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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 murres 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.

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

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

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 19*Plus* 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-