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Introduction to CCE-LTER: Responses of the California Current Ecosystem to climate forcing

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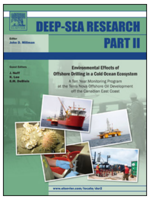

Introduction

Introduction to CCE-LTER: Responses of the California Current Ecosystem to climate forcing

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ABSTRACT

The *California Current Ecosystem* Long Term Ecological Research (CCE-LTER) site has been in existence Q2 since 2004. One of its primary objectives is to understand the response of the southern California Current ecosystem to climate forcing. The CCE-LTER site cooperates with the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program and complements CalCOFI's work through more extensive observations, process studies, and a modeling program. This special issue is focused on the long-term observations made by the CCE-LTER and CalCOFI programs, describing and understanding long-term changes in the physical, chemical, and biotic environment in the region. The papers in this issue highlight the climatological conditions during recent years and employ modeling to diagnose the principal forcing of meridional currents and eddy transport, both of which affect biotic responses. Changes in source waters in the region, and altered flushing of the Santa Barbara Basin, are considered. Temporal variations in inherent optical properties and in higher trophic levels, including seabirds and marine mammals, are presented. Key methodological developments presented include the incorporation of subsurface phytoplankton and light distributions in order to improve remotely sensed measures of primary production, and the validation of multi-frequency acoustic estimates of mesopelagic fish biomass. Results also highlight significant spatial differences across the CCE-LTER region, including cross-shore trends in microbial assemblages, and glider-resolved frontal features and zones of mixing associated with abrupt topography. Alterations to the spatial structure of the pelagic ecosystem must also be considered when evaluating future climate-related changes.

1. Introduction

A central question environmental scientists face today is: how will natural ecosystems respond to climate variability and climate change? One of the important resources available to address this question is the network of Long-Term Ecological Research (LTER) sites supported by the U.S. National Science Foundation. The LTER network includes 25 sites spanning biomes from the Arctic to the Antarctic and from the pelagic ocean to the Rocky Mountains. At all sites long-term measurements are carried out in five core areas: disturbance patterns, primary production, movement of inorganic nutrients, organic matter formation and decomposition, and studies of key populations. In addition, each site conducts intensive hypothesis-based research designed to understand processes that structure populations or mediate the fluxes of energy and matter between trophic levels. These observations and experiments are tied together with modeling at levels, ranging from organisms to the ecosystem (Robertson et al., 2012).

The California Current Ecosystem LTER (CCE-LTER) site was established in 2004. The site builds on the foundation of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program (Ohman and Venrick, 2003), as well as a suite of independent measurements. CalCOFI has made observations in the California Current System (CCS) since 1949. These observations were initially focused on small pelagic fishes in the CCS, Pacific sardine and northern anchovy, and their physical and biological environment. The 65-plus year time series has been invaluable for characterizing the response of the CCS to changing ocean climate. However, CalCOFI is primarily an ocean observing program, while CCE-LTER seeks to understand the underlying mechanisms that drive the response of the system to changing ocean climate. The central motivating questions of the CCE-LTER program are: What are the mechanisms leading to different ecosystem states in a coastal pelagic ecosystem? What is the interplay between changing ocean climate, community structure and ecosystem dynamics? Nested within these overarching questions, CCE-LTER is currently focused on the specific mechanisms leading to abrupt transitions in ecosystem state Q3 (Ohman and Venrick, 2003).

CCE-LTER uses three basic approaches to address these questions: time series observations, process studies, and modeling. One foundation of the time series observations is the CalCOFI program that currently surveys 70–85 stations off southern and central California four times a year, supplemented by several types of autonomous measurements. CCE-LTER augments CalCOFI observations to further characterize the biogeochemistry and the population structure of the pelagic ecosystem. Related programs make observations of marine mammals and seabirds. The results of these efforts

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are time series of differing length. The time series of core CalCOFI data, salinity, temperature, oxygen, zooplankton biomass and abundance, and ichthyoplankton abundance is, at the time of this writing, 66 years long. Since 1984 inorganic nutrients, chlorophyll *a* and primary production have been measured consistently. Seabirds have been enumerated since 1987 and marine mammals since 2002. The CCE-LTER program started making its observations in the fall of 2004. The main variables observed by the CCE program are concentrations of dissolved and particulate organic matter, bacterial biomass, and the biomass and population structure of phyto- and zooplankton using a variety of approaches.

CCE time series observations also include a series of autonomous measurements from *Spray* ocean gliders that operate continuously along two lines off Southern California, two interdisciplinary moorings, one in the core area of the CC and a second one off Pt. Conception, and remotely sensed data (Ohman et al., 2013b).

2. CCE-LTER special issue

The present issue of Deep-Sea Research II addresses some of the new insights that have been gained in the time series component of the CCE-LTER program since the advent of the CCE site. We do not attempt to summarize the results of other elements of the CCE program (Franks et al., 2013; Ohman et al., 2013a), but refer the reader to the CCE site bibliography for this purpose (http://cce.lternet.edu/publications).

A multidisciplinary approach is at the core of the study of ecosystems over long periods of time by members of the LTER network. This is illustrated by the diverse nature of the articles in this volume. Miller et al. (2014) provide the physical framework for the papers in this issue. They first summarize the oceanographic and climatological conditions in the CCS, describe changes in the perspectives in CCS physical processes and lastly, using the Regional Ocean Modeling System (ROMS), hindcast the physical oceanographic evolution during the CCE Process cruises. Over the last 10 years physical conditions in the CCE varied widely. The El Nino/Southern Oscillation (ENSO) varied between warm, neutral, and cool states over this time period, never reaching extremes. The North Pacific Gyre Oscillation (NPGO) was strongly positive over most of the time period, which, in our region, is indicative of enhanced upwelling. Remarkably cool conditions were observed in the CCS from late 2007 to early 2009 and from mid-2010 through 2012, which is consistent with the negative state of the PDO and the positive state of the NPGO during those intervals. Miller et al. (2014) note that the most important conceptual breakthroughs in the understanding of the dynamics of the CCS were: (a) the identification of the NPGO, which appears to control many aspects of the CCS such as salinity, chlorophyll, nutrients and oxygen; (b) the identification of a class of energetic small-scale variations in the upper ocean that are now referred to as sub-mesoscale variations that may enhance lateral and vertical mixing processes; (c) the realization that offshore Ekman pumping by wind-stress curl is equally important as coastal Ekman upwelling in supplying nutrients to the CCE; and (d) that sub-thermocline concentrations of oxygen have been declining over the last decades, driven likely by increasing stratification in the CCS and/or by changes in the oxygen content in the source of these deep waters that are advected into the region. The ROMS hindcasts of physical conditions during the CCE Process cruises showed that these cruises encountered widely varying climate states and physical conditions. Surface current fields for the 2011 and 2012 cruises will be used as a physical framework for the interpretation of the in situ biological measurements made during the process cruises.

Our ship-based observations are too coarse in space and time to resolve the physical processes that drive the CCE, in particular at the mesoscale. Davis and Di Lorenzo (2014a) utilize an eddy-resolving Regional Ocean Modeling System (ROMS) primitive equation model with terrain following coordinates to diagnose the primary processes forcing meridional currents and eddies in the California Current System (CCS) over the period from 1950 to 2008. First, the authors analyze alongshore currents in the California Current System. They consider the relative importance of local wind-stress curl (WSC) as contrasted with remote coastally-trapped waves (CTW) originating in the equatorial region, as dominant sources of the variability of mesoscale circulation and meridional transport at interannual and longer time scales. This is a problem to which modeling is well-suited because even the CalCOFI data set does not have sufficiently closely spaced stations to resolve the meandering finer-scale currents that would be linked to the wind-stress curl. Davis and Di Lorenzo (2014a) address this issue using two model configurations, both with and without coastal trapped waves of equatorial origins, to diagnose the equatorward meridional flow of the California Current. They focus on the region offshore of the narrow continental shelf. The authors find that while CTW explain much of the variation in sea-surface height in the California Current, it does not explain the variation in alongshore currents and associated transports, which instead are more closely related to wind-stress curl. This result is important for understanding the transport of nutrients, plankton, and other particles throughout the California Current System.

Davis and Di Lorenzo (2014b) illustrate another advantage of models in extending the observational record. Approximately 20 years of sea-surface height (AVISO) altimetry data were available to describe the mesoscale eddy field of the California Current, but nearly 60 years of modeled sea-surface height. Using the longer modeling record, they address the extent to which mesoscale eddy variability in the southern and northern CCS is controlled by variations in the wind-stress curl. The wind-stress curl gradient forces much of the mesoscale eddy activity in the northern sector, but relatively little of the eddy variability in the southern sector. They suggest that the eddies in the southern California (CCE-LTER) region are more related to intrinsic variability in the system. They hypothesize that southern California eddies are less directly linked to the winds because of the longer residence time of the eddies, hence greater opportunity for the eddies themselves to influence the background mean conditions, generating stronger feedbacks and lower predictability. The inference that there is greater intrinsic variability in eddy activity in the CCE-LTER region suggests that predicting future changes in eddy dynamics will be challenging.

Changes in hydrographic and chemical properties at depth in the CCS have been reported previously (Bograd et al., 2008; McClatchie et al., 2010). Bograd et al. (2014) analyze 28-year trends in dissolved nutrients and dissolved oxygen in source waters entering the CCE-LTER region to identify drivers of observed changes. Dissolved O_2 has been decreasing and nitrate, phosphate, and silicic acid have generally been increasing throughout the region at a density surface $\sigma_\theta = 25.8$, corresponding to the upper pycnocline region. At a deeper density surface ($\sigma_\theta = 26.5$) in the lower pycnocline, O_2 has also been decreasing and nitrate and phosphate increasing, but changes in silicic acid are more complex. Silicic acid has been increasing in the offshore region but decreasing in the nearshore region influenced by waters of the California Undercurrent coming from the south. This altered nutrient content of waters in the California Undercurrent is also expressed as a decline in the Si:N ratio throughout most of the region. There has also been a decline in the N:P ratio in deeper waters but an increase in N:P ratio in shallower waters. The agreement of the sign and magnitude of the shallower water trends with previously documented trends in the western and eastern subarctic Pacific (Whitney et al., 2013) suggests that these trends are linked to basin-scale climate forcing. The authors also use global ocean reanalysis products to illustrate the time lags necessary

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for circulation to propagate anomalies into the CCE-LTER region. They call attention to the possible role of altered Si:N in altering phytoplankton community composition.

Changes in oxygen and nutrients at depth have the potential to affect the biogeochemistry of the basins of the California Borderlands. Goericke et al. (2014) study the unusual biogeochemical conditions at the bottom of the Santa Barbara Basin that have been observed intermittently since 2006. During this time extremely low concentrations of nitrate and extremely high concentrations of nitrite were observed, 10 times higher than those observed previously. Such conditions are unprecedented relative to the 1984 to 2005 time period, suggesting that fundamental changes in the forcing of the bottom waters of the basin have occurred. The loss of nitrate from the system is driven by denitrification, which requires low concentrations of oxygen. Oxygen is replenished in the basin when it is flushed by dense waters that are raised above the sill of the basin by upwelling, and it declines during other times due to the remineralization of organic matter in the water column and in sediments. Indeed, the frequency of low-oxygen events in the bottom waters has increased. Increased rates of primary production and thus increased rates of sedimentation of organic matter to the bottom of the base are unlikely causes. Rather these changes are due to the decreased frequency and/or extent of flushing of the basin combined with a decrease of oxygen concentrations in these waters that enter the basin. The intermittent, dramatic increases of nitrite at the bottom of the basin likely represent a tipping point in the biogeochemical system driven by decreasing concentrations of oxygen in the bottom waters. This study thus illustrates that gradual changes in the drivers of a system can lead to a highly non-linear response of its properties, in this case concentrations of nitrite.

Near the beginning of the CCE-LTER program, a regular series of cross-shore sampling lines was established using the *Spray* ocean gliders (Sherman et al., 2001), which now includes CalCOFI lines 80 and 90 in the CCE region and line 66.7 off Monterey Bay. Johnston and Rudnick (2014) analyze an extensive series of six years of measurements of the cross-shore patterns in mixing, as inferred from Acoustic Doppler Profiler-measured shear and CTD-derived strain. They uncover a striking contrast between the patterns of mixing along the two more northern lines in comparison with the southernmost line that transits the southern California Bight and region offshore. Mixing is elevated close to shore along the two more northern lines and decays with distance offshore, while mixing along line 90 is elevated in a region located approximately 200 km from shore, near the Santa Rosa-Cortes Ridge. This zone of offshore elevated mixing, associated with rough topography, is linked to dissipation of both diurnal (D1) and semidiurnal (D2) internal tidal energy. The biological and biogeochemical consequences of such topographically-linked mixing have not been fully explored.

The same glider series, from lines 80 and 90, was independently analyzed by Powell and Ohman (2014) in order to understand the extent of co-variability of biological and physical fronts. While fronts tend to be located closer to shore along line 80, they tend to be further offshore along line 90, near the region of altered mixing identified by Johnston and Rudnick (2014). Horizontal density fronts are regions of marked changes in zooplankton acoustic backscatter and phytoplankton fluorescence, a biomass proxy. Frontal zones also tend to be regions of enhanced biomass of phytoplankton and mesozooplankton, as inferred from the glider-based sensors. These authors also illustrate the enhanced foraging success that a mobile predator could experience by searching along a frontal gradient. Because satellite imagery suggests that the incidence of Chl-*a* and sea-surface temperature fronts in the Southern California region have increased over the past 14–29 years (Kahru et al., 2012), the processes occurring at fronts are expected to become more important in the future. Such glider-derived results have contributed to making frontal processes a central focus of the current CCE-LTER experimental process cruise studies (Landry et al., 2012; Ohman et al., 2013a)

The CCE-LTER program relies primarily on observations made by ships, gliders or moorings, which are either physically located in one place or move slowly through the ocean, not allowing for a synoptic view of the system. Observations made by satellites do not suffer from this shortcoming. However, merging observations made by different satellites and relating these to in situ ocean properties is often difficult. Kahru et al. (2013) address these issues. They estimate inherent optical properties in the California Current from observations made by four different ocean color sensors (OCTS, SeaWiFS, MODISA and MERIS). Using inversion models they derive a 16-year time series for the phytoplankton absorption coefficient at 440 nm, absorption by dissolved and detrital organic matter at 440 nm, and the particle backscattering coefficient at 490 nm. The uncertainty of these derived properties is still high due to a limited number of in situ match-ups, their uneven distribution in space, and uncertainty associated with the raw sensor data. However, the time series show very interesting patterns. Along a wide band along the coast the phytoplankton absorption coefficient, a proxy for phytoplankton biomass, has been increasing over the last 16 years (1996–2012). In contrast, a significant decrease has been observed in the oligotrophic North Pacific gyre. The trend along the coast is positively correlated with increasing wind speeds, related to upwelling, suggesting likely drivers for these trends.

Over the last decade remote ocean color observations have increasingly being used not only as a proxy for chlorophyll *a* (Chl *a*) but phytoplankton carbon biomass, depth-integrated primary production (PP) and export production. For the estimation of the latter two variables the subsurface distribution of phytoplankton biomass and the physiology of the resident populations are potentially important. Jacox et al. (2013) ask how sensitive models of PP based on remotely sensed data are to the parameterization of phytoplankton physiology and the subsurface Chl *a* and light fields. The authors base their study on the 1985–2011 CalCOFI record of Chl *a* and primary production. The authors only find modest improvement to model-based estimates of PP when measured surface Chl *a* is substituted for remotely sensed surface Chl *a*. However, dramatic improvements are observed when in situ depth-resolved data for Chl *a* and light are used. The authors point out that today such in situ data are easily obtained from gliders and potentially from Bio-Argo floats. The authors show that the inclusion of glider data in the PP models substantially improves estimates of PP and suggest that this be done on a routine basis.

Taylor et al. study microbial community patterns in the CCE-LTER region using a set of samples collected between 2004 and 2010 on 25 CalCOFI cruises as part of the CCE augmented sampling. They use flow cytometry and digital epifluorescence microscopy to understand the spatial and seasonal variations of different components of the autotrophic and heterotrophic plankton $<200\ \mu m$. Although diatom biomass was elevated nearshore along line 80 and in the Santa Barbara Basin, a surprising finding is the relatively large contribution of autotrophic dinoflagellate biomass to the microplankton assemblage at all times of year. In some years (e.g., 2005–2006) dinoflagellate biomass exceeded diatom biomass, even in the upwelling regions. Autotrophic picoplankton (principally the cyanobacteria *Synechococcus* and *Prochlorococcus*) were ubiquitous, but their abundance less variable across the region. The size composition of the assemblage was consistently dominated by larger microplankton ($>20\ \mu m$) in the vicinity of Pt Conception, while the nanoplankton (2–20 μm) dominated the autotrophic assemblage everywhere else, including along line 90. The cross-shore patterns were markedly different

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along line 90, where the microplankton did not dominate biomass nearshore; peak biomass was instead found approximately 190 km from shore. This offshore peak in autotrophic biomass coincides spatially with the zone of enhanced mixing documented by Johnston and Rudnick (2014). On average, living cells (phytoplankton, heterotrophic protists, and heterotrophic bacteria) are found to comprise about half of the total particulate organic carbon present. Taylor et al. also find that the ratio of autotrophic C: Chl-*a* varies in a systematic manner with depth in the euphotic zone and, in addition, with the depth of the nitracline. These relationships will be especially valuable for CCE modeling efforts.

The last three papers of this volume study some of the higher trophic levels of the CCE: mesopelagic fishes, marine mammals, and seabirds. The importance of these trophic levels for our understanding of the ecosystem can be twofold. Such organisms may be important mediators of fluxes of energy and matter, as has recently been shown for mesopelagic fishes (Davison et al., 2013). These organisms may also be sensitive indicators of ecosystem state, because they tend to integrate changes in the ocean environment over larger space and time scales. However, estimating the biomass and abundance of these groups poses special challenges as the organisms are often sparsely and patchily distributed in space and time. Davison et al. (2014) use both trawling and active acoustics to estimate the biomass of mesopelagic fish in the CCE. The uncertainty associated with trawls is the trawl capture-efficiency of the fish which can vary with size, species, and time of day. Trawls are required for the validation of acoustic estimates of biomass, thus impacting the accuracy of acoustic estimates as well. The authors show that variations in trawl capture efficiency can affect acoustic estimates of biomass estimates 5-fold. In addition differences in acoustic backscattering among fishes (e.g., the presence and size of a swimbladder) and unknown mixtures of populations with dramatically differing backscattering characteristics also add uncertainty to such acoustic estimates. The authors carefully correct their estimates of mesopelagic fish biomass for such biases and quantify the uncertainty associated with these estimates. They conclude, consistent with their earlier studies (Davison et al., 2013), that the biomass of mesopelagic fishes of southern California is 25–37 $\mathrm{g\,m^{-2}}$. Such high levels of biomass suggest that these fish have a significant role in the ecosystem. A future question is how this role will change as their biomass has been decreasing over the last decades (Koslow et al., 2011).

Cetaceans are among the charismatic species of the marine environment and the CCS provides a habitat for numerous taxa. They are potentially impacted by human activities such as fishing, shipping, and naval operations. Campbell et al. (2014) use visual surveys carried out on CalCOFI cruises to access distributions and trends in the abundance of the six most commonly encountered cetacean species off southern California over the last decade. The unique aspect of this study is the long-term continuous observations that allow the analysis of trends with time. Blue whales, fin whales, and humpback whales were the most abundant baleen whales. Short-beaked common dolphins, Pacific white-sided dolphins, and Dall's porpoise were the most frequently encountered small cetaceans. Significant spatial and seasonal variability is observed for most species. A generalized additive model is used to estimate long-term trends accurately. No significant long-term trends are observed for blue whale, fin whale, humpback whale, short-beaked common dolphin or Dall's porpoise abundance. Pacific white-sided dolphins showed a significant decrease over the 10-year study period. Environmental parameters that correlated with this decrease are not identified; complicating the interpretation is the presence of northern and southern subpopulations of this species. The data that were collected as part of this study will be used to model and predict the habitat of these species. This model will be used by the US Navy off Southern California to minimize adverse impacts of their operations on these species.

Sydeman et al. (2014) analyze trends and interannual variability in seabirds, enumerated for the last 25 years at sea on CalCOFI cruises. They ask whether variability in seabird densities covaries with euphausiids (krill) or forage fish abundance, and whether seabirds and their prey are affected by changes in ocean stratification and upwelling. The authors use the CalCOFI ichthyoplankton data as an index for the abundance of the adult fish that spawned them, as others have before them. They find an overall decline in seabirds (combined abundance of 23 species), averaging $-2.2\%\ \mathrm{yr^{-1}}$ over the past 25 years. The decline was more pronounced along the northern line 80 than on the more southern line 90. The decline in seabirds occurred despite a temporal increase in abundance of euphausiids (*Thysanoessa spinifera* and *Euphausia pacifica*), and is instead related to the decrease in abundance of nearshore fishes, especially northern anchovy. However, in contrast to the longer term trends, Sydeman et al. (2014) find that detrended interannual variability in springtime seabird density is best explained by the density of euphausiids (*T. spinifera* and *E. pacifica*) measured in springtime plus the density of larval fish measured in the preceding winter. They also suggest that seabird density may have become more closely linked to euphausiid density after 1999. Overall, their results suggest that the effects of ocean climate on seabird abundance are mediated through the availability of their prey.

In summary, the papers in this special issue provide an introduction to some of the diverse responses of the ecosystem, studied by the CCE-LTER, to changing ocean climate. Many of the studies are based on CalCOFI data and highlight the distinct advantages to linkage of the LTER site with the deep historical perspective provided by the 66-year long CalCOFI time series. The studies illustrate the importance of conducting not merely single point measurements over time, but rather space-resolving time series that resolve spatial patterns on a regional scale. Especially in dynamic Eastern boundary current ecosystems, there are important cross-shore and regional variations that must be considered in understanding susceptibility to climate forcing. This volume also illustrates the importance of autonomous measurements, multi-frequency acoustics, and satellite remote sensing, in uncovering key elements of frontal dynamics, ocean mixing, and differential responses of the nearshore and offshore ocean to climate forcing. This collection of papers also illustrates the vital role of integration of different measurement approaches. Each method, whether shipboard, robotic vehicles, or remote sensing, has advantages and disadvantages, and the greatest understanding comes from combinations of diverse measurements spanning different time-space domains. Multiple measurement approaches also permit independent validatation.

In some cases, the new time series developed here are too short to discern and interpret temporal trends. However, as these observational programs continue into the future and continue to be assimilated into models, we have a framework for understanding both natural climate variability and the anthropogenically induced forcing that will alter the pelagic ecosystem in the future.

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