature along CalCOFI line 90 and the decline in bird abundance off southern California between 1987 and 1994. Our analyses suggest that this warming trend has continued during the 1990s. In this paper, we document increasing 10 m water temperatures along the southern (line 90) and the northern (line 80) portions of the CalCOFI grid during 1987–98 (Fig. 2; Table 4). Moreover, this study suggests that the observed warming trend is a widespread phenomenon that has affected at least the upper 100 m of the water column along the southern California Bight and off Point Conception (Fig. 3; Table 3).

The long-term warming of the CCS has two major implications for the avifauna. First, the increase in near-surface (10 m) ocean temperature is indicative of the northward shift of the subtropical water mass along the west coast of North America (Table 1). Additionally, the warming of subsurface waters (down to 100 m) suggests that the depth of the thermocline has increased off southern California in recent years (Roemmich, 1992; Roemmich and McGowan, 1995a). The deepening of the thermocline in coastal and pelagic upwelling systems reduces the supply of nutrients into surface waters, diminishes primary productivity, and stimulates a switch from a phytoplankton community dominated by large cells (e.g., *Chaetoceros* diatoms) to a smaller-celled picoplankton assemblage (e.g., *Synechococcus*) (McGowan, 1985; Fiedler et al., 1992; Lynn et al., 1995; Chavez, 1996; Chavez et al., 1999).

4.1. Migrating biogeographic domains

One of the biological changes expected in response to global warming is the poleward migration of ocean domains and species distributions (Fulton and LeBrasseur, 1985; Fields et al., 1993; Lubchenco et al., 1993; Peterson et al., 1993). In particular, the ranges of pelagic species are likely to shift in response to changes in ocean climate because their distributions are intimately related to water masses and frontal systems (Wahl et al., 1989; Ribic et al., 1992; McGowan et al., 1996; Lehodey et al., 1997).

In the North Pacific Ocean, the subtropical (SST: 20–18°C) and the subarctic (SST: 12–10°C) frontal zones delineate a narrow region of strong temperature and salinity gradients termed the Transition Domain (Favorite et al., 1976; Lynn, 1986). This oceanographic feature delimits the ranges of subarctic and subtropical species and harbors endemic zooplankton, nekton, and marine bird assemblages (Fager and McGowan, 1963; Wahl et al., 1989; Gould and Piatt, 1993; Brodeur et al., 1999). According to Gould and Piatt (1993), the Flesh-footed Shearwater (*Puffinus carneipes*) and the Stejneger's Petrel (*Pterodroma longirostris*) appear to be restricted to the central Transition Domain, though many other far ranging species aggregate within this oceanographic domain (Appendix A).

The California Current can be thought of as the southward extension of the Transition Domain, where cool, subarctic water of the North Pacific Current mixes with warm, subtropical water to the south and west (Lynn, 1986; Haury et al., 1993). Northward range expansions of subtropical zooplankton, fishes, and marine birds are commonplace off southern California during warm-water seasons (e.g., fall) and years (e.g., El Niño events), in conjunction with the latitudinal migration of the subtropical water mass (SST > 18°C). Conversely, subarctic and transition domain species migrate southward into the southern California Bight during cold-water periods (Ainley, 1976; Brinton, 1981; Squire, 1987; Norton and Crooke, 1994).

In this paper, we report long-term changes in the composition of marine bird assemblages off southern California during an 11.4-year period of substantial ocean warming (1987–98). We have documented a concurrent increase in the abundance and biomass of warm-water taxa and a decline in the importance of cold-water species between 1987–90 and 1995–98 (Tables 6 and 7). Additional evidence of long-term latitudinal range shifts off the west coast of North America include the northward migration of 25 fish spawning distributions, including meso-pelagic species like the Pacific Hake *Merluccius productus* that live and spawn at depth (100–200 m), since the 1950s (Horne and Smith, 1997; Smith and Moser, 2000). Moreover, studies of nearshore and intertidal communities suggest that these distributional shifts are not restricted to highly mobile pelagic taxa, which often respond to shifting water mass distributions rapidly and retreat once the anomalous oceanographic conditions have subsided. Sagarin and coworkers (1999), for instance, ascribed changes in intertidal communities off central California to a long-term (1931–96) air and ocean warming trend. In a similar study of reef fish assemblages in the southern California Bight, Holbrook and coworkers (1997) described a concurrent decline in northern and endemic species and an increase in southern taxa, following the warm-water regime shift of the late 1970s. These range expansions are consistent with the latitudinal migrations of water masses predicted under an ocean warming scenario (Fields et al., 1993).

The notion that seabird populations shift their distributions merely in response to physical variability (e.g., changing ocean temperature) is probably too simplistic. Instead, changes in seabird ranges and population numbers are likely influenced by shifting prey distributions and ocean productivity patterns associated with large-scale water mass distributions (Ainley and Boekelheide, 1983; Wahl et al., 1989; Veit et al., 1996; Oedekoven et al., 2001).

4.2. *Declining ocean productivity*

The deepening of the thermocline, the drop in the amount of sinking particulate organic carbon (POC), and the decrease of zooplankton and larval fish standing stocks suggest that the productivity of the CCS has declined in the last decades (Roemmich and McGowan, 1995a, b; Lynn et al., 1998; Smith and Kaufmann, 1999). Such widespread changes have also affected the avifauna of the CCS (Tables 5 and 6). Previously, Veit and coworkers (1996) reported a 42% drop in overall bird abundance off southern California between 1987 and 1994, largely caused by the 91% decrease in the abundance of the numerically dominant cold-water species, the Sooty Shearwater.

In this paper we document significant changes in the relative importance (abundance and biomass) of distinct seabird feeding guilds off southern California. Between the beginning (1987–90) and the end (1995–98) of this study, diving species declined in importance, while plunging and surface-foraging taxa increased (Tables 6 and 7). These changes are consistent with the notion of declining ocean productivity off southern California. Diving seabirds preferentially inhabit highly productive subpolar regions and boundary currents because they require dense prey aggregations to meet high energetic requirements (Ainley, 1977; Piatt, 1990; Hodum et al., 1998). These species are characterized by energetically expensive flight (Pennycuick, 1987) and high metabolic rates (Birt-Friesen et al., 1989; Costa, 1991). Conversely, taxa that feed at the surface and plunge in pursuit of prey inhabit low-productivity regions, like the subtropical gyres and tropical water masses, because they can exploit more widely distributed food resources (Ainley, 1977; Ainley and Boekelheide, 1983; Wahl et al., 1989; Ballance et al., 1997). Ultimately, the avifauna off southern California has shifted from a 'high-productivity' assemblage typical of eastern boundary upwelling systems, to a 'low-productivity' community similar to the one inhabiting the North Pacific Subtropical Gyre (Tables 1 and 2; Murphy, 1936; Abrams and Griffiths, 1981; Wahl et al., 1989; Gould and Piatt, 1993).

4.3. *Response of indicator species to the warming of the California Current*

It is clear that marine birds respond to changes in water mass distributions and ocean productivity off southern California (Ainley et al., 1976; Briggs et al., 1987; Veit et al., 1996; Hyrenbach, 2001; this study). Previously, Veit and coworkers (1996) classified seabird species as warm-water and cold-water taxa, depending on whether their abundance off southern California increased or decreased as ocean temperatures raised or dropped. This study describes concurrent changes in the importance of seabird assemblages with different temperature affinities in response to the warming of the California Current, which are in agreement with the community-level changes expected under a global warming scenario (Tables 6 and 7). However, the responses of individual bird species have been more difficult to predict, suggesting that, in addition to water temperature associations, other factors dictate the response of marine birds to long-term climatic changes. In particular, species-specific differences in ecology and life history, such as the adaptability to changing environmental conditions and the energetic cost of foraging, likely modulate the response of marine bird populations to environmental change (Anderson, 1989; Jahncke and Goya, 2000; Hyrenbach, 2001; Oedekoven et al., 2001).

For instance, an increasing abundance of warm-water species (e.g., Black-vented Shearwater) after positive near-surface temperature anomalies suggests that these birds move into the study area following the northward advection of subtropical waters. Conversely, the increase of cold-water taxa (e.g., Sooty Shearwater) several months after negative temperature anomalies has been attributed to an aggregative response to enhanced localized productivity (Fig. 6B; Veit et al., 1996).

However, seabird communities off California likely respond to changes in both local and remote oceanographic processes, ranging from shifts in coarse-meso scale (10–100s km) water mass distributions, to basin-wide (1000s km) atmospheric forcing. For instance, the immigration of Black and Least Storm-petrels and Pink-footed Shearwaters into the southern California Bight cannot be attributed solely to the northward shift of the subtropical water mass, because these bird incursions precede the warming of the CalCOFI region by three months (Fig. 6A and C). Instead, it is conceivable that decreased ocean productivity or enhanced precipitation during El Niño events disrupt seabird breeding activities in Chile (Pink-footed Shearwater, egg-laying: December–January, fledging and dispersal: March–April) and in the Sea of Cortez (Black Storm-petrels, egg-laying: May–June, fledging: September–October), causing the greater than normal northward dispersal of species that breed south of the CalCOFI grid (Harrison, 1983; Schreiber and Schreiber, 1984; Anderson, 1989; Veit et al., 1996).

4.4. *Seabird response over short and long temporal scales*

This study documents a differential numerical response of marine birds to short-term (<1 year) environmental variability during periods of contrasting oceanographic conditions (Table 10). Namely, we contrasted the cross-correlations of bird abundance and water temperature anomalies off southern California during two time periods: a persistent warming period (1987–94) and a longer time series including an additional cooling period (1995–96) followed by a subsequent warming (1997–98).

Three of the nine species investigated showed consistent short-term responses to temperature fluctuations during the initial warming period (1987–94) and the entire time series (1987–98). The Sooty Shearwater increased significantly in abundance 6–9 months after near-surface negative temperature anomalies (Veit et al., 1996; Fig. 6B). This species declined by 91% off southern California during the long-term warming period (1987–94), and then increased by 193% in response to the cold-water period during 1995–96. Similarly, the warm-water Pink-footed and Black-vented Shearwaters increased significantly in response to short-term warm-water anomalies during both time periods (Fig. 6A and C; Table 10). These three species do not breed in the CCS but visit this highly productive region seasonally

Table 10
Characteristics of the indicator seabird species discussed in this study

Species	Breeding status	Seasonal peak	Preferred habitat	Short-term response (1987–94)		Short-term response (1987–98)		References
				10 m	100 m	10 m	100 m	
Black Storm-petrel	South	Summer	Shelf/Slope	+	N.S.	N.S.	+	Harrison (1983) Tyler et al. (1993)
Black-vented Shearwater	South	Fall	Shelf/Slope	+	N.S.	+	N.S.	Harrison (1983) Tyler et al. (1993)
Cassin's Auklet	Endemic (North)	Winter	Shelf/Slope	–	N.S.	N.S.	N.S.	Harrison (1983) Tyler et al. (1993)
Sooty Shearwater	SH—Chile, New Zealand	Summer	Shelf/Slope	–	N.S.	–	N.S.	Harrison (1983) Gould and Piatt (1993)
Leach's Storm-petrel	Endemic (North)	Summer	Pelagic	+	N.S.	N.S.	–	Harrison (1983) Tyler et al. (1993) Gould and Piatt (1993)
Least Storm-petrel	South	Summer	Shelf/Slope	+	N.S.	N.S.	+	Harrison (1983) Tyler et al. (1993)
Pink-footed Shearwater	SH—Peru Current	Summer	Shelf/Slope	+	N.S.	+	+	Harrison (1983) Tyler et al. (1993) Gould and Piatt (1993)
Rhinoceros Auklet	Endemic—(North)	Winter	Shelf/Slope	–	N.S.	N.S.	N.S.	Harrison (1983) Tyler et al. (1993)
Xantus' Murrelet	Endemic—(South)	Summer	Shelf/Slope	+	N.S.	N.S.	N.S.	Harrison (1983) Tyler et al. (1993)

Breeding status describes whether the species breeds in the Southern California Bight (Endemic), in the California Current North/South of the study site (North/South), or in the Southern Hemisphere (SH). Seasonal peak and preferred habitat refer to the temporal and spatial patterns of occurrence within the CalCOFI grid between May 1987 and September 1998. Seasons are defined as follows: Winter (January–February), Spring (March–May), Summer (July–August), and Fall (September–November). Shelf/slope and pelagic waters are shallower and deeper than 2000 m respectively.
Short-term (lag <1 year) positive (+) and negative (–) responses to temperature anomalies are significant at the $\alpha = 0.05$ level.
N.S. denotes non-significant cross-correlations between seasonal anomalies of bird abundance and ocean temperature.

(Ainley, 1977; Harrison, 1983; Briggs et al., 1987; Veit et al., 1996).

We detected disparities in the sign (+ or –) and the lag of the temperature cross-correlations for the other six focal species considered in this study (Fig. 6, Table 10). These disparities were particularly striking for the Leach's Storm-petrel (Table 10). The once numerically dominant offshore seabird was significantly ($p \leqslant 0.01$) more numerous during periods of positive near-surface (10 m) temperature anomalies, and almost doubled in abundance in response to the continued warming of the California Current between 1987 and 1994 (Veit et al., 1996). However, the Leach's Storm-petrel peaked in abundance between 1991 and 1993, and declined by 71% between 1991–94 and 1995–98. Overall, the Leach's Storm-petrel declined by 54% between the beginning (1987–90) and the end (1995–98) of this study (Table 9). Over the long-term (1987–98), this species was marginally correlated ($0.01 < p \leqslant 0.05$) to negative thermocline (100 m) temperature anomalies after a lag of 3 months (Fig. 6C).

Two locally breeding alcids, the Cassin's and Rhinoceros Auklets, also were characterized by different water temperature responses during the warming period and the entire time series (Table 10). These taxa were strongly correlated ($p \leqslant 0.01$) to negative temperature anomalies early on (1987–94), and declined by 25% and 37% respectively during the initial warming period (Veit et al., 1996). Yet, these species did not increase in abundance in response to the ephemeral cold-water conditions of 1995–96 (Fig. 7B). Instead, the temperature cross-correlations of these species became non-significant when we analyzed the entire time series (1987–98), suggesting that their positive numerical response to cold-water conditions broke down sometime in the early 1990s (Table 10). Overall, these locally breeding auklets declined by 75% and 93% respectively over the long term (Table 9).

4.5. Population-level declines or redistributions

It is inherently difficult to interpret local changes in the abundance of far-ranging marine birds, because researchers in one part of the species range cannot ascertain whether local fluctuations in abundance are driven by shifting distributions or changing population numbers. In this paper, we used the short-term (<1 year) cross-correlations of bird abundance and ocean temperature to determine whether local changes in bird abundance off southern California were indicative of range shifts or shrinking populations.

The linkages between the productivity of the CCS, the diet, the reproductive performance and the demography of locally breeding marine birds is fairly well understood (Ainley et al., 1995; Bertram et al., 2000; Sydeman et al., 2001; Hedd et al., 2002). On the other hand, it has been more difficult to determine to what extent oceanographic variability in the CCS impacts far-ranging species that breed elsewhere. Therefore, it is difficult to anticipate what population-level effects, if any, the continued warming of the California Current will have on species like the Sooty and the Pink-footed Shearwater. Nevertheless, the apparent declines in resident (Cassin's and Rhinoceros Auklet) and visiting (Sooty Shearwater) cold-water species likely have very different population-level implications.

The large-scale declines in Cassin's and Rhinoceros Auklet abundance between 1987–90 and 1995–98 are suggestive of shrinking populations (Table 9). In particular, the failure of these species to increase in response to cold-water conditions during 1995–96 suggests that these breeding populations have declined over the long term (Fig. 7B). Colony-based studies of locally breeding alcid populations off central California and British Columbia provide additional evidence of ocean warming impacts on these species.

Colony-based studies of auklet foraging ecology and demography have provided a mechanistic linkage between ocean warming and the hypothesized declines of these populations. Auklet diets and reproductive success are intimately related to the magnitude of coastal upwelling and the availability of juvenile rockfish (largely short-belly rockfish *Sebastes jordani*) and cold-water euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera)*. Years of high upwelling and cool ocean temperatures enhance the reproductive success of locally breeding seabird populations. Conversely, reproductive success decreases during warm-water years with low prey abundance (Ainley et al., 1995, 1996; Sydeman et al., 2001). Thus, we hypothesize that the prolonged warming of the California Current decreased locally breeding alcid populations to the point that they could not bounce back in response to the transient cold-water conditions during 1995–96 (Bertram et al., 2000; Pyle, 2001; Sydeman et al., 2001; Hedd et al., 2002).

Concurrent at-sea and colony-based surveys suggest that the decline of Sooty Shearwaters in the CCS is partly attributable to declining breeding populations and redistribution. Surveys of colonies at the Snares Islands (Lyver et al., 1999; Scofield, 2001) and mainland New Zealand (Hamilton et al., 1997; Jones, 2000; Scofield, 2001) have documented drastic declines in Sooty Shearwater breeding populations since the mid 1980s. Additionally, at-sea surveys off central California and Washington State have not revealed localized increases in Sooty Shearwater abundance, suggestive of a northward range shift (Veit et al., 1997; Wahl and Tweit, 2000; Oedekoven et al., 2001). On the other hand, Spear and Ainley (1999) hypothesized that Sooty Shearwaters had shifted their migratory routes from the eastern to the central Pacific between 1983 and 1991. The westward shift in migration routes and the slight rebound in Sooty Shearwater abundance off southern California during the cold-water conditions of 1995–96 suggest that the decline observed between 1987 and 1994 was, at least partly, the result of emigration from the CCS. However, additional at-sea surveys during the prolonged cold-water period since the fall of 1998 have not revealed large increases in Sooty Shearwater numbers off southern California (Bograd et al., 2000; Durazo et al., 2001) comparable to the historical abundance levels recorded in the CCS during the late 1970s and early 1980s (Briggs et al., 1987; Veit et al., 1997; Wahl and Tweit, 2000). The lack of an at-sea population rebound during the late 1990s, in conjunction with evidence of declining breeding populations, suggests that there has been a global decrease in Sooty Shearwater numbers since the mid 1980s.

4.6. *Non-linear response to ocean warming*

In this paper, we document non-linear responses of bird abundance during a period of long-term warming and declining ocean productivity off southern California. We hypothesize that the disparities in the short-term (<1 year) and long-term (8–12 years) patterns of bird abundance are driven by the interplay of distinct population-level responses to ocean warming. During the warming period between 1987 and 1994, subtropical seabirds like the Black-vented Shearwater and the Black and the Least Storm-petrels immigrated into the CalCOFI region in higher numbers, apparently in response to northward shifts of subtropical waters and associated warm-water prey species (Smith, 1985; Moser and Smith, 1993). Conversely, cold-water seabirds vacated the area in search of enhanced feeding opportunities elsewhere. As a result of these redistributions, the numerically dominant cold-water species, the Sooty Shearwater, declined by 91%; while the most numerous warm-water bird, the Leach's Storm-petrel, increased by 162% off southern California (Veit et al., 1996).

The prolonged period of warm-water conditions and decreased ocean productivity also impacted the reproductive success and the survivorship of the seabirds that breed in the CCS (Ainley et al., 1996; Bertram et al., 2000; Pyle, 2001; Sydeman et al., 2001). These impacts are particularly evident in the long-term response of three locally breeding species: the two cold-water alcids (Cassin's and Rhinoceros Auklets), and the warm-water Leach's Storm-petrel (Table 10). The linkages between the productivity of the CCS and the diet and reproductive success of the auklets are well understood (Ainley et al., 1995, 1996; Sydeman et al., 2001; Hedd et al., 2002). On the other hand, the response of the Leach's Storm-petrel to ocean temperature fluctuations has not been studied. Yet, the observed decline in storm-petrel abundance is suggestive of a population decrease.

At-sea surveys suggest that the Leach's Storm-petrel responded positively to the initial warming of the CCS and declined thereafter. In spite of the instantaneous positive response to warm-water anomalies during the initial warming period (1987–94), (Table 10; Veit et al., 1996), the Leach's Storm-petrel did not increase during the 1997–98 El Niño event (Fig. 7C). Instead, this species declined by 54% between 1987–88 and 1995–98, after almost doubling in abundance between 1987–90 and 1991–94 (Table 9). We attribute the initial increase in the abundance of this warm-water species to a range expansion in response to the warming of the CalCOFI survey area. Moreover, we hypothesize that the prolonged warming of the California Current depressed this species reproductive success, eventually leading to a population decline. Unfortunately, we lack the necessary demographic data to test for changes in the reproductive success of Leach's Storm-petrel populations breeding off southern and Baja California.

The idea that environmental variability operating at different temporal scales affects populations differently is not new. Theoretical studies have shown that the rate of population decline and the probability of extinction increase with added environmental autocorrelation, particularly when the temporal scale of environmental variability (decades for the CCS) exceeds the time scale of reproduction (15–30 year seabird reproductive lifetime) of the species under consideration (Doak et al., 1994; Johst and Wissel, 1997). Thus, it is not surprising that the cold-water species that initially responded to ocean warming by shifting their distributions northwards, were eventually impacted demographically by the continued warming trend. What is perhaps more surprising is that a warm-water species, like the Leach's Storm-petrel, would respond in a similar fashion.

Holbrook and coworkers (1997) reported similar non-linear changes in reef fish assemblages off southern California between 1974 and 1993. Dominance shifted from cold-water to warm-water species, as northern and endemic southern California Bight species were replaced by southern taxa between 1976 and 1980. In spite of their affinity for warm water, southern species peaked in the late 1980s and declined abruptly during the early 1990s because they failed to recruit adequately. Overall, 95% of the species studied decreased in abundance by an average of 69%. The widespread decline of distinct fish assemblages was attributed to concurrent decreases in ocean productivity and zooplankton biomass in the southern California Bight.

This is the first time, to our knowledge, that such a non-linear response has been reported in marine birds. Previously, long-term studies of seabird distributions and reproductive success suggested that marine bird populations respond to changing ocean climate in a linear fashion (Aebischer et al., 1990; Wahl and Tweit, 2000). In other words, environmental variables and bird abundance or demography varied consistently during periods of contrasting oceanographic conditions, and reversals in environmental conditions were followed by reversals in the bird response. Thus, the sign of the correlations between the driving environmental variables and the bird responses were consistent through time. For instance, Aebischer and coworkers (1990) described a long-term (1955–87) link between Black-legged Kittiwake (*Rissa tridactyla*) reproductive success and ocean climate in the North Atlantic. The Kittiwakes experienced a decline in reproductive success between 1960 and 1980, concurrent with a decrease in westerly winds and a drop in zooplankton abundance and fish stocks. From 1980 to 1987 these trends reversed, suggesting that westerly wind, zooplankton abundance, fish prey stocks, and bird reproductive success remained positively correlated throughout the entire time series.

Similarly, in the northeast Pacific, at-sea bird communities off Washington State (1972–98) have changed consistently with respect to ocean temperature fluctuations. Fourteen of the 24 coastal species studied showed significant changes in abundance before and after the 1977 and the 1989 shifts in oceanographic conditions (Miller et al., 1994; Beamish et al., 1999). Of these, the five species that responded significantly to both regime shifts did so in a consistent fashion, either decreasing or increasing in response to the progressive warming of the northeastern Pacific. The two auklets and the Sooty Shearwater declined as ocean temperature increased (Wahl and Tweit, 2000).

4.7. *Implications*

Whether the warming of the California Current is part of a low-frequency (period >40 years) cycle or a continued trend is unclear (Folland et al., 1999; Bograd et al., 2000; Levitus et al., 2000). Regardless of the nature of this warming trend, the observed changes may have important implications for marine bird populations globally. Because the avifauna off California is composed of both locally breeding species and far-ranging seasonal visitors, the warming of the California Current could potentially affect bird species throughout the Pacific Ocean. Specifically, the far-ranging Shearwater and petrel species that complete their molt in the North Pacific (e.g., Sooty and Buller's Shearwater *Puffinus bulleri*; Chu, 1984; Briggs et al., 1987) and the subarctic taxa that over-winter in the CCS (e.g., Northern Fulmar *Fulmarus glacialis*, Black-legged Kittiwake; Briggs et al., 1987) may be particularly susceptible to this decline in ocean productivity.

Additionally, the study of marine bird communities can improve our understanding of how climate change may affect other highly mobile marine predators. The distributions of nektonic predators, including tunas and salmon, are influenced by dynamic water-mass boundaries and large-scale circulation and production regimes (Sund et al., 1981; Squire, 1987; Brodeur and Ware, 1995; Lehodey et al., 1997). Furthermore, marine birds, cetaceans and large predatory fish exploit the same marine food webs, and often rely on the same prey resources that are affected by these climatic perturbations (Brodeur and Pearcy, 1992; Brodeur et al., 1996; Furness and Camphuysen, 1997; Sydeman et al., 2001). In particular, the non-linear responses to environmental change described in this study highlight the need to improve our understanding of the behavioral and demographic responses of upper-trophic predators to oceanographic variability. More specifically, this paper stresses three interrelated aspects that deserve additional study: (1) the way that ocean productivity affects the distribution and aggregation of prey; (2) how prey dispersion influences the distribution, prey selection and foraging effort of upper-trophic predators; and, (3) whether enhanced foraging effort impacts top predator reproductive success and survivorship.

Acknowledgements

This research was completed as part of the first author's requirements for a Ph.D. at the Scripps Institution of Oceanography. We gratefully thank the captains and crews of the R.V. *David Starr Jordan*, R.V. *New Horizon* and R.V. *Roger Revelle*, the Scripps Institution of Oceanography and the CalCOFI organization for their logistical support. Particularly, we thank M. Mullin, T. Hayward and J. McGowan for their vision and commitment to make this seabird time series possible. CalCOFI and NMFS technicians collected the CTD information used to characterize changes in ocean climate. C. Alexander, J. Dunn, C. Elphick, R. Foster, B. Leventhal, M. Lippsmeyer, K. Molina, R. Morgan, P. Pyle, R. Reitsch, E. Root, R. Russell, D. Sidley, K. Stowe, O. Williams conducted seabird observations throughout the years. S. Bograd, P. Dayton, P. Franks, G. Hunt, J. Jaffe and two anonymous reviewers provided helpful comments on an earlier draft of this manuscript. This research was supported by NSF OCE 90-19394 to R. Veit and J. McGowan.

Appendix A

List of 68 bird species analyzed in this study. All weights taken from Dunning (1993). Feeding methods described by Ashmole (1971) and Wahl et al. (1989) (see Table 11).

Table 11
List of 68 bird species analyzed in this study

Taxa	Species	Weight (g)	Water temp. affinity	Feeding method	% Numbers	% Biomass
Ancient Murrelet		206	–	D	0.011	0.004
Arctic Loon		3355		D	0.242	1.567
Arctic Tern		110		P	0.075	0.016
Ashy Storm-petrel		36.9		S	0.311	0.022
Black-footed Albatross		3148		S	0.529	3.209
Black-legged Kittiwake		407	–	S	0.472	0.370
Black Storm-petrel		59	+	S	1.259	0.143
Black Tern		54.2[a]		P	0.001	0.000
Bonaparte's Gull		281		S	2.173	1.176
Brandt's Cormorant		2103		D	0.802	3.248
Brown Pelican		3438		P	1.839	12.182
Band-rumped Storm-petrel		41.8		S	0.023	0.002
Buller's Shearwater		380		P	0.089	0.065
Black-vented Shearwater		276	+	D	4.732	2.516
Cassin's Auklet		188	–	S	3.285	1.190
California Gull		606.5		S	6.408	7.488
Caspian Tern		655		P	0.055	0.069

Table 11 (*continued*)

Taxa	Species	Weight (g)	Water temp. affinity	Feeding method	% Numbers	% Biomass
Common Murre		992.5	–	D	0.418	0.798
Cook's Petrel		178.5	+	SS	0.996	0.343
Common Tern		120		PL	0.034	0.008
Double-crested Cormorant		1674		DI	0.050	0.161
Eared Greebe		292		DI	0.019	0.011
Elegant Tern		257		PL	0.113	0.056
Flesh-footed Shearwater		568		PL	0.005	0.005
Forster's Tern		158		PL	0.023	0.007
Forked-tailed Storm-petrel		55.3	–	SS	0.027	0.003
Glaucous-winged Gull		1412.5		SS	0.023	0.063
Herring Gull		1135		SS	0.324	0.709
Horned Greebe		453		DI	0.003	0.003
Horned Puffin		619	–	DI	0.001	0.001
Heermann's Gull		500	+	SS	0.427	0.411
Juan-Fernandez Petrel		434[b]	+	SS	0.001	0.001
Leach's Storm-Petrel		39.8	+	SS	14.253	1.093
Loons	Common and Pacific Loon	2896.5[c]		DI	0.785	4.383
Large Greebes	Western and Clark's Greebe	1477[d]		DI	0.079	0.225
Least Storm-petrel		20.5	+	SS	0.336	0.013
Long-tailed Jaeger		296.5		K	0.069	0.039
Laysan Albatross		3041.5		S	0.093	0.547
Marbled Murrelet		222	–	D	0.001	0.000
Mew Gull		403.5		S	0.041	0.032
Mottled Petrel		316		S	0.002	0.001
Northern Fulmar		544	–	S	0.719	0.754
Parakeet Auklet		258	–	D	0.020	0.010
Parasitic Jaeger		464.5		K	0.122	0.109
Pelagic Cormorant		1868		D	0.033	0.117
Pink-footed Shearwater		721		P	4.015	5.578
Phalaropes	Red and Red-necked Phalarope	46.9[e]	+	S	23.214	2.098
Pigeon Guillemot		487		D	0.644	0.604
Pomarine Jaeger		694	–	K	0.206	0.276
Ring-billed Gull		518.5		S	0.230	0.230
Red-billed Tropicbird		750		P	0.065	0.094
Rhinoceros Auklet		520	–	D	0.916	0.917
Red-necked Greebe		1023		D	0.530	1.044
Royal Tern		470		P	0.056	0.051
Red-throated Loon		1551		D	0.022	0.065
Red-tailed Tropicbird		624	+	P	0.026	0.031
Sabine's Gull		191		S	0.102	0.037
Sooty Shearwater	Sooty and Short-tailed Shearwater	787[f]	–	D	20.994	31.833
South-polar Skua		1156		K	0.030	0.068
Stejneger's Petrel		178.5[g]		S	0.006	0.002
Thick-billed Murre		964	–	D	0.001	0.002
Thayer's Gull		996		S	0.031	0.059
Tufted Puffin		779	–	D	0.500	0.750
Western Gull		1011		S	6.677	13.006
Wilson's Storm-petrel		32		S	0.227	0.014
Wedge-rumped Storm-petrel		39.8[h]	+	S	0.010	0.001

Table 11 (*continued*)

Taxa	Species	Weight (g)	Water temp. affinity	Feeding method	% Numbers	% Biomass
Wedge-tailed Shearwater		388	+	S	0.025	0.019
Xantus' Murrelet	Xantus' and Craveri's Murrelet	167[i]	+	S	0.151	0.049

(D) Diving, (P) Plunging, (K) Kleptoparasitism, and (S) Surface-feeding. Relative abundance (%) and biomass (%) calculated as the proportion of total bird numbers and biomass contributed by each taxa between May 1987 and September 1998. Warm (+) and cold (−) water temperature affinities were considered.

[a] Used body mass of the similarly sized White-winged Black Tern.

[b] Used body mass of the similarly sized Dark-rumped Petrel.

[c] Used average body mass of Pacific and Common Loons.

[d] Used body mass of the most abundant species, the Western Greebe.

[e] Used average body mass of Red and Red-necked Phalaropes.

[f] Used body mass of the most abundant species, the Sooty Shearwater.

[g] Used body mass of the similarly sized Cook's Petrel.

[h] Used body mass of the similarly sized Leach's Storm-petrel.

[i] Used body mass of most abundant species, the Xantus' Murrelet.

References

Abrams, R.W., Griffiths, A.M., 1981. Ecological structure of the pelagic seabird community in the Benguela Current Region. Marine Ecology Progress Series 5, 269–277.

Aebischer, N.J., Coulson, J.C., Colebrook, J.M., 1990. Parallel long-term trends across four marine trophic levels and weather. Nature 347, 753–755.

Ainley, D.G., 1976. The occurrence of seabirds in the coastal region of California. Western Birds 7, 33–68.

Ainley, D.G., 1977. Feeding methods of seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. In: Llano, G.A. (Ed.), Adaptations Within Antarctic Ecosystems. Gulf Publishing Company, Houston, pp. 669–686.

Ainley, D.G., Boekelheide, R.J., 1983. An ecological comparison of oceanic seabird communities of the South Pacific. Studies in Avian Biology 8, 2–23.

Ainley, D.G., Sydeman, W.J., Norton, J., 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Marine Ecology Progress Series 118, 69–79.

Ainley, D.G., Spear, L.B., Allen, S.G., 1996. Variation in the diet of Cassin's Auklet reveals spatial, seasonal and decadal occurrence patterns of euphausiids off California, USA. Marine Ecology Progress Series 137, 1–10.

Anderson, D.J., 1989. Differential responses of boobies and other seabirds in the Galapagos to the 1986-87 El Niño—Southern Oscillation event. Marine Ecology Progress Series 52, 209–216.

Antonov, J., Levitus, S., Boyer, T.P., Conkright, M., O'Brien, T., Stephens, C., 1998. World Ocean Atlas 1998 Vol. 2: Temperature of the Pacific Ocean. NOAA Atlas NESDIS 28. US Government Printing Office, Washington.

Ashmole, N.P., 1971. Sea bird ecology and the marine environment. In: Farner, D.S., King, R.J. (Eds.), Avian Biology, Vol. 1. Academic Press, New York, pp. 223–286.

Ballance, L.T., Pitman, R.L., Reilly, S.B., 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology 78, 1502–1518.

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V., Kurashov, V., 1999. The regime concept and natural trends in the production of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 56, 516–526.

Bertram, D.F., Jones, I.L., Cooch, E.G., Knechtel, H.A., Cooke, F., 2000. Survival rates of Cassin's and Rhinoceros Auklets at Triangle Island, British Columbia. Condor 102, 155–162.

Birt-Friesen, V.L., Montevecchi, W.A., Cairns, D.K., Macko, S.A., 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. Ecology 70, 357–367.

Bograd, S.J., DiGiacomo, P.M., Durazo, R., Hayward, T.L., Hyrenbach, K.D., Lynn, R.J., Mantyla, A.W., Schwing, F.B., Sydeman, W.J., Baumgartner, T., Lavaniegos, B., Moore, C.S., 2000. The state of the California Current, 1999–2000: forward to a new regime? California Cooperative of Oceanographic Fisheries Investigations Reports 41, 26–52.

Briggs, K.T., Tyler, W.B., Lewis, D.B., Carlson, D.R., 1987. Bird communities at sea off California. Studies in Avian Biology 11, 1–74.

Brinton, E., 1981. Euphausiid distributions in the California Current during the warm-water-spring of 1977–78, in the context of a 1949–1966 time-series. California Cooperative Oceanic Fisheries Investigations Reports 22, 135–154.

Brinton, E., 1996. Will the '96 drill head on up the hill, and spill like jill? Or: the '93–'96 krill increases have reached levels which, in the past, have preceded abrupt declines off southern California. California Cooperative Oceanic Fisheries Investigations Annual Conference, Pacific Grove, CA, Abstracts, V-7.

Brodeur, R.D., Pearcy, W.G., 1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. Marine Ecology Progress Series 84, 101–119.

Brodeur, R.D., Ware, D.M., 1995. Interdecadal variability in distribution and catch rates of epipelagic nekton in the Northeast Pacific Ocean. Canadian Special Publications Fisheries and Aquatic Sciences 121, 329–356.

Brodeur, R.D., Frost, B.W., Hare, S.R., Francis, R.C., Ingraham Jr., W.J., 1996. Interannual variations in zooplankton biomass in the Gulf of Alaska, and covariation with California Current zooplankton biomass. California Cooperative Oceanic Fisheries Investigations Reports 37, 80–99.

Brodeur, R.D., McKinnell, S., Nagasawa, K., Pearcy, W., Radchenko, V., Tagaki, S., 1999. Epipelagic nekton of the North Pacific Subarctic and Transition Zones. Progress in Oceanography 43, 365–397.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London.

Chavez, F.P., 1996. Forcing and biological impact of the 1992 El Niño in central California. Geophysical Research Letters 23, 265–268.

Chavez, F.P., Strutton, P.G., Friederich, G.E., Feely, R.A., Feldman, G.C., Foley, D.G., McPhaden, M.J., 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997–98 El Niño. Science 286, 2126–2131.

Chelton, D.B., Bernal, P.A., McGowan, J.A., 1982. Large-scale interannual physical and biological interactions in the California Current. Journal of Marine Research 40, 1095–1125.

Chu, E.W., 1984. Sooty Shearwaters off California: diet and energy gain. In: Nettleship, D.N., Sanger, G.A., Springer, P.F. (Eds.), Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Canadian Wildlife Service, Ottawa, pp. 64–71.

Costa, D.P., 1991. Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history. American Zoologist 31, 111–130.

Dickson, R.R., Lamb, H.H., Malmberg, S.A., Colebrook, J.M., 1975. Climatic reversals in the northern North Atlantic. Nature 256, 479–482.

Doak, D.F., Klepetka, B., Kareiva, P., 1994. Modeling population viability for the desert tortoise in the western Mohave Desert. Ecological Applications 4, 446–460.

Dunning, J.B., 1993. CRC Handbook of Avian Body Masses. CRC Press, Boca Raton.

Durazo, R., Baumgartner, T.R., Bograd, S.J., Collins, C.A., De La Campa, S., Garcia, J., Gaxiola-Castro, G., Huyer, A., Hyrenbach, K.D., Loya, D., Lynn, R.J., Schwing, F.B., Smith, R.L., Sydeman, W.J., Wheeler, P., 2001. The State of the California Current, 2000–2001: evidence of a new regime? California Cooperative of Oceanic Fisheries Investigations Reports 42, 29–60.

Efron, B., Tibshirani, R., 1993. An Introduction to the Bootstrap. Chapman and Hall, New York.

Fager, E.W., McGowan, J.A., 1963. Zooplankton species groups in the North Pacific. Science 140, 453–461.

Fargion, G.S., McGowan, J.A., Stewart, R.H., 1993. Seasonality of chlorophyll concentrations in the California Current: a comparison of two methods. California Cooperative of Oceanic Fisheries Investigations Reports 34, 35–50.

Favorite, F., Dodimead, A.J., Nasu, K., 1976. Oceanography of the Subarctic Pacific region, 1960–71. Bulletin of the International North Pacific Fisheries Commission 33, 1–187.

Fiedler, P., Chavez, F.P., Reilly, S., 1992. Physical and biological effects of Los Niños in the ETP, 1986–1989. Deep-Sea Research I 39, 199–219.

Fields, P.A., Graham, J.B., Rosenblatt, R.H., Somero, G.N., 1993. Effects of expected global climate change on marine faunas. Trends in Ecology and Evolution 8, 361–366.

Folland, C.K., Parker, D.E., Colman, A.W., Washington, R., 1999. Large scale models of ocean surface temperature since the late nineteenth century. In: Navarra, A. (Ed.), Beyond El Niño: Decadal and Interdecadal Climate Variability. Springer, New York, pp. 75–102.

Fulton, J.D., LeBrasseur, R.J., 1985. Interannual shifting of the Subarctic Boundary and some of the biotic effects on juvenile salmonids. In: Wooster, W.S., Fluharty, D.L. (Eds.), El Niño North: El Niño Effects in the Subarctic Pacific Ocean. University of Washington Press, Seattle, pp. 237–252.

Furness, R.W., Camphuysen, C.J., 1997. Seabirds as monitors of the marine environment. ICES Journal of Marine Science 54, 726–737.

Gould, P.J., Piatt, J.F., 1993. Seabirds of the central North Pacific. In: Vermeer, K., Briggs, K.T., Morgan, K.H., Siegel-Causey, D. (Eds.), The Status, Ecology, and Conservation of Marine Birds of the North Pacific. Canadian Wildlife Service, Ottawa, pp. 27–38.

Griffiths, A.M., Siegfried, W.R., Abrams, R.W., 1982. Ecological structure of a pelagic seabird community in the Southern Ocean. Polar Biology 1, 39–46.

Hamilton, S.A., Moller, H., Robertson, C.J.R., 1997. Distribution of Sooty Shearwater (*Puffinus griseus*) breeding colonies along the Otago Coast, New Zealand, with indicators of countrywide population trends. Notornis 44, 15–25.

Harrison, P., 1983. Seabirds: An Identification Guide. Mifflin Company, Boston.

Haury, L.R., Venrick, E.L., Fey, C.L., Niiler, P.P., McGowan, J.A., 1993. The Ensenada Front, July 1985. California Cooperative Oceanic Fisheries Investigations Reports 34, 69–88.

Hayward, T.L., 1997. Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. Trends in Ecology and Evolution 12, 150–154.

Hayward, T.L., Venrick, E.L., 1998. Nearsurface pattern in the California Current: coupling between physical and biological structure. Deep-Sea Research II 45, 1617–1638.

Hayward, T.L., Cummings, S.L., Cayan, D.R., Chavez, F.P., Lynn, R.J., Mantyla, A.W, Niiler, P.P., Schwing, F.B., Veit, R.R., Venrick, E.L., 1996. The state of the California Current in 1995–1996: continuing declines in zooplankton biomass during a period of nearly normal circulation. California Cooperative Oceanic Fisheries Investigations Reports 37, 22–37.

Hedd, A., Ryder, J.L., Cowen, L.L., Bertram, D.F., 2002. Inter-annual variation in the diet, provisioning and growth of Cassin's Auklet at Triangle Island, British Columbia: responses to variation in ocean climate. Marine Ecology Progress Series 229, 221–232.

Heinemann, D., 1981. A range-finder for pelagic bird censusing. Journal of Wildlife Management 45, 489–493.

Hilborn, R., Mangel, M., 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton.

Hodum, P.J., Sydeman, W.J., Visser, G.H., Weathers, W.W., 1998. Energy expenditure and food requirement of Cassin's Auklets provisioning nestlings. Condor 100, 546–550.

Holbrook, S.J., Schmitt, R.J., Stephens Jr., J.S., 1997. Changes in an assemblage of temperate reef fishes associated with a climatic shift. Ecological Applications 7, 1299–1310.

Horne, J.K., Smith, P.E., 1997. Space and time scales in Pacific hake recruitment processes: latitudinal variation over annual cycles. California Cooperative Oceanic Fisheries Investigations Reports 38, 90–102.

Hunt Jr., G.L., Pitman, R.L., Naughton, M., Winnet, K., Newman, A., Kelly, P.R., Briggs, K.T., 1981. Distributions, status, reproductive ecology, and foraging habits of breeding seabirds and seasonal status of seabirds of the southern California Bight. Investigators' Reports. Book 2, Part III: Summary of Marine Mammal and Seabird Surveys of the Southern California Bight Area, 1975–78. US Natl. Tech. Info. Serv. Publ. PD-81-148-205, pp. 1–399.

Hyrenbach, K.D., 2001. Marine bird distribution and abundance off southern California: pattern and process at multiple scales. Ph.D. Dissertation, University of California, San Diego.

Jahncke, J., Goya, E., 2000. Responses of three booby species to El Niño 1997–1998. Waterbirds 23, 102–108.

Johst, K., Wissel, C., 1997. Extinction risk in a temporally correlated fluctuating environment. Theoretical Population Biology 52, 91–100.

Jones, C., 2000. Sooty Shearwater (*Puffinus griseus*) breeding colonies on mainland South Island, New Zealand: evidence of decline and predictors of persistence. New Zealand Journal of Zoology 27, 327–334.

Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., Picaut, J., 1997. El Niño Southern Oscillation and tuna in the western Pacific. Nature 389, 715–718.

Levitus, S., Antonov, J.I., Boyer, T.P., Stephens, C., 2000. Warming of the world ocean. Science 287, 2225–2229.

Lubchenco, J.S., Navarrete, S., Tissot, B.N., Castilla, J.C., 1993. Possible ecological responses to global climate change: nearshore benthic biota of northeastern pacific coastal ecosystems. In: Mooney, H.A. (Ed.), Earth System Responses to Global Change: Contrasts Between North and South America. Academic Press, San Diego, pp. 147–165.

Lynn, R.J., 1986. The subarctic and northern subtropical fronts in the Eastern North Pacific Ocean in Spring. Journal of Physical Oceanography 16, 209–222.

Lynn, R.J., Bliss, K.A., Eber, L.E., 1982. Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-t, stability, dynamic height, oxygen and oxygen saturation in the California Current, 1950–1978. California Cooperative Oceanic Fisheries Investigations Atlas 30, 1–513.

Lynn, R.J., Schwing, F.B., Hayward, T.L., 1995. The effect of the 1991–93 ENSO on the California Current System. California Cooperative of Oceanic Fisheries Investigations Reports 36, 57–71.

Lynn, R.J., Baumgartner, T., Garcia, J., Collins, C.A., Hayward, T.L., Hyrenbach, K.D., Mantyla, A.W., Murphree, T., Shankle, A., Schwing, F.B., Sakuma, K.M., Tegner, M.J., 1998. The state of the California Current 1997–1998: transition to El Niño conditions. California Cooperative of Oceanic Fisheries Investigations Reports 39, 25–50.

Lyver, P.O., Moller, H., Thompson, C., 1999. Changes in Sooty Shearwater *Puffinus griseus* chick production and harvest precede ENSO events. Marine Ecology Progress Series 188, 237–248.

Manly, B.F.J., 1991. Randomization and Monte Carlo Methods in Biology. Chapman and Hall, London.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Metereological Society 78, 1069–1079.

McGowan, J.A., 1985. El Niño 1983 in the Southern California Bight. In: Wooster, W.S., Fluharty, D.L. (Eds.), El Niño North: El Niño Effects in the Subarctic Pacific Ocean. University of Washington, Seattle, pp. 166–184.

McGowan, J.A., Chelton, D.B., Conversi, A., 1996. Plankton patterns, climate, and change in the California Current. California Cooperative Oceanic Fisheries Investigations Reports 37, 45–68.

McGowan, J.A., Cayan, D.R., Dorman, L.M., 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281, 210–217.

Miller, A.J., Cayan, D.R., Barnett, T.P., Graham, N.E., Oberhuber, J.M., 1994. The 1976–77 climate shift of the Pacific Ocean. Oceanography 7, 21–26.

Montevecchi, W.A., Myers, R.A., 1995. Prey harvest of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Marine Ecology Progress Series 117, 1–9.

Moser, H.G., Smith, P.E., 1993. Larval fish assemblages of the California Current region and their vertical and horizontal distributions across a front. Bulletin of Marine Science 53 (2), 645–691.

Murphy, R.C., 1936. The oceanic birds of South America. American Museum of Natural History, New York.

Norton, J.G., Crooke, S.J., 1994. Occasional availability of dolphin, *Coryphaena hippurus*, to southern California commercial passenger fishing vessel anglers: observations and hypotheses. California Cooperative Oceanic Fisheries Investigations Reports 35, 230–239.

Oedekoven, C.S., Ainley, D.G., Spear, L.B., 2001. Variable responses of seabirds to change in marine climate: California Current, 1985–1994. Marine Ecology Progress Series 212, 265–281.

Pennycuick, C.J., 1987. Flight of seabirds. In: Croxall, J.P. (Ed.), The Feeding Ecology of Seabirds and Their Role in Marine Ecosystems. Cambridge University Press, Cambridge, pp. 43–62.

Peterson, C.H., Barber, R.T., Skilleter, G.A., 1993. Global warming and coastal ecosystem response: how northern and southern hemispheres may differ in the Eastern Pacific Ocean. In: Mooney, H.A. (Ed.), Earth System Responses to Global Change: Contrasts Between North and South America. Academic Press, San Diego, pp. 17–34.

Piatt, J.F., 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. Studies in Avian Biology 14, 36–51.

Polovina, J.J., Mitchum, G.T., Graham, N.E., Mitchell, P.C., DeMartini, E.E., Flint, E.B., 1994. Physical and biological consequences of a climate event in the Central North Pacific. Fisheries Oceanography 3, 15–21.

Pyle, P., 2001. Age of first breeding and natal dispersal in a declining population of Cassin's Auklet. Auk 118, 996–1007.

Reid, J.L., Roden, G.I., Willie, J.G., 1958. Studies of the California Current System. California Cooperative of Oceanic Fisheries Investigations Reports 5, 27–57.

Ribic, C.A., Ainley, D.G., Spear, L.B., 1992. Effects of El Niño and La Niña on seabird assemblages in the equatorial Pacific. Marine Ecology Progress Series 80, 109–124.

Roemmich, D., 1992. Ocean warming and sea level rise along the southwest US coast. Science 257, 373–375.

Roemmich, D., McGowan, J.A., 1995a. Climatic warming and the decline of zooplankton in the California Current. Science 267, 1324–1326.

Roemmich, D., McGowan, J.A., 1995b. Sampling zooplankton: correction. Science 268, 352–353.

Sagarin, R.D., Barry, J.P., Gilman, S.E, Baxter, C.H., 1999. Climate-related change in an intertidal community over short and long time scales. Ecological Monographs 69, 465–490.

Schneider, D.C., Duffy, D.C., 1985. Scale-dependent variability in seabird abundance. Marine Ecology Progress Series 25, 211–218.

Schneider, D.C., Piatt, J.F., 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Marine Ecology Progress Series 32, 237–246.

Schwing, F.B., Hayward, T.L., Sakuma, K.M., Murphee, T., Mascarenas, A.S., Larios Castillo, S.I., Mantyla, A.W., Cummings, S.L., Chavez, F.P., Baltz, K., Ainley, D.G., 1997. The state of the California Current, 1996–1997: mixed signals from the tropics. California Cooperative Oceanic Fisheries Investigations Reports 38, 22–47.

Schreiber, R.W., Schreiber, E.A., 1984. Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 perspectives. Science 225, 713–716.

Scofield, R.P., 2001. Sooty Shearwater (*Puffinus griseus*) survival in unharvested populations. Ph.D. Dissertation, University of Otago, New Zealand.

Smith, P.E., 1985. A case history of an anti-El Niño to El Niño transition on plankton and nekton distributions and abundances. In: Wooster, W.S., Fluharty, D.L. (Eds.), El Niño North: El Niño Effects in the Subarctic Pacific Ocean. University of Washington, Seattle, pp. 121–142.

Smith Jr., K.L., Kaufmann, R.S., 1999. Long-term discrepancy between food supply and demand in the deep Eastern North Pacific. Science 284, 1174–1177.

Smith, P.E., Moser, H.G., 2000. The effects of basin-wide climatic shifts on four California Current recurrent groups of fish larvae. Abstract 120, Section 2. Beyond El Niño: A Conference on Pacific Climate Variability and Marine Ecosystem Impacts, from the Tropics to the Arctic. March 23–26, 2000. La Jolla, California.

Spear, L.B., Ainley, D.G., 1998. Morphological differences relative to ecological segregation in petrels (Family: Procellariidae) of the Southern Ocean and Tropical Pacific. Auk 115, 1017–1033.

Spear, L.B., Ainley, D.G., 1999. Migration routes of Sooty Shearwaters in the Pacific Ocean. Condor 101, 205–218.

Squire, J.L., 1987. Relation of sea surface temperature changes during the 1983 El Niño to the geographical distribution of some important recreational pelagic species and their catch temperature parameters. Marine Fisheries Review 49 (2), 44–57.

Sund, P.N., Blackburn, M., Williams, F., 1981. Tunas and their environment in the Pacific: a review. Oceanography and Marine Biology Annual Reviews 19, 443–512.

Sverdrup, H.U., Johnson, M.J., Fleming, R.H., 1942. The Oceans: Their Physics, Chemistry and General Biology. Prentice Hall, Englewood Cliffs.

Sydeman, W.J., Hester, M.M., Thayer, J.A., Gress, F., Martin, P., Buffa, J., 2001. Climate change, reproductive performance and diet composition of marine birds in the California Current system, 1969–1997. Progress in Oceanography 49, 309–329.

Tasker, M.L., Jones, P.H., Dixon, T., Blake, B.F., 1984. Counting seabirds at sea from ships: a review of the methods employed and a suggestion for a standardized approach. Auk 101, 567–577.

Tegner, M.J., Dayton P, K., Edwards, P.B., Riser, K.L., 1996. Is there evidence for long-term climatic change in southern California kelp forests? California Cooperative Oceanic Fisheries Investigations Reports 37, 111–126.

Tyler, W.B., Briggs, K.T., Lewis, D.B., Ford, R.G., 1993. Seabird distribution and abundance in relation to oceanographic processes in the California Current System. In: Vermeer, K., Briggs, K.T., Morgan, K.H., Siegel-Causey, D. (Eds.), The Status, Ecology, and Conservation of Marine Birds of the North Pacific. Canadian Wildlife Service, Ottawa, pp. 48–60.

Veit, R.R., Pyle, P., McGowan, J.A., 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current System. Marine Ecology Progress Series 139, 11–18.

Veit, R.R., McGowan, J.A., Ainley, D.G., Wahl, T.R., Pyle, P., 1997. Apex marine predator declines ninety percent in association with changing oceanic climate. Global Change Biology 3, 23–28.

Venrick, E.L., McGowan, J.A., Cayan, D.R., Hayward, T.L., 1987. Climate and chlorophyll a: long-term trends in the Central North Pacific. Science 238, 70–72.

Wahl, T., Tweit, B., 2000. Seabird abundances off Washington, 1972–1998. Western Birds 31, 69–88.

Wahl, T.R., Ainley, D.G., Benedict, A.H., DeGange, A.R., 1989. Association between seabirds and water masses in the northern Pacific Ocean in summer. Marine Biology 103, 1–11.

Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall, New Jersey.