



Ecosystem responses to short-term climate variability in the Gulf of the Farallones, California

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ABSTRACT

We conducted an integrated study from physics to upper trophic-level predators in the Gulf of the Farallones, California. We hypothesized that decreased zooplankton abundance for upper trophic-level predators in the Gulf of the Farallones during 2004 and 2005 was a response to reduced upwelling-favorable winds and primary production. Based on their trophic ecology, we hypothesized that planktivorous auklets and omnivorous murrens will show differential responses to upwelling variability. We examined these hypotheses by analyzing time series on oceanographic variables associated to upwelling and the biological responses at low, mid and high trophic-levels. We found that reduced upwelling-favorable wind was correlated with anomalously high SST and low chlorophyll *a* concentration from July 2004 to August 2005. During 2005, low chlorophyll concentrations were related to reduced krill abundance in the upper water column and decreased seabird abundance in the vicinity of the breeding colony in the study area. Decreased krill abundance was associated with late timing of nesting and reduced breeding success, with auklets showing a more pronounced response. This study shows how short-term climate variability can affect primary through tertiary productivity, and supports an interpretation of “bottom-up” control of ecosystem dynamics.

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1. Introduction

The California Current System (CCS) is one of the most productive marine environments in the world (Barber and Smith, 1981; Carr, 2002; Hill et al., 1998). High productivity in the CCS is the result of coastal upwelling, an oceanic response to winds along the coastline, which causes offshore Ekman transport, shallowing the thermocline and bringing cold nutrient-rich water to the euphotic zone thus enhancing primary production (Chavez, 1996). Wind forcing is determined by the relative position and intensity of the North Pacific High, the Aleutian Low and the North American Thermal Low pressure systems, resulting in strong equatorward winds during spring and summer (Batchelder et al., 2002; Winant et al., 1988). Variability in upwelling forcing mechanisms is likely to have bottom-up indirect effects on mid and high trophic-level organisms (Chavez et al., 2002; McGowan et al., 1998; Ware and Thompson, 2005).

Mid-trophic-level species, such as euphausiids (krill), are a critical pathway for energy transfer in marine food webs (Mangel and Nichol, 2000; Mackas et al., 2001). In the CCS, *Euphausia pacifica*

and *Thysanoessa spinifera* are the dominant species of krill (Dorman et al., 2005; Gomez-Gutierrez et al., 2005). These two krill species are important prey items of many higher trophic organisms in the CCS, including salmon (Brodeur et al., 2003; Brodeur and Pearcy, 1992), rockfish (Brodeur and Pearcy, 1984; Chess et al., 1988), hake (Buckley and Livingston, 1997; Tanasichuk et al., 1991), marine birds (Sydeman et al., 2001), and mammals (Croll et al., 1998).

Marine birds are conspicuous upper trophic-level predators that forage directly on krill or forage on other prey that feed on krill (Sydeman et al., 1997, 2001). In the central CCS, Cassin's auklets (*Ptychoramphus aleuticus*) and common murrens (*Uria aalge*) are the dominant resident seabird species (Ainley et al., 1994; PRBO & USFWS, unpublished data). Cassin's auklets are small birds [150–200 g of wet weight (WW)], which dive 20–80 m in search of prey (Manuwal and Thoresen, 1993; Nettleship, 1996). They feed on crustacean zooplankton and generally more than 80% of their diet is composed of krill (Ainley et al., 1996a; Abraham and Sydeman, 2004). Auklets breed in early spring when *E. pacifica* is abundant and available near the nesting sites and mean annual productivity (number of chicks produced per pair each year) is positively correlated with the abundance of both *E. pacifica* and *T. spinifera* (Abraham and Sydeman, 2004). In most years there is a switch in consumption of these species approximately midway through the breeding season (Abraham and Sydeman, 2006). Auklets feed heavily on *E. pacifica* early in the breeding season and gradually

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switch to a diet of *T. spinifera*, a slightly larger but significantly less abundant euphausiid, later in the breeding season (Abraham and Sydeman, 2006). This switch in prey consumption is more pronounced when sea surface temperatures (SST) in March are cold, suggesting that oceanographic conditions during winter influence the availability of *E. pacifica*, which in turn affects timing of nesting and breeding success (Abraham and Sydeman, 2006). Common murrens are large seabirds (945–1044 g WW) that dive 60–70 m (max. 180 m) in search of prey (Burger and Simpson, 1986; Nettleship, 1996). Murrens feed on northern anchovy (*Engraulis mordax*) and juvenile rockfish (mainly *Sebastes jordani*) during the chick-rearing period (Ainley et al., 1996b; Sydeman et al., 1997, 2001). However, there is evidence that murrens are zooplanktivorous during the egg formation period, shifting trophic-level and diet between winter/spring and summer from krill to fish (Sydeman et al., 1997).

Several authors have suggested that these two krill species may be negatively affected by warm SSTs (Brinton, 1981; Marinovic et al., 2002; Brinton and Townsend, 2003). The distributions of *E. pacifica* and *T. spinifera* in the CCS contract northward in response to warm ENSO years (Brinton, 1981; Marinovic et al., 2002), and the abundance of *E. pacifica* has been shown to decrease during warm PDO regimes (Brinton and Townsend, 2003). Several studies have reported changes in seabird distribution, abundance and phenology due to warm SST (Ainley et al., 1994, 1995; Veit et al., 1996; Oedekoven et al., 2001; Sydeman et al., 2001; Hyrenbach and Veit, 2003). The relative abundance of cold water species, such as Cassin's auklets and common murrens, decreased in ENSO years (Ainley et al., 1994, 1995), and an overall decline in population abundance and reproductive performance has been associated with ocean warming trends over interdecadal scales (Oedekoven et al., 2001; Sydeman et al., 2001).

Recent evidence suggests tight coupling between climate forcing, primary production, and food web dynamics in the CCS at time scales shorter than interannual (Sydeman et al., 2006). The study of climate variability and ecological responses at these short time scales may provide insights into trophic dynamics that would otherwise be missed at larger scales. Herein, we test the hypothesis that decreased prey availability for upper trophic-level predators in the Gulf of the Farallones during late 2004 and 2005 was a response to reduced upwelling-favorable winds and primary production. Because the Cassin's auklet appears to be more dependent on zooplankton prey than murrens are, we hypothesized that the short-term climate response of auklets would be more extreme. We predicted that krill abundance would be positively related to primary production, which, in turn would be related to upwelling-favorable winds and cooler ocean temperatures. We also predicted that at-sea abundance of upper trophic-level predators that rely heavily on krill, such as Cassin's auklets, would be positively associated with krill abundance, whereas other foragers, such as common murrens, which have greater diet diversity, would be less related to krill abundance.

2. Materials and methods

2.1. Study area and survey design

We conducted 10 (3-day ea.) research cruises on the R/V John H. Martin (Moss Landing Marine Laboratories, Moss Landing, CA, USA) from May to October 2004 and February to October 2005 (Table 1). The survey grid consisted of nine east–west transect lines that extended from the 1000-m isobath to within several kilometers from the coast (Fig. 1). The survey grid covered most of the offshore region of Cordell Bank and Gulf of the Farallones National Marine Sanctuaries. During each cruise, we conducted Conductivity–Tem-

Table 1

Date, along-track distance (km), area surveyed and total number of birds feeding and sitting on the water during cruises carried out in the Gulf of the Farallones and Cordell Bank regions in 2004 and 2005

Year	Month	Dates	Distance (km)	Area (km ²)	Birds (total)
2004	May	20–22	282.1	84.6	5248
	July	26–28	294.6	49.1	2610
	September	21–23	293.4	72.0	887
	October	21–23	232.2	69.6	1525
2005	February	22–24	232.5	53.0	1060
	April	21–27	228.4	68.5	4828
	May	26–28	293.6	88.1	903
	June	22–25	277.0	83.1	1294
	July	26–28	291.4	87.4	3684
	October	20–22	232.1	52.7	435

perature–Depth (CTD) casts at oceanographic stations, surveyed abundance of zooplankton using hydroacoustics, and counted marine birds using standardized strip transects.

2.2. Buoy data

We obtained hourly meteorological data on wind speed (m s⁻¹), wind direction (degrees clockwise from true north) and sea-surface temperature (SST, °C) from the National Data Buoy Center for stations 46013 (Bodega: 38°13.5'N, 123°19'W) and 46026 (San Francisco: 37°45.5'N, 122°50'W). Data for station 46013 spans April 1981–December 2005. Data for station 46026 extends from July 1982 to December 2005. Wind direction was rotated 40° into alignment with the coastline and wind speed and direction were decomposed into across-shore and alongshore components (Dorman et al., 2005). Hourly values were averaged to daily values and linear interpolation was used to estimate single missing data points. Daily values were then averaged to monthly values. Monthly values were averaged across years 1981/1982–2003 to estimate the long-term mean and 95% confidence intervals. These means were used to estimate monthly anomalies in alongshore wind and SST at Bodega and San Francisco during 2004 and 2005.

2.3. Hydrographic data

We conducted CTD casts using a Sea-Bird Electronics SBE 19Plus SEACAT Profiler at 15 oceanographic stations along transect lines 2, 4 and 6 (Fig. 1). We binned downcast data to 1 m depth intervals using SBE Data Processing Software version 5.31 (Sea-Bird Electronics, Bellevue, Washington, USA). We contoured vertical sections of temperature and salinity along transect lines using triangulation with linear interpolation in SURFER version 7 (Golden Software, Golden, CO, USA).

2.4. Chlorophyll *a* concentration

Chlorophyll *a* concentrations were derived from SeaWiFS Level-3 Standard Mapped Images at monthly 9 km resolution for a 2 × 2 degree box (latitude 37–39°N, longitude 122–124°W). Data was extracted from satellite images using the wam_series tool from WIM Automation Module software, version 6.31 (Wimsoft, San Diego, CA). Monthly values were averaged across years (1997–2005) to estimate the mean and 95% confidence intervals. Means were used to estimate monthly anomalies in chlorophyll *a* concentration during 2004 and 2005.

2.5. Krill abundance index

We used a SIMRAD EK-60 echosounder equipped with 38, 120 and 200 kHz transducers to determine the abundance of krill. Sam-

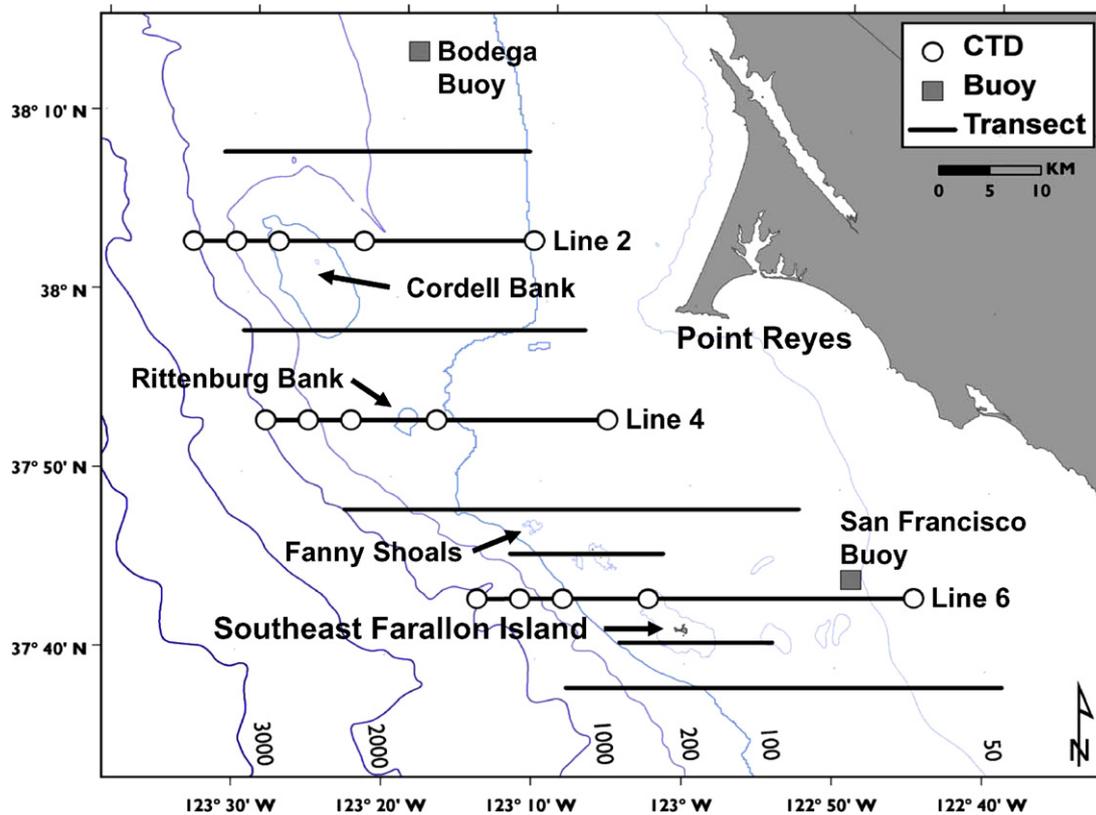


Fig. 1. Map of study area indicating survey lines, CTD and location of the National Data Buoy Center buoys used in this study.

pling was done during the day, under calm conditions (winds $<5\text{--}8\text{ m s}^{-1}$) and cruising at $18\text{--}22\text{ km h}^{-1}$ to minimize noise from surface bubbles and waves. Following others, we assumed that the 38 kHz transducer detects large organisms and negligible amounts of krill, while the 120 and 200 kHz transducers detect most krill, as well as smaller and larger organisms (Coyle and Cooney, 1993; Fiedler et al., 1998). We corrected for noise through subtraction of time-varied estimations of noise, and thresholded data below -81 dB to eliminate moderate backscatter from non-biological sources and organisms smaller than krill (Coyle et al., 1992; Croll et al., 1998; Lawson et al., 2004; Macaulay et al., 1995). We calculated an index of krill abundance by averaging volume backscatter from the 120 and 200 kHz transducers, and subtracting backscatter from organisms larger than krill detected by the 38 kHz (Fiedler et al., 1998). For analysis, we averaged volume backscatter from transects into 3 km intervals that closely matched spatial resolution of the seabird data, and across the upper 50 and 200 m of the water column.

2.6. Marine bird at-sea abundance

We used standardized strip transects to count marine birds from the flying bridge of the R/V John H. Martin (eye height = 5 m above the sea surface) while the ship was underway cruising at $18\text{--}22\text{ km h}^{-1}$. Birds were counted continuously during daylight hours in a 100 m arc from directly ahead of the vessel to 90° off the side with best visibility (i.e. lowest glare) and logged into a portable computer. Observers switched to a snapshot method of counting birds to minimize the overestimate of numbers present when large numbers of birds were encountered (Tasker et al., 1984). Marine bird behaviors were recorded as flying, on water, and feeding; for the purpose of this analysis, we used birds feeding and on water which we assumed had previously fed in the vicinity of where they were resting. We binned the data at 3 km intervals

and estimated densities (birds km^{-2}) by dividing the number of birds by the area surveyed.

2.7. Marine bird timing of nesting and breeding success

We studied Cassin's auklets breeding in artificial burrows (i.e. nest boxes) and common murrelets breeding at the Upper Shubrick Colony on Southeast Farallon Islands (SEFI). After 30 days of incubation, auklet nest boxes were checked every 1–5 days to determine hatching and fledging dates. We used hatch-date data for first breeding attempts only; data from second breeding attempts was not included. Murre nesting sites were checked daily to determine hatching and fledging dates. For both species, breeding success was calculated as the number of chicks fledged per breeding pair in each year. Annual mean laying date and breeding success were averaged across years from 1972 to 2003 to estimate the long-term mean (Abraham and Sydeman, 2004; PRBO, unpublished data).

2.8. Data analysis

We used ANOVA to examine variability in monthly alongshore wind and SST from 1981/1982 to 2005, in alongshore wind and SST anomalies from 2004 to 2005, and in chlorophyll *a* concentration from 1997 to 2005. We used Pearson correlation (r_p) to examine relationships between oceanographic variables (alongshore wind and SST) and chlorophyll *a* concentration (sample size >90). We used Ordered Logistic Regression (OLR; Hosmer and Lemeshow, 2000) with backward stepwise procedures for model selection to examine krill and marine bird abundances at a 3 km resolution. We categorized prey and predator abundance indices into four levels as follows: absence data was scored as '0', presence data was scored as '1', '2', or '3' using the 33rd and 66th percentiles as break points. We used Arc-GIS 9.1 (ESRI, Redlands, CA) to esti-

mate at 3 km along-track horizontal resolution mean bottom depth and an index of bathymetry gradient [bathymetry, (max depth – min depth)/max depth]. Variables included in the OLR models were year, month surveyed (as squared variable), and latitude, longitude, depth and bathymetry. We used *t*-tests to examine whether auklet and murre laying dates and breeding success in 2004 and 2005 were equal to the long-term mean. We used Spearman rank correlation (r_s) to examine relationships between oceanographic (monthly anomalies in alongshore wind and SST) and biological variables (monthly chlorophyll *a* concentration, krill and marine bird abundance) from January 2004 to December 2005 (sample size ≤ 24).

3. Results

3.1. Seasonal cycle in wind and SST in the Gulf of the Farallones

Fig. 2 shows the mean ($\pm 95\%$ CI) seasonal cycle in alongshore wind and SST from 1981/1982 to 2005 at the Bodega and San Francisco buoys, respectively. The predominant alongshore wind was negative at both locations indicating equatorward flow during much of the year. Poleward flow was common during November–February. Monthly alongshore wind was significantly stronger (more negative) at Bodega than San Francisco and showed significant variation between months and years (three-way ANOVA: $F[\text{buoy}]_{1,499} = 79.663$, $p < 0.001$; $F[\text{month}]_{11,499} = 58.067$, $p < 0.001$; $F[\text{year}]_{24,499} = 2.619$, $p < 0.001$; $r^2 = 0.617$). The mean monthly alongshore wind increased rapidly (became more negative) in strength from January to May, reaching maximum strength from May to June, and gradually decreasing thereafter (Fig. 2). We found that monthly SST was significantly colder at Bodega than San Francisco and showed significant variation between months and years (three-way ANOVA: $F[\text{buoy}]_{1,498} = 85.524$, $p < 0.001$; $F[\text{month}]_{11,498} = 51.494$, $p < 0.001$; $F[\text{year}]_{24,498} = 11.450$, $p < 0.001$; $r^2 = 0.655$). The

mean monthly SST at Bodega decreased from March to June in response to the winds, this pattern was less noticeable at the San Francisco buoy; SST at both locations increased from June to September and decreased thereafter (Fig. 2).

3.2. Anomalous winds and SST in 2004 and 2005

Fig. 3 shows monthly anomalies in alongshore wind and SST from 2004 to 2005 at the Bodega buoy compared to the mean 1981–2003 climatology. We found no significant variation in alongshore wind anomalies among buoys and months (two-way ANOVA: $F[\text{buoy}]_{1,35} = 0.105$, $p = 0.747$; $F[\text{month}]_{11,35} = 2.001$, $p = 0.059$; $r^2 = 0.387$). The alongshore wind anomalies were positive – with a few exceptions – from July 2004 to August 2005 and beyond the 95% CI (weak equatorward wind) in July, August and October 2004 and May and December 2005 (Fig. 3). We found no significant variation in SST among buoys and significant variation between months (ANOVA: $F[\text{buoy}]_{1,35} = 0.064$, $p = 0.802$; $F[\text{month}]_{11,35} = 2.460$, $p = 0.021$; $r^2 = 0.437$). SST anomalies were positive from July 2004 to August 2005, except for September 2004. Moreover, 7 months had SST anomalies significantly warmer than the monthly 95% CI; highest SST anomalies were observed during March and May 2005 (Fig. 3).

3.3. Variability in chlorophyll *a* concentration

Chlorophyll *a* concentration from 1997 to 2005 showed significant variation between months and years (ANOVA: $F[\text{month}]_{11,80} = 5.594$, $p < 0.001$; $F[\text{year}]_{8,80} = 5.412$, $p < 0.001$; $r^2 = 0.565$). Chlorophyll *a* concentration anomalies from 2004 to 2005 were significantly higher than the maximum 95% CI in March, April, November and December 2004 and September 2005 and significantly lower than the minimum 95% CI in July 2004 and January, March, May and July 2005 (Fig. 3). Monthly chlorophyll

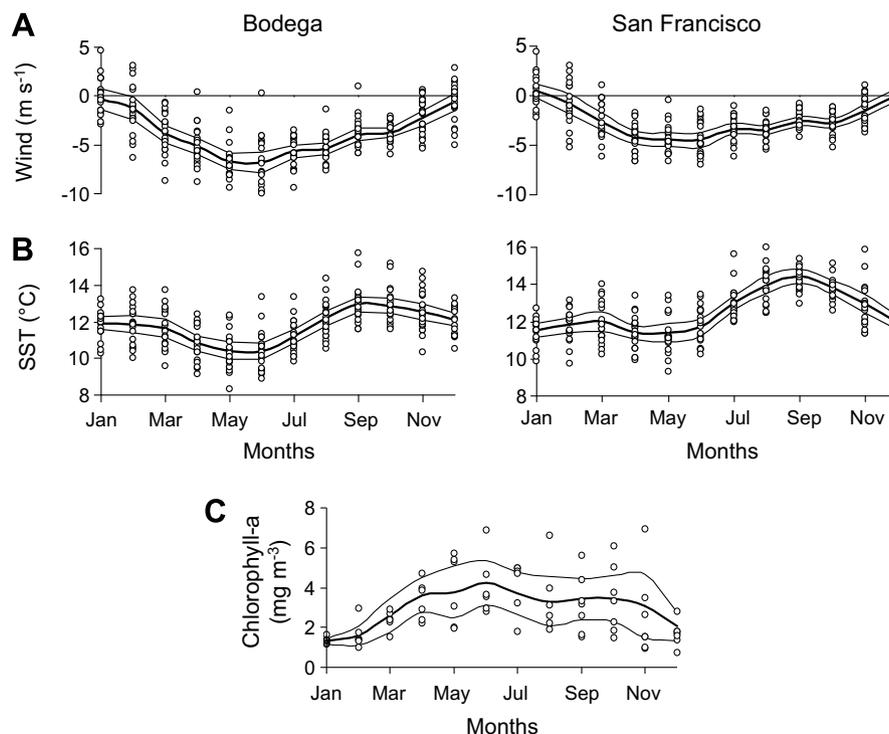


Fig. 2. Seasonal cycle in monthly averaged alongshore wind velocity (A) and sea surface temperature (B) from 1981/1982 to 2005 at the Bodega and San Francisco buoys, and monthly averaged chlorophyll *a* concentration (C) from 1997 to 2005 in a 2×2 degree box centered at Point Reyes. Continuous lines indicate the mean (middle bold line) and 95% confidence intervals.

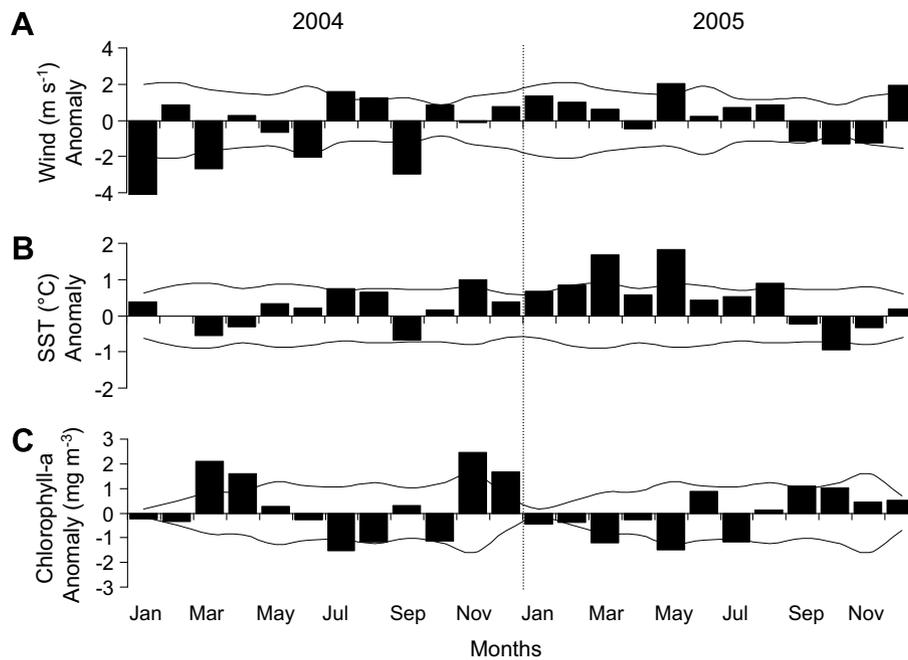


Fig. 3. Monthly anomalies in alongshore wind (A), sea surface temperature (B) and chlorophyll *a* concentration (C) from 2004 to 2005 at the Bodega buoy. Continuous lines indicate 95% confidence intervals based on mean seasonal cycle from 1981 to 2005.

a concentration from 1997 to 2005 was negatively correlated with alongshore wind at both buoys (Bodega: $r_p = -0.402$, $n = 92$, $p < 0.01$; San Francisco: $r_p = -0.413$, $n = 90$, $p < 0.01$) and SST at Bodega ($r_p = -0.229$, $n = 92$, $p < 0.05$) but not at San Francisco ($r_p = -0.067$, $n = 90$, $p > 0.05$), indicating that high primary productivity was related to the upwelling of cold water, which is more intense near Bodega.

3.4. Oceanographic conditions during 2004 and 2005

Strong equatorward winds resulted in upwelling during May 2004, causing the observed pattern of warm-fresh water offshore and cold-salty water nearshore (Fig. 4). Strong equatorward winds continued into June and then relaxed in July. By July 2004, stratification was apparent with a shallow thermocline. Short wind episodes continued into August followed by a long moderate equatorward wind event in September. The September 2004 cruise showed warm-fresh water over most transects, with some evidence of upwelling in the form of shallower inshore isohalines and haloclines. A relatively long wind reversal, with southern winds occurred a few days prior to the October 2004 cruise, resulted in a stratified water column with evidence of inshore downwelling.

Warm-fresh water occupied most of our survey area during the winter cruise in February 2005 (Fig. 5). We observed a shallow layer of fresh water flowing north on the inshore side of the study area, which was likely the result of poleward winds prior to the cruise. The vertical profiles of the water changed dramatically during the spring. The April 2005 cruise showed cold-salty water occupying most of the line with clear evidence of upwelling near shore. This cruise was conducted after a strong episode of equatorward winds that marked the start of the spring transition; however, winds did not last long and were followed by short episodes of strong poleward winds. The May 2005 cruise showed cold-salty water over the shelf but it was deeper as the upper layer of warm-fresh water thickened and pushed down the pycnocline. Two relatively strong wind events and a relaxation in winds followed this cruise. The equatorward winds probably resulted in off-

shore transport of surface waters in June 2005, as the upper layer of warm-fresh water was thinner than in May and comparable to that of April. However, the relaxation in winds resulted in flat isotherms and isohalines which indicated little upwelling occurred near shore. The cruise in July 2005 was carried out after a long relaxation in winds, which explained the presence of a layer of warm water over most of the shelf; the cold-salty water was below a relatively deep pycnocline. Most cold-salty water was absent from the shelf during the fall cruise in October 2005.

3.5. Krill abundance index

The krill index in the upper 50 m of the water column showed significant variation by year, month, latitude, and longitude, but not with bottom depth or bathymetry [OLR; Likelihood Ratio Statistic (LRX²) = 170.13, $n = 899$, d.f. = 7, $p < 0.001$; Table 2]. The krill index in the upper 200 m showed significant variation by year, month, latitude, longitude, depth and bathymetry (OLR; LRX² = 173.98, $n = 912$, d.f. = 7, $p < 0.001$; Table 2). The krill index in 2005 was significantly lower than 2004 in the upper 50 m and upper 200 m, representing an overall decrease of 61% and 52%, respectively. The krill index in the upper 50 m during May 2005 represented just 9% of the May 2004 value; the krill index in the upper 50 m in July and October 2005 represented 96% and 84% of the krill measured during the same months in 2004 (Fig. 6).

The krill index in the upper 50 m varied non-linearly with month, and showed a negative association with latitude and a positive association with longitude (Table 2). This suggested greater abundance of prey near the surface in the southeastern region of our study area, east of Southeast Farallon Island (SEFI) and in proximity to San Francisco Bay. In May 2004, we found greater krill index values in the upper 50 m near Cordell and Rittenburg Banks, and in the vicinity of SEFI. In July and October 2004, and May, July and October 2005, greater values of krill index in the upper 50 m were found in the vicinity of SEFI and in the southeast most section of our study area (Fig. 7).

The krill index in the upper 200 m also varied non-linearly with month, and showed negative associations with latitude, longitude

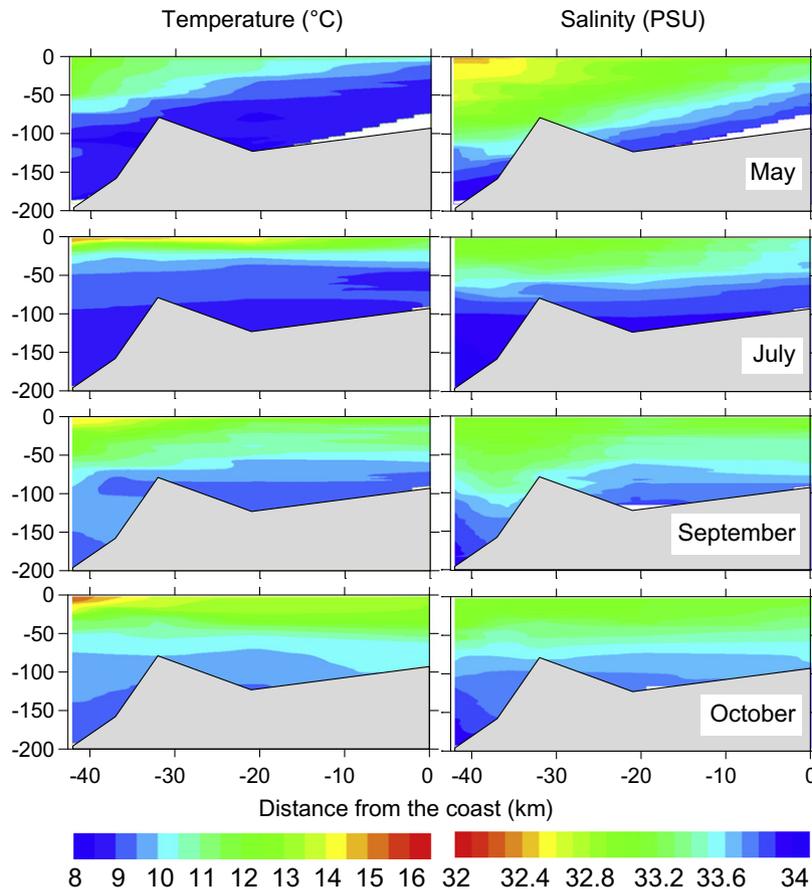


Fig. 4. Vertical section of temperature and salinity along line 2 in cruises carried out during 2004.

and bottom depth, and a positive association with bathymetry (Table 2). This indicated an overall greater abundance of prey in the southwestern region of our study area, over the shelf-edge in areas with steep changes in bottom topography. In 2004, most cruises indicated greater values of krill index along the outer continental shelf and shelf-break regions. A similar pattern was observed in May 2005. In July and October 2005, we found few large aggregations of krill that appear to concentrate in the vicinity of the Farallones archipelago in July, and the archipelago and Cordell Bank in September (Fig. 7).

3.6. Marine bird abundance and distribution at-sea

The relative abundance of Cassin's auklets feeding and sitting on the water showed significant variation by year, month, and bathymetry but not with either latitude, longitude and depth (OLR; $LRX^2 = 48.47$, $n = 205$, $d.f. = 7$, $p < 0.001$; Table 3). Densities of foraging Cassin's auklets and common murres were significantly lower in 2005 than 2004. Cassin's auklet densities decreased by 81% from $36.2 \text{ birds km}^{-2}$ in 2004 to $6.7 \text{ birds km}^{-2}$ in 2005. We found that during May and July 2005 the abundance of Cassin's auklets represented 4.9% and 1.5% of the densities found in same months during 2004, respectively (Fig. 6). Cassin's auklet abundance showed a non-linear association with month and a positive linear association with bathymetry suggesting greater densities of birds in late spring-early summer near areas with steep changes in bottom topography (Table 3). Cassin's auklets foraged over the outer continental shelf from Cordell Bank to SEFI (Fig. 8). In May and July 2004, we found high densities of foraging birds near Fanny Shoals and the Farallon Islands. In July 2004 we found high densi-

ties around the Farallon Islands and over Cordell Bank. Few birds remained into September and October and were found foraging in scattered groups near the shelf-edge area. We found no aggregation of birds in 2005 that was comparable in size to those found in 2004. The few birds observed in 2005 were foraging along the edge of the shelf in most surveys, including over Rittenburg Bank and Fanny Shoals in April, and Cordell Bank and the Farallon Islands in May and June.

The abundance of common murres feeding and sitting on the water showed significant variation by year and longitude but not by month surveyed, latitude, depth or bathymetry (OLR, $LRX^2 = 52.64$, $n = 409$, $d.f. = 7$, $p < 0.001$). Annual average densities of common murre declined only slightly (by 6.4%) from $34.1 \text{ birds km}^{-2}$ in 2004 to $31.9 \text{ birds km}^{-2}$ in 2005. Seasonally, the abundance of common murres during May 2005 was only 29.8% of the densities found in May 2004, while the density in July 2005 was more than twice that of July 2004 (Fig. 6). Common murre abundance showed a positive linear association with longitude indicating greater densities closer to shore in the eastern region of our study area (Table 3). Common murres foraged over the continental shelf south from Point Reyes and inshore from SEFI (Fig. 8). In 2004, we found high densities of birds east of Fanny shoals and near the Farallon Islands in May and July. Foraging birds moved inshore and few remained near Fanny Shoals and SEFI in September and October. In 2005, birds continued to forage inshore of SEFI in February and dispersed north near Cordell Bank and west to the shelf-edge in April (distributions not shown). The distribution of birds in May 2005 was very different from 2004. We observed fewer birds in May 2005, and instead of foraging on the shelf, we found them foraging near the shelf-edge and west of Point Reyes. High

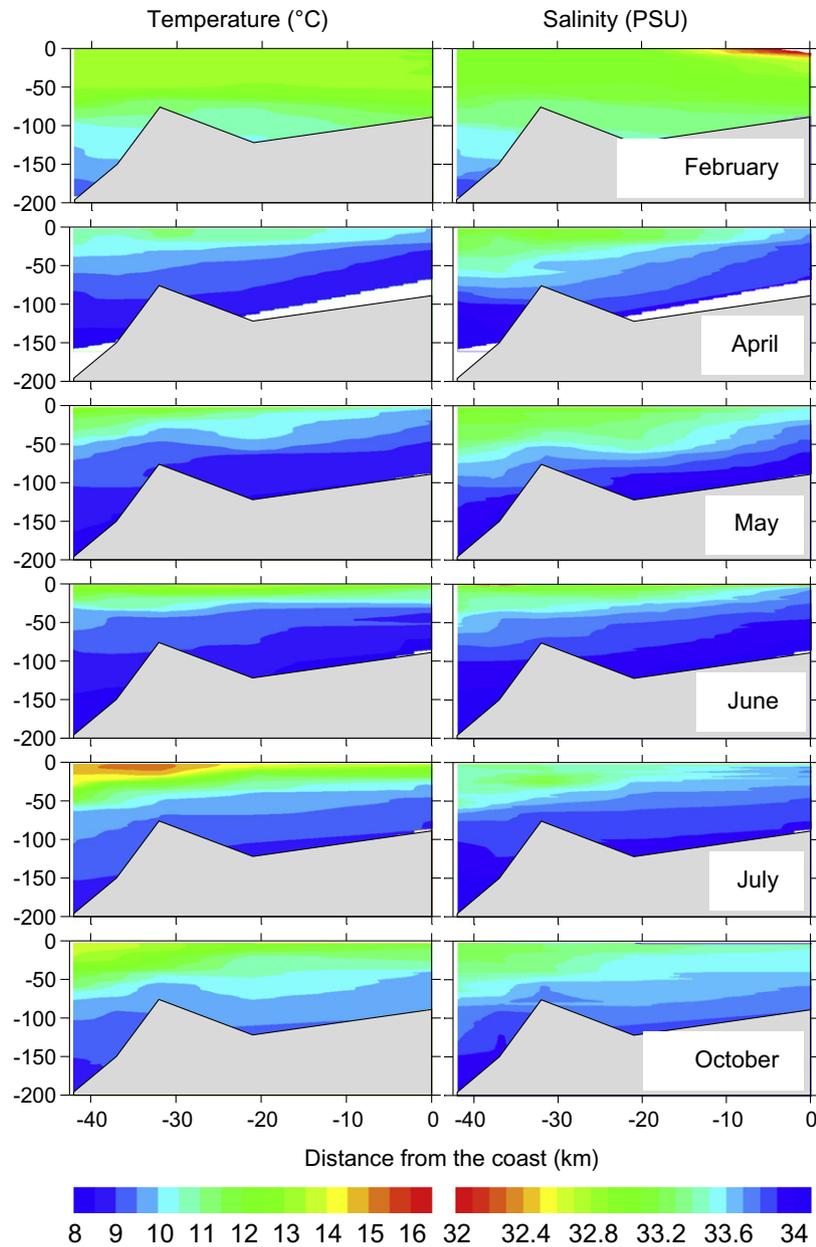


Fig. 5. Vertical section of temperature and salinity along line 2 in cruises carried out during 2005.

Table 2

Coefficient, standard error and significance values of variables included in ordered logistic regression analysis of krill abundance index in the upper 50 and 200 m of the water column

Depths	Variable	Coefficient	Standard error	p value
Upper 50 m	Year	-0.7138	0.1430	<0.001
	Month	-0.6890	0.1356	<0.001
	Month ²	0.0526	0.0102	<0.001
	Latitude	-2.3717	0.7413	0.0010
	Longitude	1.7149	0.5981	0.0040
	Depth	-0.0004	0.0004	0.2350
	Bathymetry	0.0002	0.0003	0.5050
Upper 200 m	Year	-0.8310	0.1414	<0.001
	Month	-0.6252	0.1421	<0.001
	Month ²	0.0406	0.0106	<0.001
	Latitude	-3.0891	0.7552	<0.001
	Longitude	-4.0092	0.6311	<0.001
	Depth	-0.0037	0.0004	<0.001
	Bathymetry	0.0033	0.0008	<0.001

densities of birds were found foraging in the shelf-area in June and July; fewer birds remained over the shelf into October.

3.7. Marine bird timing of nesting and breeding success

Timing of nesting of Cassin's auklets and common murres in 2004 was not significantly different from the long-term mean (t -test; auklets: $t = 0.165$, $p = 0.870$; murres: $t = -1.895$, $p = 0.060$), whereas in 2005 it was significantly later (t -test; auklets: $t = 5.165$, $p < 0.001$; murres: $t = 18.494$, $p < 0.001$) (Table 4). We found that breeding success in 2004 was not significantly different from the long-term mean for Cassin's auklets (t -test; $t = 1.190$, $p = 0.246$) and common murres (t -test; $t = 0.737$, $p = 0.462$). However, we found that in 2005 breeding success was significantly lower than the long-term mean for common murres (t -test; $t = -7.046$, $p < 0.001$) and the lowest value ever recorded for Cassin's auklets (zero breeding success).

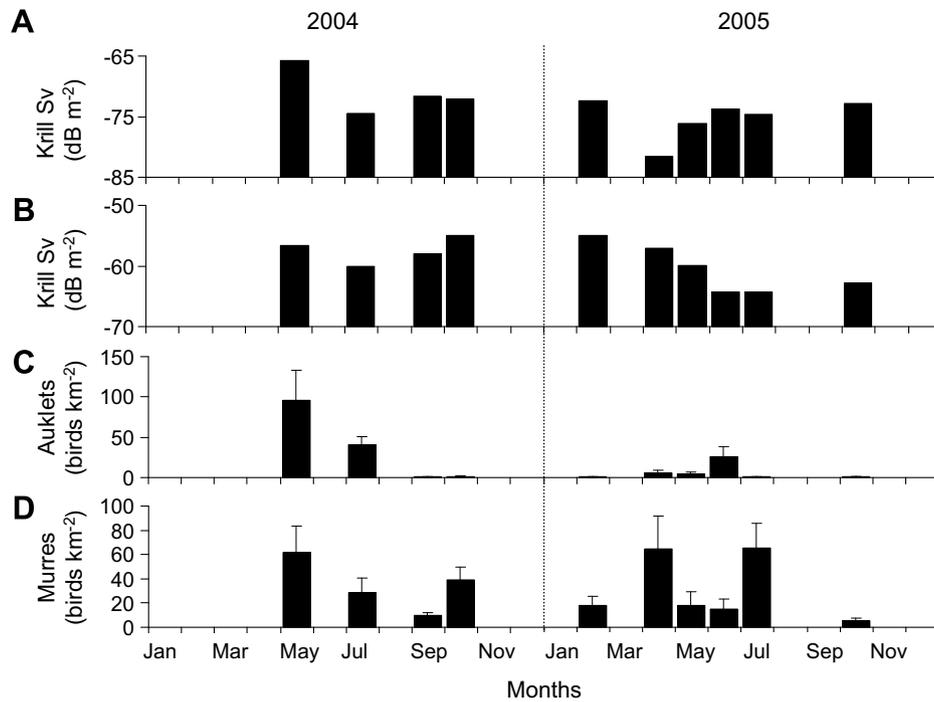


Fig. 6. Volume backscatter (upper quartile) of krill index in the upper 50 m (A) and 200 m (B) and mean (± 1 SE) densities of Cassin’s auklets (C) and common murres (D) during cruises conducted in 2004 and 2005.

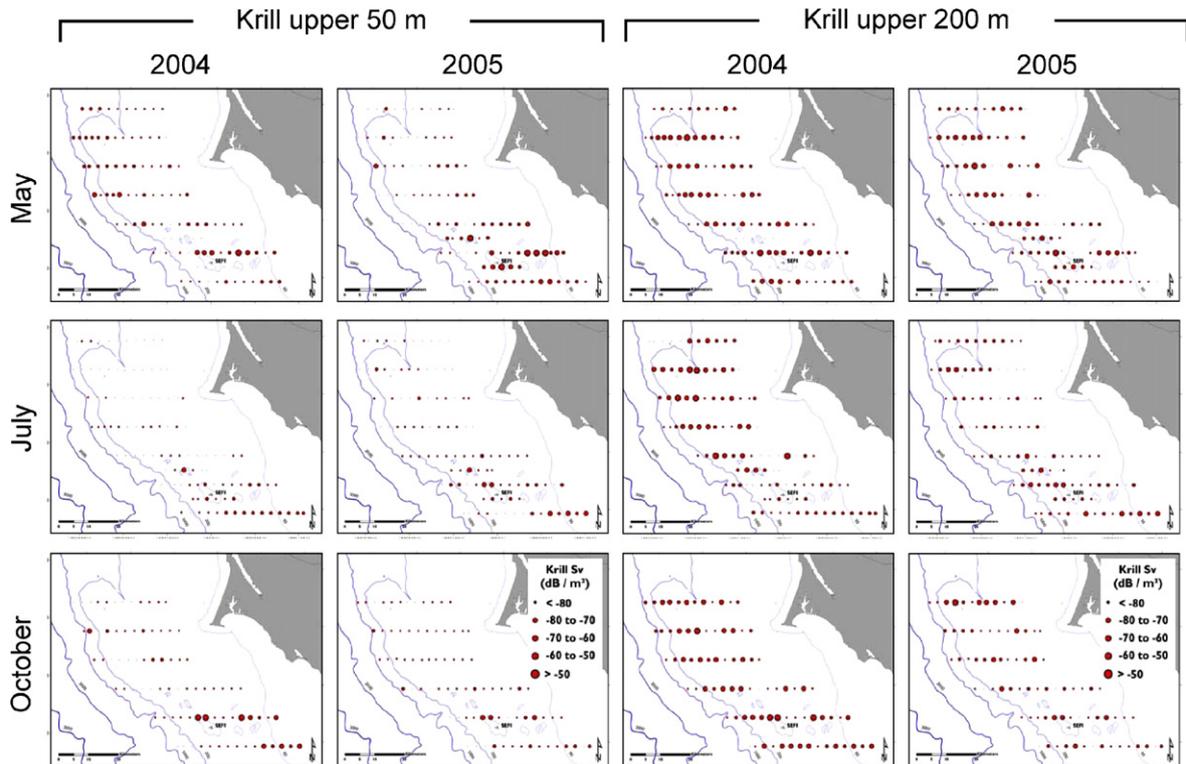


Fig. 7. Spatial distribution of krill backscatter index in the upper 50 m (left) and 200 m (right) during May, July and October cruises conducted in 2004 and 2005.

3.8. Ecosystem response to climate forcing

Alongshore wind anomalies were positively correlated with SST anomalies, indicating that anomalously weak equatorward winds resulted in high SST. Chlorophyll *a* concentration anomalies were

negatively correlated with alongshore wind and SST anomalies at Bodega (Table 5), indicating that low chlorophyll *a* concentration was associated with weak equatorward winds and high SST at this location. We found a weak negative correlation between krill abundance in the upper 50 m of water column and SST anomalies

at both buoys and a positive trend between krill abundance and chlorophyll *a* concentration (Table 5), indicating that krill abun-

dance in the upper water column was greater in cold water with high chlorophyll *a* concentration. We found no correlation between krill abundance in the upper 200 m and SST or chlorophyll *a* concentration (Table 5). Correlations between the monthly abundance of Cassin's auklet and common murres and the monthly abundance of krill in the upper 50 and 200 m of the water column were not significant (Table 5).

Table 3
Coefficient, standard error and significance values of variables included in ordered logistic regression analysis of Cassin's auklet and common murre abundance

Species	Variable	Coefficient	Standard error	p value
Auklet	Year	-1.2530	0.3160	<0.001
	Month	0.9047	0.3635	0.0130
	Month ²	-0.0891	0.0273	0.0010
	Latitude	-2.4207	1.8406	0.1880
	Longitude	-1.4812	1.8284	0.4180
	Depth	-0.0009	0.0008	0.2890
	Bathymetry	0.0036	0.0016	0.0300
Murre	Year	-0.5543	0.2135	0.0090
	Month	0.1245	0.2262	0.5820
	Month ²	-0.0189	0.0172	0.2730
	Latitude	2.1837	1.3319	0.1010
	Longitude	4.9165	1.0136	<0.001
	Depth	-0.0001	0.0008	0.9090
	Bathymetry	0.0019	0.0015	0.1920

4. Discussion

We predicted that primary production would depend strongly on the strength of upwelling producing winds responsible for nutrient input to the system. We found that reduced equatorial winds led to high SST (i.e., limited nutrient supplies) and resulted in anomalously low surface chlorophyll *a* concentrations, as registered by SeaWiFS, in the Gulf of the Farallones from July 2004 to August 2005. Low primary production due to reduced upwelling and decreased nutrient input has been observed in nearby Monterey Bay during ENSO years (Chavez et al., 2002; Kudela and Chavez, 2000). Monterey Bay, and much of the coastal waters in the CCS, is

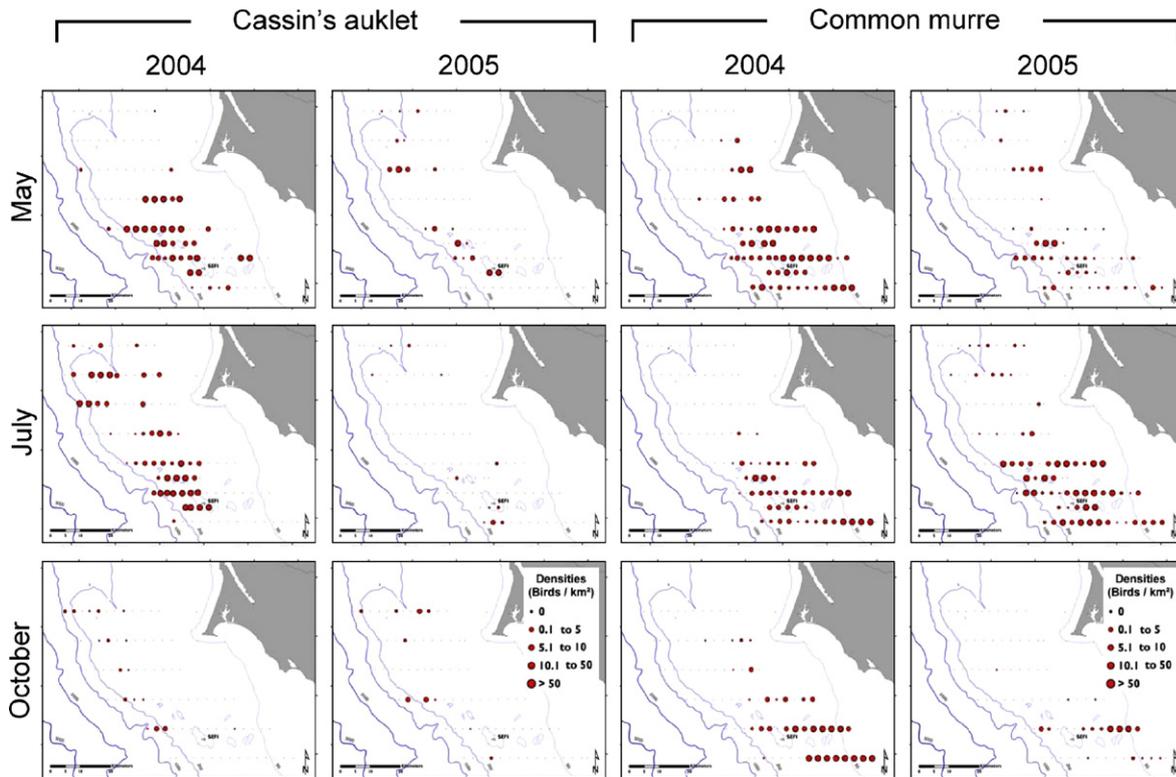


Fig. 8. Spatial distribution of Cassin's auklet (left) and common murres (right) during May, July and October cruises conducted in 2004 and 2005.

Table 4
Timing [mean ± SE (sample size)] of nesting (egg laying) and breeding success of Cassin's auklets and common murres in 2004 and 2005 relative to the long-term mean (ns = non significant, *significant at $p < 0.001$)

		Timing of nesting		Nesting success	
		Julian day	Difference	Proportion	Difference
Auklet	1972–2003	107.14 ± 3.6 (32)	–	0.72 ± 0.04 (32)	–
	2004	107.36 ± 1.31 (42)	0.22 (ns)	0.64 ± 0.07 (42)	-0.08 (ns)
	2005	133.50 ± 5.10 (16)	26.36 (*)	–	-0.72
Murre	1972–2003	134.08 ± 1.5 (32)	–	0.68 ± 0.04 (32)	–
	2004	132.69 ± 0.73 (167)	-1.38 (ns)	0.70 ± 0.03 (201)	0.02 (ns)
	2005	145.05 ± 0.59 (179)	10.97 (*)	0.44 ± 0.03 (209)	-0.24 (*)

Table 5

Results from Spearman rank correlations between oceanographic (monthly anomalies in alongshore wind and SST) and biological variables (monthly anomalies in chlorophyll *a* concentration, krill abundance index and marine bird abundances) in 2004 and 2005

		Bodega		San Francisco		Chlorophyll	Krill		<i>n</i>
		Wind	SST	Wind	SST		50 m	200 m	
Bodega	Wind								24
	SST	0.581							24
San Francisco	Wind	0.883	0.470						24
	SST	0.494	0.814	0.500					24
Chlorophyll		-0.530	-0.521	<i>-0.400</i>	<i>-0.365</i>				24
Krill	50 m		<i>-0.600</i>		<i>-0.588</i>	0.418			10
	200 m		0.103		<i>-0.067</i>	<i>-0.067</i>			10
Birds	Auklets		0.091		<i>-0.188</i>	<i>-0.006</i>	<i>-0.006</i>	0.055	10
	Murres		0.333		0.261	<i>-0.552</i>	<i>-0.321</i>	0.091	10

Bold fonts indicate $p < 0.01$, bold-italic fonts indicate $p < 0.05$, and italic fonts indicate $p < 0.10$. Sample unit month decreases because we only carried out cruises in 10 out of 24 months.

typically dominated by a diatom community that thrives in cold nutrient-rich waters. Inflows of warm nutrient-depleted waters are associated with a mixed oceanic phytoplankton community (Bolin and Abbott, 1963). Environmental conditions in 2005 led to changes in phytoplankton in Monterey Bay from a diatom dominated community to a more diverse oligotrophic community (Sullivan, J.M., Rhines, J.E.B., personal communication). Due to its proximity and similar ecology to Monterey Bay, the Gulf of the Farallones may have experienced a similar shift to a low-productivity phytoplankton community during the later portion of our study period.

We predicted that krill abundance would be positively related to primary production. We found that low chlorophyll *a* concentration and anomalously high SST were associated with low krill abundance in the upper water column during 2005. We also found that krill abundance in the upper 200 m was low in 2005, but did not show a direct correlation with chlorophyll *a* and SST. These krill abundance trends were corroborated by net sampling from springtime CalCOFI lines off central California (Point Reyes to Point Sur) that showed decreased abundance of *E. pacifica* and *T. spinifera* in 2005 as compared to 2004 (Sydeman et al., 2006). Similarly to this study, an overall decrease in zooplankton abundance coincident with decreased upwelling and high SST was observed in Monterey Bay during the 1997/1998 El Niño (Marinovic et al., 2002). The rapid decline in zooplankton during 1997/1998 was the result of a major decline in *E. pacifica* (Marinovic et al., 2002).

We predicted that at-sea abundance of Cassin's auklets would be positively associated with krill abundance, and that the association would be relatively stronger than that between murres and krill. We found that low euphausiid availability had negative effects on both species, but as predicted, effects were stronger on the obligate planktivores (auklets) than on the relative omnivores (murres) in terms of at-sea abundance in the study area and reproductive success. Decreased upwelling had no effect on seabirds in 2004 because anomalies started near the end of the breeding season. Krill abundance began to decline by the end of the chick-rearing period, but may have still been sufficiently available to feed adults and fledge chicks. Our July 2004 cruise showed auklets foraging north of the colonies and near Cordell Bank. Foraging near Cordell Bank probably required more energy than along the shelf-edge close to the breeding colonies as observed in May 2004.

The at-sea distribution, abundance and timing and success of auklet and murre breeding in 2005 differed from observations in 2004. We hypothesize that a series of upwelling-related events transpired that resulted in later than usual breeding and differences in spatial distribution within the central California region. Although a brief period of seasonally normal upwelling occurred in April 2005 led to near normal chlorophyll concentration, this

productivity was apparently not reflected in krill abundance. Near-surface (upper 50 m) krill abundance in 2005 (annual average) was only 40% of the 2004 abundance. The year-to-year reduction in krill abundance was greater for the upper 50 m estimate than the upper 200 m estimate. This is important because it is the prey within the upper 50 m which is most attractive to auklets and which they are most likely to key to as foraging predators. Because suitable euphausiid prey were relatively scarce in 2005, esp. near the surface in May 2005 (only 9% of May 2004 levels), auklets delayed their time of nesting by 26 days compared to 2004 or the long-term average – mid-May instead of mid-April. Murres also delayed their breeding in 2005 by ca. 11 days compared to 2004. Similar late timing of nesting of auklets and murres was observed during the 1983, 1992 and 1998 ENSO events (Abraham and Sydeman, 2004; PRBO & USFWS, unpublished data). Springtime ocean conditions (temperatures, ocean productivity) are critical for auklets and murres because that is when the birds are accumulating energy for and/or recovering from egg production (Sydeman et al., 2006). By May 20, auklets had abandoned their nests (prior to hatch of the eggs). This abandonment occurred because upwelling winds were particularly weak for most of the preceding 5 months, surface temperatures were elevated, and prey (krill) were very scarce near the nesting colonies. These anomalous conditions were reinforced by 'atmospheric blocking' in the Gulf of Alaska, which shifted the jet stream to the south (Schwing et al., 2006), and caused an extended period of southerly winds and storminess during the first few weeks of May (Sydeman et al., 2006). Low auklet breeding success (but not complete abandonment) was observed during the 1983, 1990, 1992 and 1997 ENSO events (Abraham and Sydeman, 2004). By June 2005, upwelling-favorable winds increased, SST was near average, chlorophyll was above average and prey abundance in the upper 50 m increased. A few birds responded with a new breeding attempt at this time, but were unsuccessful as conditions quickly worsened again in July. Despite the anomalous conditions, murres continued attending the colony throughout 2005, but their breeding success declined by 24%. This decline in breeding success was much less severe than the total failure experienced by the auklets. In fact, murre breeding success in 2005 was higher than during the 1983, 1992 and 1998 ENSO events (PRBO & USFWS, unpublished data). This differential response between seabird species was likely due to the ability of murres to forage both in deeper habitats and on more diverse prey (including fish) in addition to euphausiids. The critical role of winter oceanographic conditions and its influence on timing of nesting and breeding success was previously recognized for auklets on SEFI but not for murres (Abraham and Sydeman, 2006).

This study shows how anomalous "bottom-up" forces can shape the ecology of upper trophic-level predators on relatively short

temporal scales. Upwelling-favorable winds regulate the overall amount of nutrients available for primary production; this in turn determines the abundance of prey available for upper trophic-level predators. Seasonal wind anomalies can create mismatches between prey availability and predator demand for prey, leading, at times, to complete loss of an annual cohort, as observed for auklets in 2005. Mobile zooplankton (krill) and upper trophic-level predators (marine birds) have the ability to act in response to short-term changes in climate and food resources. As evidenced by the response of marine birds in this study, it is apparent that the timing of the climate anomalies, and not just their magnitude, play a large role in the structure and dynamics of the ecosystem. Timing of anomalous weather may have a similar effect on other upper trophic-level predators, and likely on krill as well, depending on the seasonality of their reproductive cycle and the pattern of climate variation.

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