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Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997

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Abstract

We studied the effects of low-frequency climate change on the reproductive performance of 11 species of marine bird in the southern California Current system, 1969–1997. Reproductive performance of Brown Pelican (*Pelecanus occidentalis*) and Double-crested Cormorant (*Phalacrocorax auritus*) in southern California demonstrated an increase in the 1970s and early 1980s, attributable to recovery from organochlorine contamination (primarily DDE). Brandt's Cormorant (*Phalacrocorax penicillatus*) in central California was the only species to demonstrate a secular increase in performance through time, a pattern that remains unexplained. Ashy Storm-petrel (*Oceanodroma homochroa*) and Pelagic Cormorant (*Phalacrocorax pelagicus*) demonstrated curvilinear patterns of change, with decreasing reproductive performance in the past decade. All other species including Western Gull (*Larus occidentalis*), Pigeon Guillemot (*Cephus columba*), Xantus's Murrelet (*Synthliboramphus hypoleucus*), Common Murre (*Uria aalge*), Cassin's Auklet (*Ptychoramphus aleuticus*) and Rhinoceros Auklet (*Cerorhinca monocerata*) showed diminishing reproductive performance through time. Patterns of change for the murre and auklets were not significant, presumably because of a lack of reproductive variation for these species, which display a conservative breeding effort (i.e. single-egg clutches). Changes in the birds' abilities to provision young and maintain chick survival during May–July each year appeared most closely related to overall changes in reproductive performance. Dietary change indicated a decline in use of juvenile rockfish (*Sebastes* spp.) by marine birds in central California. There was also significant interannual variability in consumption of juvenile rockfish and the euphausiid *Thysanoessa spinifera*. Patterns of change in marine bird reproductive performance were generally concordant between southern and central California after considering the period of recovery for Brown Pelican and Double-crested Cormorant. The decline in reproductive performance and changes in diet composition do not appear directly related to the polarity reversal of the Pacific Decadal Oscillation

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in 1976/1977. Instead, reproductive performance and dietary characteristics indicate substantial change in the late 1980s, suggesting another regime-shift at that time. © 2001 Elsevier Science Ltd. All rights reserved.

Contents

1. Introduction	310
2. Methods	312
2.1. Components of productivity	313
2.2. Diet composition	314
2.3. Statistical analyses	314
3. Results	314
3.1. Temporal trends in reproductive performance—central California	314
3.2. Temporal trends in reproductive performance—southern California	317
3.3. Components of performance—SFI seabird community	317
3.4. Diet composition	318
4. Discussion	319
Acknowledgements	327
References	327

1. Introduction

In recent years, much has been written about low-frequency (i.e., >year-to-year) spatial and temporal change in physical and biological attributes of Pacific Ocean coastal marine ecosystems (Bakun, 1990; McGowan, 1990; Beamish & Bouillon, 1993; Miller, Cayan, Barnett, Graham, & Oberhuber, 1994; Francis & Hare, 1994; MacCall, 1996; Hayward, 1997; Mantua, Hare, Zhang, Wallace, & Francis, 1997; Zhang, Wallace, & Battisti, 1997). In particular, a mid 1970s climate event associated with a shift in location and intensification of the Aleutian Low pressure system has been the subject of numerous reports. This broad-scale event resulted in increased westerly winds along the North American continent, increased coastal ocean surface temperatures, and altered thermocline depths throughout much of the north Pacific Ocean (Graham, 1994; Trenberth & Hurrell, 1994). Mantua et al. (1997) and Zhang et al. (1997) extended these observations by analyzing a variety of climatological variables from the Pacific basin, finding general coherency in patterns of environmental and biotic change on interdecadal time scales. They coined the term ‘Pacific Decadal Oscillation’ (PDO) for the change in state associated with intensification of the Aleutian Low, and concluded that polarity reversals of the PDO have had major effects on ecosystem productivity throughout the Pacific Ocean during the past century. Reversals of the PDO state occurred in the mid 1920s, late 1940s, and mid 1970s thereby suggesting a half-cycle of ~25 yr to the PDO and corresponding ecosystem production regimes.

The California Current system (CCS) is a large marine ecosystem extending from southern British Columbia to Point Conception, California (Hickey, 1979). The southern CCS has been the subject of much investigation concerning climate change and ecosystem response; sea level, sea surface temperature, and biological characteristics of California coastal waters have continued to increase and/or change throughout the 1990s (Roemmich, 1992; Roemmich & McGowan, 1995; Hayward, 1997). Reports from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program have demonstrated significant reductions in many populations of mid- and upper-trophic level organisms; zooplankton biomass declined by as much as 80% from 1951 to 1995 (Roemmich & McGowan, 1995; Hayward, 1997), and some pelagic marine bird populations, notably Sooty Shearwaters (*Puffinus griseus*), decreased as much as 90% from 1987 to 1994 (Veit, Pyle, & McGowan, 1996). Other species, such as Pacific sardine (*Sardinops sajax*) have increased (MacCall, 1996).

To date, studies in the southern CCS have tended to focus on ecosystem response to climate change in the Southern California Bight and adjacent areas (many based on the CalCOFI program). Ecosystem response at more northerly latitudes may or may not be similar. Mesoscale physical processes vary temporally and spatially with latitude in the CCS (GLOBEC, 1992), influencing ecosystem productivity on relatively small spatial scales. In central and northern California marine productivity may remain stable near upwelling centers (e.g., coastal promontories) if the timing and intensity of this process has remained favorable to food web development through time. Alternatively, ecosystem response near highly productive upwelling centers may be accentuated as a result of interactions between mesoscale and basin-wide oceanographic processes. Because time-series data on biological attributes of central and northern California waters are limited, few reports have discussed low-frequency ecosystem response in this region. Barry, Baxter, Sagarin, and Gilman (1995) investigated compositional changes in rocky intertidal communities in Monterey Bay and found species-specific changes in abundance related to species' zoogeographical affinities; many southern species increased through time, while northern species decreased. Ainley, Veit, Allen, Spear, and Pyle (1995b) demonstrated interannual variability in the pelagic marine bird community from Monterey Bay through the Gulf of the Farallones from 1986 to 1994; however, trends between southern and northern species were inconsistent. Notably, both pelagic bird studies (Ainley et al., 1995b; Veit et al., 1996) occurred entirely within the warm regime that dominated the CCS after 1976/1977.

In relation to revealing the potential influence of regime shifts and ecosystem change on marine birds, the time-series examined to date are limited in duration. In the highly variable southern CCS, research based on time-series of 10 yr or less will suffer from an inability to distinguish interannual from longer-term trends. Moreover, both pelagic seabird projects reported above were initiated in the mid 1980s, years of relatively high ecosystem productivity in the southern CCS (Hayward et al., 1996). Therefore, there may be problems with overly-influential data points early in each time-series, especially given the use of regression analyses to infer trends. Marine bird population size and density estimates at sea may be less sensitive to changes in oceanic conditions than other population parameters such as fecundity (reproductive performance) and/or behavioral attributes (Cairns, 1987; Furness & Monaghan, 1987; Montevecchi, 1993; Monaghan, 1996). Life histories of many marine bird species are conservative; adult survival is maximized at the expense of reproduction (Erikstad, Fauchald, Tverra, & Steen, 1998), and reproductive and behavioral parameters fluctuate on a similar time scale in response to environmental changes. As shown by

Veit et al. (1996), changes in seabird populations lag behind environmental change, thereby suggesting that estimates of abundance are potentially less useful as a real-time indicator of climatic events than demographic parameters.

Marine bird reproductive performance (the number of offspring produced per breeding pair per year) varies significantly on interannual (Montevecchi, 1993; Ainley, Sydeman, & Norton, 1995a) and longer time scales (Aebischer, Coulson, & Colebrook, 1990; Polovina et al., 1994). Marine bird reproductive performance fluctuates in relation to prey availability (Anderson, Gress, & Mais, 1982; Ainley et al., 1995a). Most seabirds feed extensively on macrozooplankton (e.g., copepods and euphausiids), small schooling fish (e.g., anchovy, sardine, sandlance, herring etc.), 0-age class large predatory fish (e.g., salmonids, hake, rockfishes) or other invertebrates (squids). Therefore, the reproductive performance of marine birds at colony sites can be used as a biological indicator of change in prey populations. If studies are of sufficient duration, seabird reproductive performance should provide information on ecosystem response on multiple time scales (interannual to interdecadal). The reproductive performance of many seabirds is easily measured, and provides real-time information on feeding conditions for breeding birds, from the initiation of reproduction through incubation of eggs and caring for dependent young, which often lasts for 6+ months. Therefore, this parameter serves as an integrated measurement of prey availability over a substantial period of time within each year.

Herein, we examine temporal trends in the reproductive performance of marine birds from the southern CCS including information from the Southern California Bight and central California upwelling domain. We analyzed data collated from seabird monitoring programs conducted by Point Reyes Bird Observatory (PRBO) and U.S. Fish and Wildlife Service (USFWS) on the Farallon Islands in central California, and by Channel Islands National Park (CINP), PRBO, and the University of California at Davis (UCD) on Santa Barbara and West Anacapa islands in southern California. Our goals are:

1. To establish the significance of species-specific trends in reproductive performance in relation to the mid 1970s climate change event;
2. To examine components of reproductive performance (i.e., number of eggs laid, proportion of eggs hatched, and proportion of chicks raised to independence) to determine which life history stage is most closely associated with changes in overall reproductive performance,
3. To examine concordance in performance patterns between species and oceanographic domains in the southern CCS; and
4. To evaluate dietary characteristics and how changes in prey use may be related to long-term ecosystem changes.

2. Methods

We monitored reproductive performance of 11 species at the following locations: Ashy Storm-petrel *Oceanodroma homochroa* (Southeast Farallon Island; SFI), Brandt's Cormorant, *Phalacrocorax penicillatus* (SFI), Pelagic Cormorant, *P. pelagicus* (SFI), Double-crested Cormorant, *P. auritus* (West Anacapa Island; WAI), Brown Pelican *Pelicanus occidentalis* (WAI), Western Gull

Larus occidentalis (Santa Barbara Island; SBI, and SFI), Common Murre *Uria aalge* (SFI), Pigeon Guillemot, *Cephus columba* (SFI), Cassin's Auklet, *Ptychoramphus aleuticus* (SFI), Xantus's Murrelet, *Synthiloboramphus hypoleucus* (SBI), and Rhinoceros Auklet, *Cerorhinca monocerata* (SFI). General life history and foraging characteristics for each species is provided (Table 1). With the exception of Brown Pelican and Double-crested Cormorant, a sample of focal breeding pairs was studied throughout each nesting season at each colony to determine reproductive performance. For each species, individual nest sites were monitored ($n=15\text{--}500$ nests per species per year) at 1–7 day intervals for breeding activity. Fledging was assumed with departure of young from the colony. Reproductive performance was defined as the number of offspring departing the colony per breeding pair per year. For the Brown Pelican and Double-crested Cormorant, reproductive performance was assessed by conducting whole-colony counts of the number of large young and total number of nests each year; reproductive performance was then calculated as the number of large young divided by the total number of nesting attempts.

2.1. Components of productivity

We examined interannual variability in components of reproductive performance: mean clutch size, mean hatching success, and mean fledging success for species breeding on SFI (this information is not available for most species in southern California). The number of eggs laid per breeding female was taken as a measure of clutch size. Hatching success was calculated as the proportion of eggs hatched; fledging success equaled the proportion of chicks hatched that eventually fledged. Clutch size provides information on the condition of females during the egg-laying period (early spring, March–April). Hatching success provides information concerning the birds' abilities to incubate, protect eggs, and find food during incubation (spring, April–May). Fledging

Table 1
Life-history and foraging characteristics of breeding marine bird populations in the California Current marine ecosystem

Species	Clutch size	Dispersion	Foraging habitat	Diet
Ashy Storm-petrel	1	Resident, endemic	Shelf break	Zooplankton, larval fish
Brandt's Cormorant	2–5	Resident, endemic	Neritic, estuaries	Fish
Pelagic Cormorant	2–5	Resident	Neritic, benthic	Fish
Double-crested Cormorant	2–4	Resident	Neritic, estuaries	Fish
Brown Pelican	1–3	Resident, endemic	Neritic, surface	Fish
Western Gull	1–3	Resident	Shelf	Zooplankton, fish, refuse
Common Murre	1	Resident	Shelf	Zooplankton, fish
Pigeon Guillemot	1–2	Migratory	Neritic, benthic	Fish
Cassin's Auklet	1	Resident	Shelf	Zooplankton, larval fish
Xantus's Murrelet	1–2	Resident, endemic	Shelf	Zooplankton, larval fish
Rhinoceros Auklet	1	Resident	Shelf break	Fish

success provides information concerning the birds' abilities to provision themselves and their young and protect young from predators during the nestling period (May–July).

2.2. *Diet composition*

To quantify food habits of birds breeding on SFI, we observed adults feeding chicks. Common Murres and Pigeon Guillemots carry single prey items in their beaks to provision chicks, and diet items can be identified, often to species, by observers situated in blinds near breeding colonies. We conducted observations on approximately 75–150 pairs of murres and 50–75 pairs of guillemots throughout the chick-rearing period (murres: late May through early July; guillemots: late June through mid-August) each year. To quantify food habits of Rhinoceros Auklets, we collected food items from adults captured in mist nets opened near dusk, monitored continuously (~1.5 h), and closed just after night fall. We conducted at least three capture sessions at each of three locations on SFI from 15 June to 30 August. Diet of Cassin's Auklets was based on 50–100 regurgitations collected each year from parents returning to feed chicks at night. We attempted to obtain 10 diet samples every 7–10 days throughout the chick-rearing period (mid-May through July) each year. Each regurgitation was weighed and frozen for analysis. During analysis, otoliths, squid beaks, and whole bodies of crustaceans were separated, identified and enumerated; to aid identifications we used collections maintained at PRBO, Southwest Fisheries Science Center (La Jolla, California) or Moss Landing Marine Laboratory (Moss Landing, California). Analysis of Cassin's Auklet diet composition for the years 1993–1997 was performed by M. Galbraith at the Institute of Ocean Sciences (Sidney, British Columbia).

2.3. *Statistical analyses*

We used robust locally weighted regression (LOWESS, Cleveland, 1993) with 90% band widths to illustrate trends in reproductive performance for each species at each location through time. Trends in reproductive performance were tested using the Cochran–Orcutt regression procedure; year and year-squared were considered in analyses to test for curvature in time trends. The Cochran–Orcutt procedure estimates a linear regression for the dependent variable (reproductive performance) against an independent variable (year) that is corrected for serially correlated residuals using the Cochran–Orcutt iterative process (Chatterjee & Price, 1991). We used Principal Component Analysis (PCA) to build a marine bird community response variable encompassing the reproductive performance of each species on SFI from 1972 to 1997. We did not use PCA for the southern California time-series because each series differed in longevity. Trends in principal components through time were tested. Statistical tests were performed using the package STATA (Anon, 1997); *P*-values of <0.05 were assumed to be significant.

3. Results

3.1. *Temporal trends in reproductive performance—central California*

The reproductive performance of SFI seabirds reveals dissimilar patterns of change among species. Patterns appear related to species-specific foraging costs and life history strategies.

Among species laying a single-egg clutch each year, only the Ashy Storm-petrel showed a significant pattern of change in reproductive performance through time (Table 2); for this species, reproductive performance increased slightly through the mid 1980s and decreased sharply thereafter [Fig. 1(a)]. Patterns of change for Common Murre [Fig. 1(b)], Cassin's Auklet [Fig. 1(c)] and Rhinoceros Auklet [Fig. 1(d)] were all not significant. However, LOWESS regression lines and linear regression coefficients (β) for each species were negative; for Cassin's Auklet, reproductive performance tended to increase slightly in the late 1990s.

For species laying more than one egg per clutch, each demonstrated significant time-trends in reproductive performance, but patterns of change varied (Table 2). Brandt's Cormorant was the only species to demonstrate an increase in productivity through time [Fig. 2(a)]; this relationship was significant when excluding the severe El Niño years of 1983 and 1992 ($\beta_1=0.038$, $P=0.006$, $n=24$). Reproductive failure in El Niño years was due to near-zero breeding effort (i.e., very few nest attempts) rather than a major drop in performance after egg laying per se. Similarly, breeding effort in the Pelagic Cormorant was essentially zero in 1978, 1983, 1990, and 1992. Excluding these years, reproductive performance followed a pattern of increase through the mid-1980s, followed by a decline thereafter [$\beta_1=0.675$, $P=0.034$, $\beta_2=-0.004$, $P=0.033$, $n=22$; Fig. 2(b)]. Reproductive performance of Western Gull [Fig. 2(c)] and Pigeon Guillemot [Fig. 2(d)] demonstrated significant linear decreases through time (Table 3).

PCA resulted in two significant principal components, one that we interpreted to reflect all species except the storm-petrel, and the second which appeared to reflect mostly storm-petrel reproductive performance (Table 3). This analysis revealed a linear decline in the marine bird

Table 2

Results of Cochrane–Orcutt regression analyses on time-trends in reproductive performance for seabirds in central and southern California. Results from linear and quadratic regression analyses (coefficients and P values) are reported for each species^a

	Linear	Quadratic
<i>a. Central California</i>		
Ashy Storm-petrel	-0.005 (0.436)	0.238 (0.033); -0.001 (0.031)
Common Murre	-0.006 (0.336)	ns
Cassin's Auklet	-0.005 (0.326)	ns
Rhinoceros Auklet	-0.014 (0.310)	nd
Brandt's Cormorant	0.031 (0.108)	ns
Pelagic Cormorant	-0.008 (0.545)	ns
Western Gull	-0.037 (0.001)	ns
Pigeon Guillemot	-0.018 (0.013)	ns
<i>b. Southern California</i>		
Western Gull	-0.071 (<0.001)	nd
Xantus's Murrelet	-0.034 (0.017)	nd
Brown Pelican ^b	0.010 (0.391)	ns
Double-crested Cormorant	0.058 (0.001)	0.805 (0.025); -0.005 (0.039)

^a ns: neither coefficient varied from zero ($P>0.05$); nd: not determined due to length of time-series.

^b A regression including year, year-squared, and year-cubed was significant [$\beta_1=6.04$, $P=0.043$, $\beta_2=-0.070$, $P=0.048$, $\beta_3=0.0003$, $P=0.050$; refer to Fig. 3(c)].

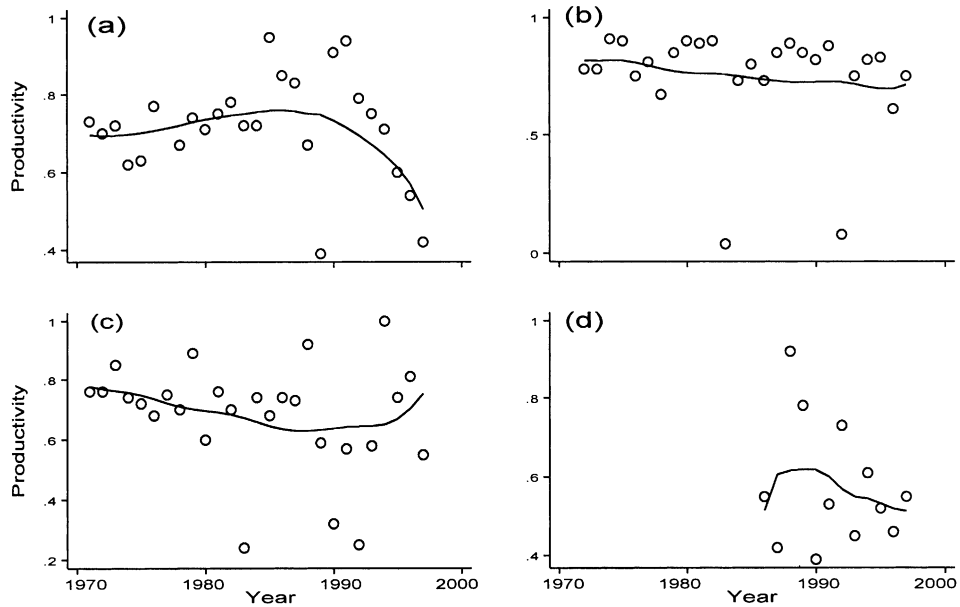


Fig. 1. Interdecadal temporal trends in the reproductive performance of species laying a single egg per clutch at Southeast Farallon Island (SFI): (a) Ashy Storm-petrel; (b) Common Murre; (c) Cassin's Auklet; and (d) Rhinoceros Auklet. Points show mean annual values of reproductive performance. Lines reflect robust locally weighted regressions (LOWESS) through time. See text for analytical details.

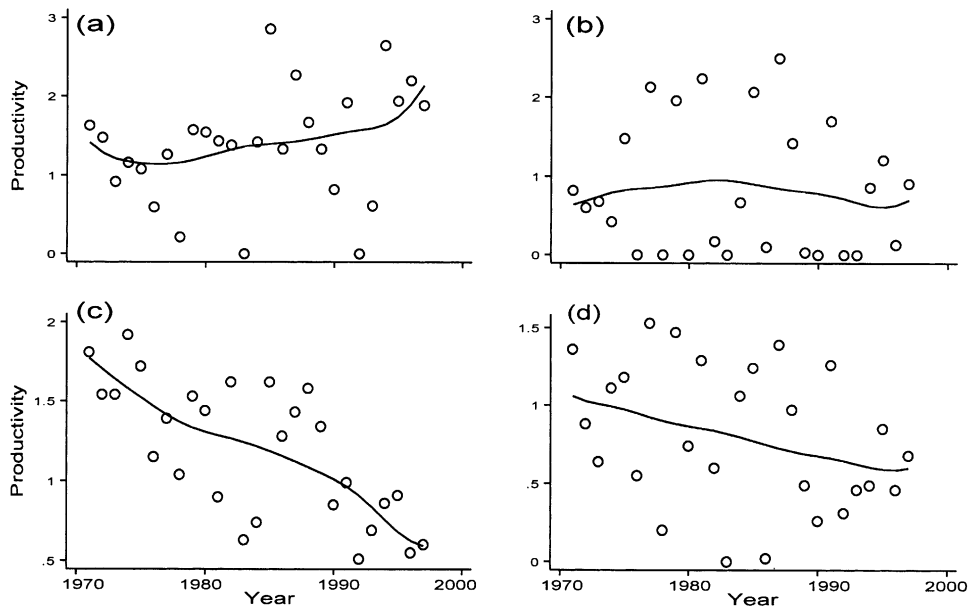


Fig. 2. Interdecadal temporal trends in the reproductive performance of species laying multiple eggs per clutch at SFI: (a) Brandt's Cormorant; (b) Pelagic Cormorant; (c) Western Gull; and (d) Pigeon Guillemot. See Fig. 1 for additional details.

Table 3

Results of principle components analysis (PCA) of reproductive performance of seven species of marine bird (excluding Rhinoceros Auklet due to length of time-series) on Southeast Farallon Island, 1972–1997. The year 1977 was excluded from analysis due to incomplete data

<i>a. Eigenvalues</i>	Eigenvalue	Proportion	Cumulative proportion
PC 1	3.56	0.51	0.51
PC 2	1.23	0.17	0.68
<i>b. Factor loadings</i>		PC 1	PC 2
Ashy Storm-petrel		0.04	0.77
Common Murre		0.43	–0.22
Cassin's Auklet		0.40	–0.35
Brandt's Cormorant		0.41	–0.11
Pelagic Cormorant		0.41	0.39
Western Gull		0.34	–0.06
Pigeon Guillemot		0.45	0.25

community reproductive performance over the past 25 yr, although the trend was not statistically significant ($\beta_1 = -0.047$, $P = 0.360$). On the other hand, the trend in PC2 was significant, and reflected the same pattern of increase and decrease as the time-series for the storm-petrel alone.

3.2. Temporal trends in reproductive performance—southern California

Time-series from southern California demonstrated significant temporal variation in reproductive performance. Western Gull [Fig. 3(a)] and Xantus's Murrelet [Fig. 3(b)] reproductive performance demonstrated a significant linear decline from 1985 to 1997 (Table 2). Brown Pelican and Double-crested Cormorant reproductive performance also varied significantly through time (Table 3). For pelicans, there was a significant increase through the mid 1980s and a slight decrease thereafter [Fig. 3(c)]. For cormorants the pattern was slightly different: overall, there was a linear increase in productivity which plateaued in recent years [Fig. 3(d)].

3.3. Components of performance—SFI seabird community

Change in Ashy Storm-petrel reproductive performance between 1971 and 1997 was related to significant changes in fledging success and non-significant variability in hatching success [Table 4, Fig. 4(a,b)]. Hatching success in the 1990s was low, and appears to be responsible for the decline in storm-petrel reproductive performance in recent years. Hatching and fledging success for Common Murres did not change significantly through time [Fig. 4(c,d)]. Hatching success was reduced to approximately 30% of eggs laid during El Niño 1983 and 1992, but in most years remained above 80%. Fledging success also was much reduced during El Niño, but was typically above 90%. The pattern of hatching success for Cassin's Auklets was similar to the murre, with little change through time except during severe oceanographic events [Fig. 4(e)]. However, fledging success dropped noticeably from the 1970s to the 1980s, and was then variable in the 1990s with four years (1991–1993, and 1997) showing success of about 65% and three others (1994–

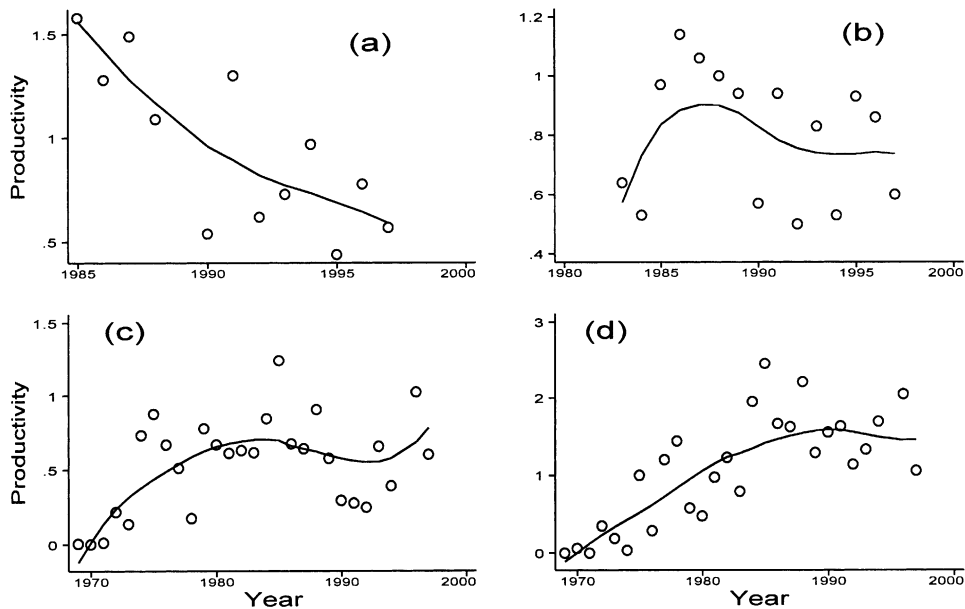


Fig. 3. Interdecadal temporal trends in the reproductive performance of marine birds in southern California (all laying multiple egg clutches): (a) Western Gull on Santa Barbara Island; (b) Xantus's Murrelet on Santa Barbara Island; (c) Brown Pelican on West Anacapa Island; and (d) Double-crested Cormorant on West Anacapa Island.

1996) demonstrating success of about 85% [Fig. 4(f)]. The year 1990 stands out as being anomalously low with fledging success of only 40%. Interannual variability in hatching and fledging success for Rhinoceros Auklets was considerable, but there were no temporal trends in either measurement [Fig. 4(g,h)].

For species laying more than one egg per clutch, we also examined temporal trends in mean clutch size. For Brandt's Cormorants, there was a significant increase in hatching success through time, but no change in clutch size or fledging success [Table 4, Fig. 5(a–c)]. For Pelagic Cormorants, fledging success followed a similar pattern to performance, increasing throughout the 1970s and early 1980s and decreasing thereafter; there was no systematic change, though there was considerable interannual variability, in clutch size and hatching success [Fig. 5(d–e)]. For Western Gulls [Fig. 5(g–i)] and Pigeon Guillemots [Fig. 5(j–l)], there were significant decreases in fledging success through time, but no significant trends in clutch size or hatching success. For both species, there was a slight change in clutch size, with this parameter increasing for the gull and decreasing for the guillemot.

3.4. Diet composition

Information concerning chick diet composition for Common Murre [Fig. 6(a)], Rhinoceros Auklet [Fig. 6(b)], and Pigeon Guillemot [Fig. 6(c)] revealed a similar pattern of use for juvenile rockfish (*Sebastes* spp.) as prey (although lack of time-series data for Rhinoceros Auklet prior to 1987 makes this pattern less obvious for that species). In all species, there was a decline in the use of rockfish during the 1990s. Prior to 1989, young-of-the-year rockfish were the primary prey

Table 4

Results of Cochrane–Orcutt regressions on components of reproductive performance for SEFI marine birds, 1971–1997. Results of linear and quadratic regression analyses (coefficients and *P* values) are presented. See Table 2 for explanations

	Linear	Quadratic
<i>a. Clutch size</i>		
Brandt's Cormorant	0.001 (0.885)	ns
Pelagic Cormorant	−0.021 (0.072)	ns
Western Gull	0.008 (0.109)	ns
Pigeon Guillemot	−0.009 (0.072)	ns
<i>b. Hatching success</i>		
Ashy Storm-petrel	−0.002 (0.684)	0.171 (0.074); −0.001 (0.071)
Common Murre	−0.003 (0.487)	ns
Cassin's Auklet	−0.002 (0.345)	ns
Rhinoceros Auklet	−0.010 (0.474)	nd
Brandt's Cormorant	0.010 (0.012)	ns
Pelagic Cormorant	−0.0001 (0.973)	ns
Western Gull	−0.001 (0.581)	ns
Pigeon Guillemot	−0.0002 (0.929)	ns
<i>c. Fledging success</i>		
Ashy Storm-petrel	0.005 (0.018)	0.098 (0.009); −0.001 (0.013)
Common Murre	−0.004 (0.424)	ns
Cassin's Auklet	−0.005 (0.164)	ns
Rhinoceros Auklet	−0.001 (0.952)	nd
Brandt's Cormorant	0.001 (0.857)	ns
Pelagic Cormorant ^a	0.380 (0.031)	0.380 (0.031); −0.002 (0.032)
Western Gull	−0.019 (0.001)	ns
Pigeon Guillemot	−0.010 (0.015)	ns

^a The years 1980, 1982, and 1986 were excluded from analysis because of small sample size; few nests were available for analysis because hatching success was low in these years.

fed to nestlings except during El Niño years (1973, 1976, 1983, 1986) and other years of anomalously warm-water (1978). After 1988, juvenile rockfish comprised 50% or less of the nestling diet for each species, except Rhinoceros Auklet in 1991 and Pigeon Guillemot in 1993. In years when juvenile rockfish were not utilized as prey, there was a corresponding increase in the use of alternative prey. For Cassin's Auklet, there was interannual variability in the use of the euphausiid *Thysanoessa spinifera*. This species was the dominant prey item in 1977, 1979, 1981, and 1995–1997 [Fig. 6(d)]. There was a corresponding increase in the use of alternative prey when *T. spinifera* was not used. The use of *T. spinifera* exceeded 80% of the diet composition in 1977 and 1996.

4. Discussion

In the southern CCS, upper trophic level predators have been shown to respond rapidly to basin-scale interannual variability in atmospheric–oceanographic conditions (Ainley et al., 1995a;

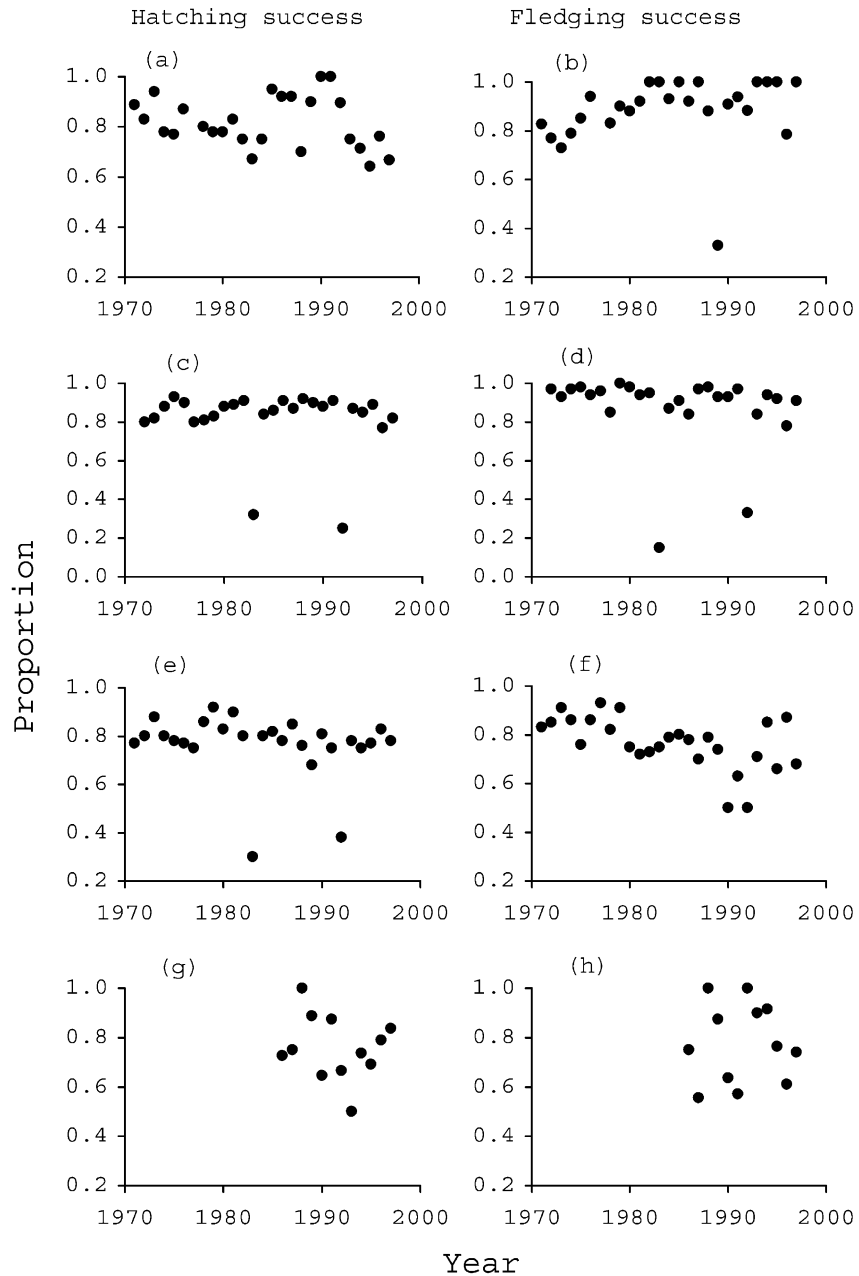


Fig. 4. Interdecadal changes in components of reproductive performance for SFI seabirds laying one egg per clutch. Illustrated are mean annual values of hatching success and fledging success for (a,b) Ashy Storm-petrel, (c,d) Common Murre, (e,f) Cassin's Auklet, and (g,h) Rhinoceros Auklet.

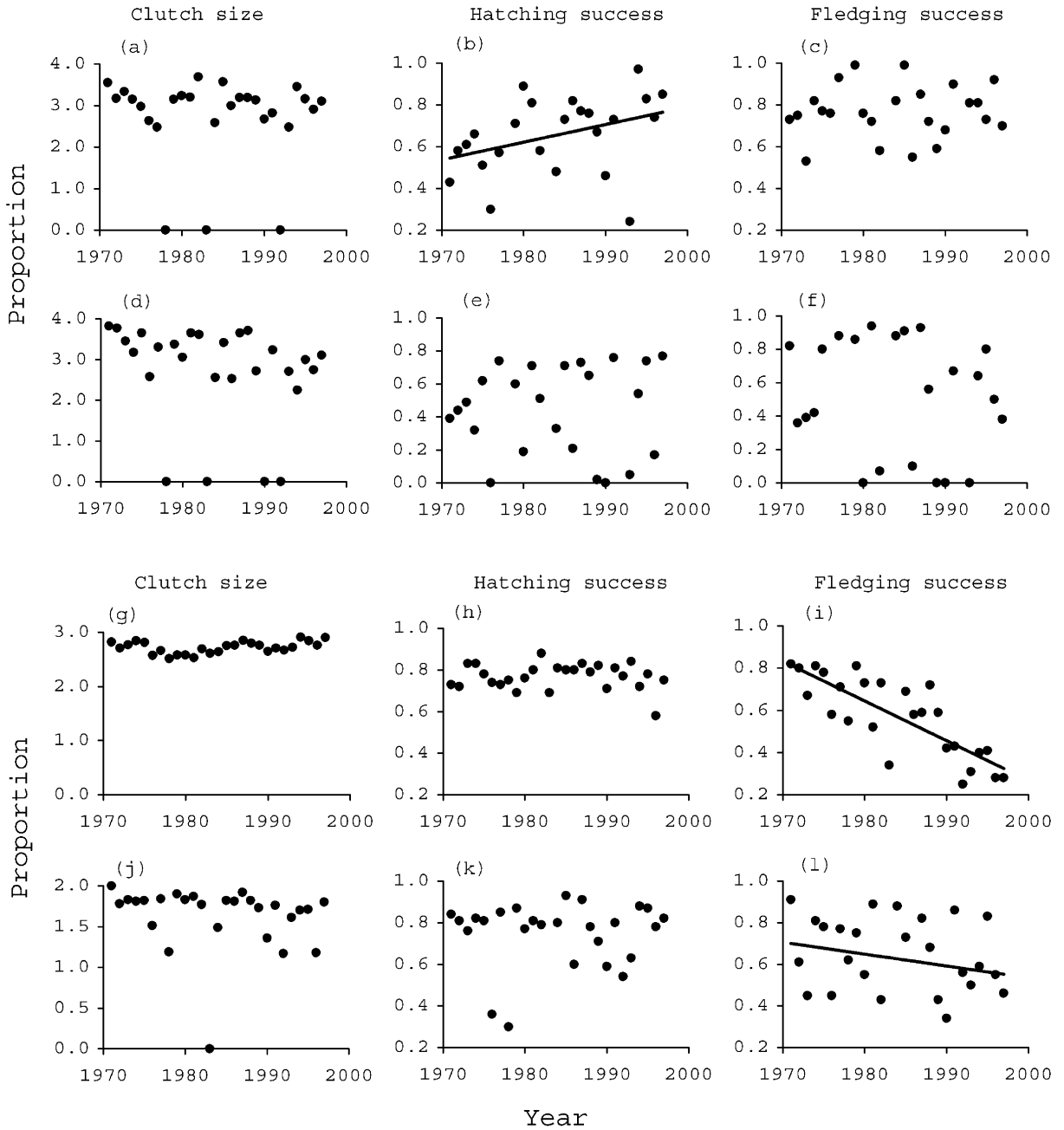


Fig. 5. Interdecadal changes in components of reproductive performance for SFI seabirds laying more than one egg per clutch. Illustrated are mean annual values of clutch size, hatching success and fledging success for (a–c) Brandt’s Cormorant, (d–f) Pelagic Cormorant, (g–i) Western Gull, and (j–l) Pigeon Guillemot.

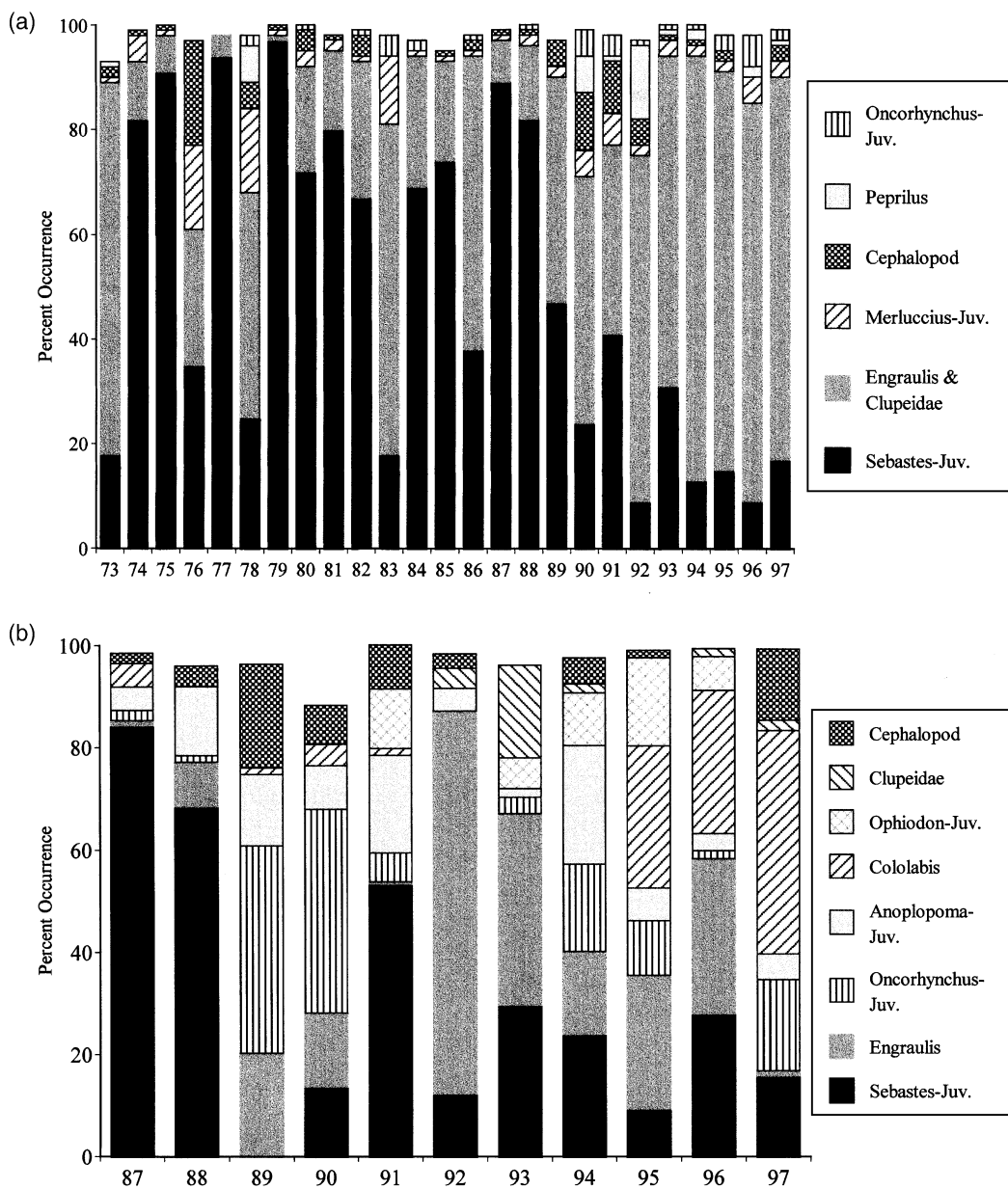


Fig. 6. Changes in the chick diet composition (% by number) for marine birds in central California, 1972–1997; (a) Common Murre, (b) Rhinoceros Auklet, (c) Pigeon Guillemot, and (d) Cassin's Auklet.

Veit et al., 1996; Sydeman & Allen, 1999). This study was developed to expand upon previous studies and to investigate the response of marine birds to lower-frequency (interdecadal) change, similar to that reported by Aebischer et al. (1990) for Black-legged Kittiwakes *Rissa tridactyla* in the North Atlantic Ocean. This study was also undertaken to compliment previous investigations of changes in the abundance of marine birds at-sea in relation to marine climate change (Ainley

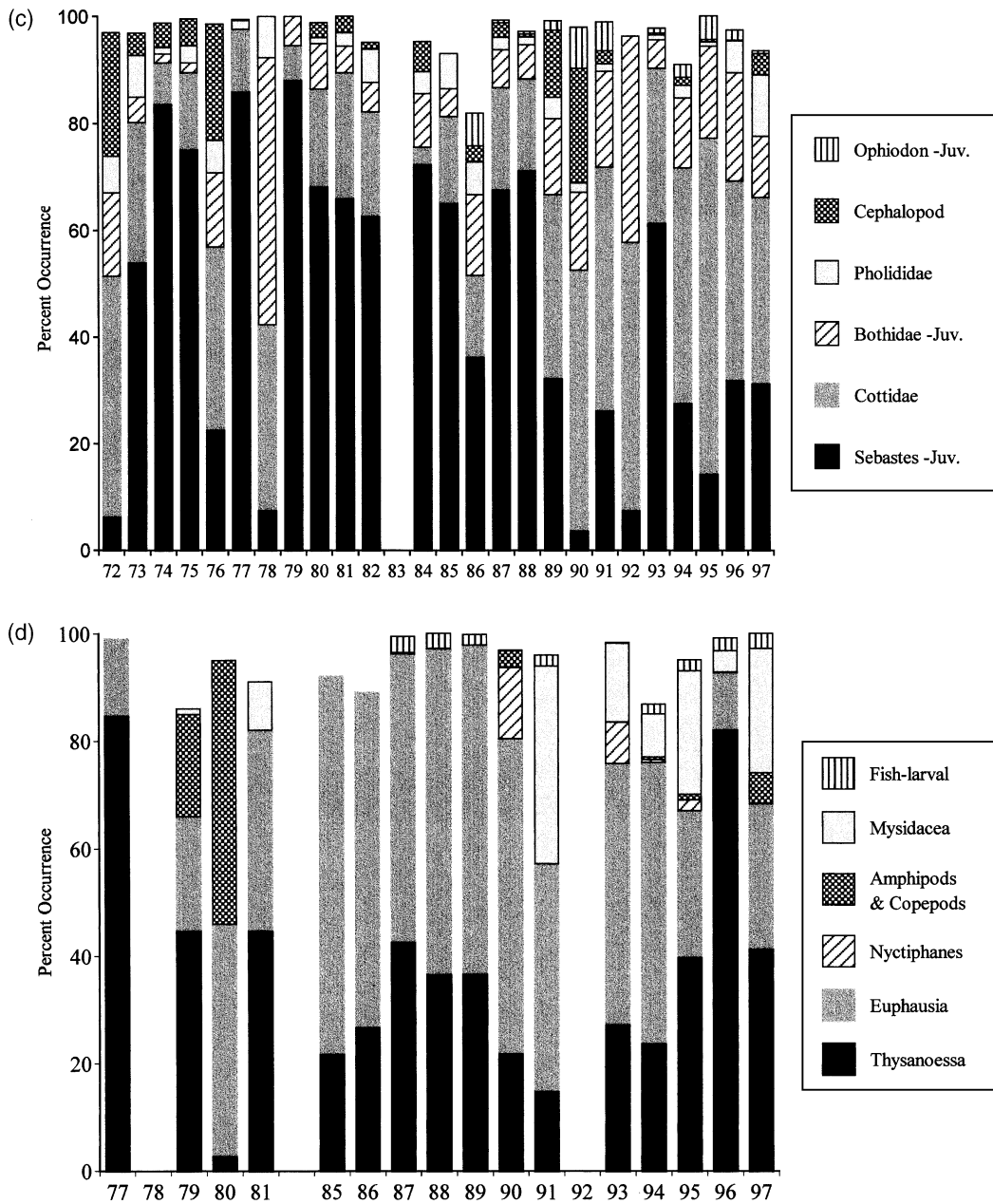


Fig. 6 (continued)

et al., 1995b; Veit et al., 1996). Some of the on-colony time-series presented herein (SFI and WAI) are of much longer duration (nearly 30 yr) than either time-series concerning birds at-sea in California. Therefore, in this study we were able to investigate change during the 1970s and early 1980s, as well as the mid 1980s to mid 1990s period. Finally, another objective was to

compare information on marine bird reproductive performance from the Southern California Bight and central California regions, oceanographic domains influenced by different physics and biophysical coupling mechanisms.

Ainley et al. (1995b) and Veit et al. (1996) demonstrated that one species, the Sooty Shearwater, had become less abundant in California waters between 1986/1987 and 1994. Temporal trends for other species were not as clear, with some species increasing in abundance, while there was little change for others. Ainley et al. (1995b) concluded that warm-water species increased in the upwelling-dominated, cold-water environment of central California during a period of recent ocean warming. Thus, similar to the conclusions of Barry et al. (1995), Ainley et al. (1995b) suggested that marine birds showed different patterns based on zoogeographic affinities. In our study, we expected to observe similar differences among the breeding bird community, especially when comparing species endemic to the California Current with others having their distribution centered at more northerly latitudes. We observed species-specific temporal differences in reproductive performance, but these trends are not consistent with a zoogeographical explanation. Although there were declining trends in the reproductive performance for the sub-arctic Common Murre, Cassin's Auklet, and Rhinoceros Auklet, these changes were not statistically significant, even though these cold-water species should have been strongly influenced by the ocean warming that occurred during the period. Murres and auklets have the most conservative life history strategy of all the study species in that they produce only a single egg per clutch (Ashy Storm-petrel also lays only one egg per clutch each year). Murres and auklets are also capable of foraging over large areas from the colony on daily provisioning trips.

Reproductive performance declined linearly and significantly for the Western Gull, Xantus's Murrelet, and Pigeon Guillemot. Moreover, there were significant curvilinear patterns, indicating decline after the mid 1980s, in the reproductive performance of the Ashy Storm-petrel and Pelagic Cormorant. Pigeon Guillemots and Pelagic Cormorants are widely distributed throughout the Pacific Rim, but they are the most neritic species, often foraging in benthic habitats close to breeding colonies. Foraging costs for these species may be high during the chick rearing phase of reproduction as they lay multi-egg clutches and make frequent provisioning trips to the nest each day (Ainley & Boekelheide, 1990). The Western Gull is nearly endemic to the CCS and has diverse foraging strategies, including the use of human refuse. SFI Western Gulls forage on euphausiids during the egg formation period, but switch to surface schools of 0-age class rockfish and anchovies during chick rearing (Ainley & Boekelheide, 1990; Sydeman, Hobson, Pyle, & McLaren, 1997). In southern California, changes for the Brown Pelican and Double-crested Cormorant were curvilinear, indicating, at best, that the pattern of increase in reproductive performance for these species ended in the mid-1980s. Patterns of change for these latter species reflect recovery from eggshell thinning caused by DDE (the metabolite of DDT) in the marine environment, rather than a positive change in oceanographic and prey conditions in the Southern California Bight in the 1970s (Gress, 1995). In summary, for all species except Brandt's Cormorant trends in reproductive performance appeared to be level or negative after the mid-1980s.

The result of increasing Brandt's Cormorant productivity is interesting. This species, like Ashy Storm-petrel, Western Gull, Xantus's Murrelet and Brown Pelican, is essentially endemic to the CCS. We are uncertain why Brandt's Cormorant shows a pattern different from the other species, but suspect it may relate to their foraging in estuarine and coastal neritic habitats. Nur and Sydeman (1999) found no indication of negative density-dependence in Brandt's Cormorant repro-

ductive performance, even though the SFI breeding population has decreased by about 50% since the early 1970s (PRBO unpublished data). Instead, this species may be using alternative prey resources that could explain relatively high levels of reproductive performance from 1994 to 1997 [Fig 2(a)]. We are uncertain what alternative prey they are now exploiting.

Information on components of reproductive success (clutch size, hatching success of eggs, and fledging success of chicks) indicates which life history stage is most closely associated with overall changes in reproductive performance. We identified the ability of birds to provision chicks, as well as themselves, as provided by mean annual values of fledging success, as a principal determinant of reproductive performance for Western Gulls, Pigeon Guillemots, and Pelagic Cormorants. Changes in hatching success, reflective of occurrences during incubation, apparently explained the positive change in reproductive performance of Brandt's Cormorants.

Prey availability is the primary determinant of variability in fledging success and overall reproductive performance for these species. First, consider the Pelagic Cormorant and Pigeon Guillemot. There is little evidence that predation plays a role in chick survival for these species on SFI (Ainley & Boekelheide, 1990). Guillemots nest in relatively small, protected cavities, where island predators, which on SFI are restricted to gulls, cannot enter. Pelagic Cormorants nest on isolated cliff ledges where aerial predators could be a problem. During the early chick phase when gulls could take exposed young, one parent remains at the site all the time. However, when prey availability diminishes, Pelagic Cormorants are one of the first species to leave young exposed and/or abandon nesting attempts entirely. Therefore, changes in food resources may result in changes in behavior that can lead to predation, but without deterioration in feeding conditions, predation would be unlikely to occur. Second, consider the Western Gull. This species nests on the open ground and can be cannibalistic towards neighboring offspring. However, except when dependent young become large, one parent almost always stays on the territory to protect chicks. Predation may occur when chicks wander from territories; previous studies have shown that wandering is more likely to occur when chicks are malnourished under poor feeding conditions (Hunt & Hunt, 1976). Therefore, even for gulls predation appears to be mediated via changes in marine prey availability. A similar mechanism has been hypothesized to account for the effects of predation on the reproductive performance of Xantus's Murrelets (Sydeman, 1999). More generally, Anderson et al. (1982) and Ainley et al. (1995a) provide quantitative relationships for the effect of varying prey resources on the reproductive performance for these seabird species. Long-term dietary information for the murre, auklets, and guillemot (Fig. 6) and direct measurements of change in zooplankton and some fish stocks (Roemmich & McGowan, 1995; MacCall, 1996) support the conclusion that changes in prey resources are leading to changes in seabird reproductive performance in the southern CCS.

To characterize the marine bird community response, we created a combined performance variable using PCA. We found an overall negative trend in marine bird reproductive performance, but the pattern did not appear as a step-wise change in reproductive performance in 1976/1977 that could be associated with change in the PDO at that time. However, our ability to resolve change in seabird reproductive performance is hampered by lack of time-series prior to 1976 (only 7 yr). Moreover, based on the PCA for SFI birds, an apparent peak in reproductive performance occurred in 1979, with all subsequent years falling below this value. Thus, it is possible that ecosystem response in central California, especially for upper trophic level organisms that may store fat and protein reserves, could be lagged to the 1976/1977 regime shift. Indeed 1977 and

1979 were highly productive years for marine birds in central California, whereas 1978 was one of the worst years on record next to the severe El Niños of 1983 and 1992 (Ainley et al., 1995a). Effects of the 1976/1977 event could be lagged to the prey resources for seabirds; in particular, rockfish juvenile production could have been increasing through this period as a result of good recruitment in the 1960s and early 1970s (A. MacCall, personal communication). Alternatively, upwelling characteristics that promote food web development in the vicinity of the SFI may have been favorable in these years, thereby masking effects of change in the PDO.

According to Polovina et al. (1994) and Polovina, Mitchum, and Evans (1995), the ecosystem-level effects of the 1976/1977 regime shift had ended by 1988, but this is apparently not true for the southern CCS. Roemmich and McGowan (1995), Hayward (1997), McGowan, Cayan, & Dorman (1998) and others have noted increases in ocean temperatures and corresponding ecosystem changes continuing through the mid 1990s. The marine bird diet and performance time-series for both southern and central California presented herein support these observations and also indicates continuing ecosystem changes through 1997. In recent years, there are hints of a positive trend in the reproductive performance for the planktivorous Cassin's Auklet and piscivorous Brandt's Cormorant and Brown Pelican. Therefore, based on a variety of time-series, from zooplankton to birds, indications are that low-frequency oceanographic change, which may or may not be related to the PDO, is still affecting the southern CCS.

Notably, our study indicates a noticeable change in diet composition for SFI seabirds starting in 1989. Prior to that time, variability in diet composition appeared to reflect change in oceanographic conditions and prey availability on the interannual time scale. Studies by the National Marine Fisheries Service (NMFS, Tiburon/Santa Cruz Laboratory) confirm the pattern illustrated by the marine bird diets by showing a decline in juvenile rockfish captured in standardized mid-water trawl surveys in central California after 1988 (S. Ralston et al., NMFS Santa Cruz Laboratory, unpublished data). One of the most interesting results of the dietary analyses concerns the use of the euphausiid *Nyctiphanes simplex* by breeding Cassin's Auklets to provision their chicks. In the southern CCS, the Cassin's Auklet is an obligate planktivore, though a very small percentage of its diet may be composed of larval fish and squid (Ainley, Spear, & Allen, 1996; Sydeman et al., 1997). The euphausiids *T. spinifera* and *E. pacifica* dominated the chicks' diet in almost all years, and before 1990, *N. simplex* had not been recorded in any significant amounts. In the 1990s, *N. simplex* was found in the diet in 4 of 7 yr, suggesting that this species may be a tracer of the 1989 climate event. *N. simplex* is normally restricted to subtropical waters (Brinton, 1981). The years of greatest prevalence of *N. simplex* in the diet were 1990, and 1993–1995 (with no data available for 1992). Trenberth and Hoar (1996) suggested that during the period 1990–1995, an extended El Niño event persisted in the Pacific Ocean. The appearance of *N. simplex* in the Cassin's Auklet diet may be explained by this mechanism.

The marine bird diet composition time-series clearly indicates ecosystem change between 1988 and 1989. A number of other reports have now suggested that a regime shift occurred in 1989 (Beamish et al., 1999; Hare & Mantua, 2000; Mackas, Thompson, & Galbraith, 2001; McFarlane, King, & Beamish, 2000; McFarlane & Beamish, 2001). One of the perplexing questions concerns why the breeding success of seabirds of the southern CCS either did not respond to the 1976/1977 event, or responded in a manner that is undetectable with the information at hand. This is something to consider in greater detail and highlights the multidimensional nature of ecosystem response to regime shifts. A regime shift in 1989 also has implications for the previous marine

bird studies. Ainley et al. (1995b) and Veit et al. (1996) concluded that climate change had influenced the at-sea avifauna of the southern CCS. Our study supports this conclusion, but indicates that the ecosystem change they detected was probably related to the 1988/1989 regime shift rather than the regime shift of 1976–1977. Greater integration of seabird and fisheries oceanography programs will enhance our abilities to pinpoint the timing of spatial and temporal variability in climate-driven changes to marine bird populations.

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