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Climate–ecosystem change off southern California: Time-dependent seabird predator–prey numerical responses

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A R T I C L E I N F O

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A B S T R A C T

Climate change may increase both stratification and upwelling in marine ecosystems, but these processes may affect productivity in opposing or complementary ways. For the Southern California region of the California Current Ecosystem (CCE), we hypothesized that changes in stratification and upwelling have affected marine bird populations indirectly through changes in prey availability. To test this hypothesis, we derived trends and associations between stratification and upwelling, the relative abundance of potential prey including krill and forage fish, and seabirds based on the long-term, multi-disciplinary CalCOFI/CCE-LTER program. Over the period 1987 through 2011, spring and summer seabird density (all species combined) declined by ~2% per year, mostly in the northern sector of the study region. Krill showed variable trends with two species increasing and one deceasing, resulting in community reorganization. Nearshore forage fish, dominated by northern anchovy (*Engraulis mordax*) as well as offshore mesopelagic species, show declines in relative abundance over this period. The unidirectional decline in springtime seabird density is largely explained by declining nearshore fish abundance in the previous season (winter). Interannual variability in seabird density, especially in the 2000s, is explained by variability in krill abundance. Changes in the numerical responses of seabirds to prey abundance correspond to a putative ecosystem shift in 1998–1999 and support aspects of optimal foraging (diet) theory. Predator–prey interactions and numerical responses clearly explain aspects of the upper trophic level patterns of change in the pelagic ecosystem off southern California.

1. Introduction

Ocean warming accompanied by increasing density stratification is projected by coupled atmosphere–ocean global climate models (Solomon et al., 2007). Generally, large-scale empirical observations support model predictions (Belkin, 2009; Levitus et al., 2009), but substantial spatial variability may be observed at smaller (e.g., regional) scales (Burrows et al., 2011). Eastern boundary current ecosystems, where upwelling-favorable winds may be enhanced by global warming (Bakun, 1990), provide an exception; in these regions upwelling intensification may lead to ocean cooling. While the global warming-upwelling intensification hypothesis remains equivocal, in some regions of the world observations of upwelling-favorable wind intensification are compelling (Narayan et al., 2010; García-Reyes and Largier, 2010).

Ecosystem responses to simultaneous changes in temperature/stratification and upwelling are difficult to predict. Upwelling intensification could increase isopycnal shoaling and nutrient input leading to enhanced productivity, but excessive upwelling could also increase fish mortality via excessive turbulence or advection (Cury and Roy, 1989). Increased stratification could impede the efficacy of upwelling, thereby diminishing nutrient input and primary productivity (Roemmich and McGowan, 1995; Sarmiento et al., 2004), though in some upwelling regions stratification has been positively related to nitrate concentrations and proxies of phytoplankton biomass (Aksnes and Ohman, 2009, Kahru et al., 2012); these observations also have been supported by recent models (Rykaczewski and Dunne, 2010). To date, a few model experiments have addressed the ecosystem consequences of increasing stratification and upwelling (Auad et al., 2006; Di Lorenzo et al., 2005), but this interaction has yet to be adequately investigated using observations.

The California Current Ecosystem (CCE) is an eastern boundary current system where upwelling and stratification have been studied for decades and related to multiple trophic levels including phytoplankton (Aksnes and Ohman, 2009; Chavez and Messié, 2009; Venrick, 2012), zooplankton (Hooff and Peterson, 2006; Lavaniegos and Ohman, 2007), forage fish (Brodeur et al., 2006;

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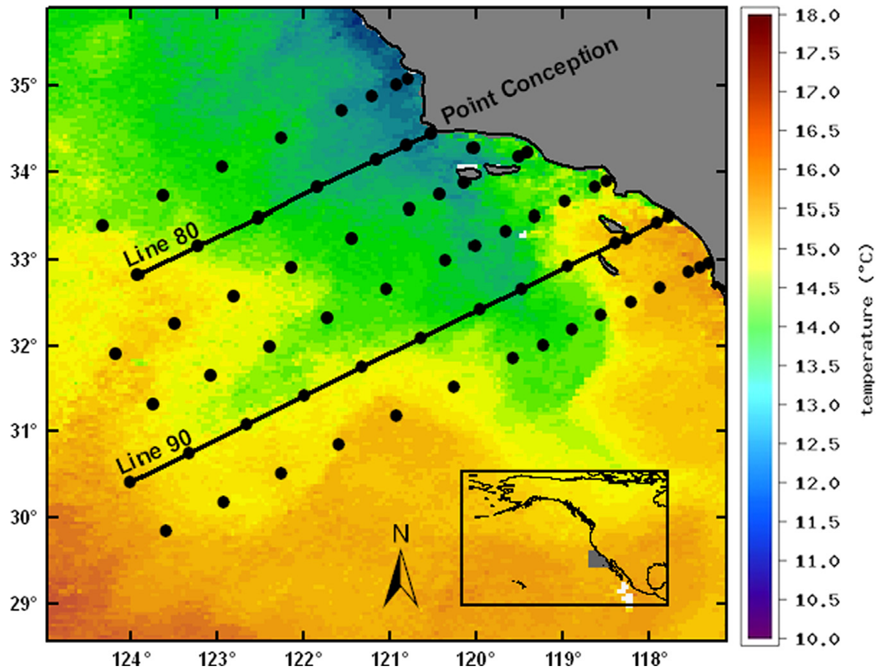

Fig. 1. Map showing CalCOFI/CCE-LTER grid overlaid on AVHRR SST image from 30 May 2000.

MacCall, 2009), and upper trophic level fish, seabirds, and marine mammals (Black et al., 2011; García-Reyes et al., 2013; Sydeman and Allen, 1999; Thompson et al., 2012). It is well known that upwelling in the CCE is spatially heterogeneous with major regional variation (Checkley and Barth, 2009; Bjorkstedt et al., 2011). One of the largest upwelling cells in the CCE is located off Point Conception, California, a large coastal promontory near the northern boundary of the Southern California Bight (SCB) region (Fig. 1). Cold, newly-upwelled waters deflected off Point Conception under northwesterly wind forcing spread southward in the vicinity of the Channel Islands, but typically remain well to the north of the California–Mexico border. Stratification in this region has increased over time (Roemmich and McGowan, 1995; Lavaniegos and Ohman, 2007; Aksnes and Ohman, 2009; see also Palacios et al., 2004 for the central California region), but it is unclear whether the pattern of change is best explained by trends in ocean warming or inter-decadal variability related to variation in the Pacific Decadal Oscillation and North Pacific Gyre Oscillation (Bograd and Lynn, 2003). Decadal-scale variability can be a dominant signal in the region (Di Lorenzo and Ohman, 2013). Because the SCB is characterized by spatial heterogeneity in water mass structure and a north–south ecotone where cold, upwelled waters meet warm and strongly stratified sub-tropical waters from the south (Hayward and Venrick, 1998), this region provides an unparalleled opportunity to study and resolve climate-related stratification and upwelling-ecosystem dynamics across physical and ecological boundaries where changes in pelagic ecosystems may be most apparent.

The California Cooperative Oceanic Fisheries Investigations (CalCOFI), supplemented recently by the California Current Ecosystem Long-Term Ecological Research (CCE-LTER) program, has been studying the pelagic ecosystem of the SCB since 1949, resulting in one of the longest-running multi-disciplinary, multi-trophic level studies in the world. Approximately 65 years of information (1949 through present) is available on physical oceanographic processes, hydrographic conditions, and plankton communities (Peña and Bograd, 2007). Studies of seabird communities were initiated in 1987 and now provide a 25-year time series for these taxa (Hyrenbach and Veit, 2003; Veit et al., 1996, 1997). Hyrenbach and Veit demonstrated that declines in various seabird populations, indexed by density at sea, were related to ocean warming, but these authors did not examine seabird numerical responses to variation in potential prey populations. More recently, Lavaniegos and Ohman (2007) showed that stratification negatively impacted zooplankton, specifically pelagic tunicates, in this region. Hsieh et al. (2009) showed negative relationships between an index of stratification and the abundance of larval mesopelagic fish in the region. Subsequently, Koslow et al. (2011, 2013) confirmed the decline in mesopelagic fish, which they attributed to shoaling of the oxygen minimum zone, and also demonstrated declines in many nearshore pelagic schooling species, including northern anchovy (*Engraulis mordax*). In this study, we hypothesize that changes in stratification and upwelling affect seabirds indirectly through intermediate trophic levels represented by zooplankton, specifically krill, and forage fish. To test this hypothesis, we derived trends and associations between upwelling, stratification, potential prey populations, and seabird density using the CalCOFI/CCE-LTER data set. Our specific questions are: (1) What are the temporal trends in seabird, krill, and forage fish populations? (2) Are trends and interannual variability in krill and forage fish related to changes in seabirds? (3) Are changes in seabirds and prey related to changes in stratification, upwelling, and the interaction between these variables? (4) Are changes in seabird abundance best explained by monotonic or cyclical changes in prey and/or physical properties? This study is important as understanding predator–prey relationships is key to the ecosystem-approach to fisheries management (Cury et al., 2011; Hunsicker et al., 2011; Smith et al., 2011).

2. Methods

The study region is located in the southern sector of the CCE. Six transect lines extending as far as 700 km offshore have been regularly sampled during the CalCOFI program, resulting in data that can be used to resolve spatial and temporal changes in the distribution and abundance of pelagic organisms and the environment simultaneously. Along these transects, permanent hydrographic and