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Habitat compression and expansion of sea urchins in response to changing climate conditions on the California continental shelf and slope (1994–2013)

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ABSTRACT

Echinoid sea urchins with distributions along the continental shelf and slope of the eastern Pacific often dominate the megafauna community. This occurs despite their exposure to naturally low dissolved oxygen (DO) waters ($<60\ \mu mol\ kg^{-1}$) associated with the Oxygen Limited Zone and low-pH waters undersaturated with respect to calcium carbonate ($\Omega_{CaCO3}<1$). Here we present vertical depth distribution and density analyses of historical otter trawl data collected in the Southern California Bight (SCB) from 1994 to 2013 to address the question: Do changes in echinoid density and species' depth distributions along the continental margin in the SCB reflect observed secular or interannual changes in climate? Deep-dwelling burrowing urchins (*Brissopsis pacifica*, *Brisaster* spp. and *Spatangus californicus*), which are adapted to low-DO, low-pH conditions appeared to have expanded their vertical distributions and populations upslope over the past decade (2003–2013), and densities of the deep pink urchin, *Strongylocentrotus fragilis*, increased significantly in the upper 500 m of the SCB. Conversely, the shallower urchin, *Lytechinus pictus*, exhibited depth shoaling and density decreases within the upper 200 m of the SCB from 1994 to 2013. Oxygen and pH in the SCB also vary inter-annually due to varying strengths of the El Niño Southern Oscillation (ENSO). Changes in depth distributions and densities were correlated with bi-monthly ENSO climate indices in the region. Our results suggest that both a secular trend in ocean deoxygenation and acidification and varying strength of ENSO may be linked to echinoid species distributions and densities, creating habitat compression in some and habitat expansion in others. Potential life-history mechanisms underlying depth and density changes observed over these time periods include migration, mortality, and recruitment. These types of analyses are needed for a broad suite of benthic species in order to identify and manage climate-sensitive species on the margin.

1. Introduction

Continental margin ecosystems in eastern boundary upwelling regions such as the west coast of North America experience dynamic natural variations in biogeochemical cycles on various spatiotemporal scales. Oscillations in ocean-atmosphere coupled processes occur naturally on millennial (Moffitt et al., 2015), decadal (Mantua et al., 1997), and interannual (Bjerknes, 1966) time-scales; these can have basin-wide effects on population dynamics and global climate change variables such as seawater pH, dissolved oxygen (DO), and temperature (reviewed in Levin et al., 2015). The Southern California Bight (SCB) is a 700-km long region influenced by the upwelling of cold, nutrient-rich, deep water characterized by relatively low DO, low pH, and high carbon dioxide (CO_2). Benthic and epibenthic organisms may already be functioning at their physiological limits at the seawater-seafloor interface where the continental slope intersects with a permanent dissolved Oxygen Minimum Zone (OMZ) and Carbon Maximum Zone (Paulmier et al., 2011), therefore making these regions particular 'hotspots' of future climate change (Gruber, 2011).

Oxygen Limited Zones (OLZs) are the regions above and beneath the OMZ where DO concentrations of $<60\ \mu mol\ kg^{-1}$ are often considered hypoxic habitat for marine organisms (Gilly et al., 2013), although this threshold may not be relevant for organisms with very low metabolic oxygen demands (Seibel, 2011; Somero et al., 2016). Time-series analysis from 1984 to 2006 of quarterly cruise data in the SCB collected by the

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California Cooperative Ocean Fisheries Investigations (CalCOFI) reveal oxygen declines, with an average decrease in DO of ~1 μmol kg^{-1} yr^{-1} at 200-m stations and a shoaling of the OLZ boundary of >80 m at some inshore stations (Bograd et al., 2008). An updated analysis of these data (1984–2010) showed a decrease of 0.76 μmol kg^{-1} yr^{-1} at the 25.8 kg m^{-3} isopycnal (Bograd et al., 2015). Due to microbially-mediated remineralization processes, similar reductions in pH and increases in pCO_2 are expected to have accompanied the expansion of low oxygen zones in the SCB (Gilly et al., 2013; Gruber, 2011; Paulmier et al., 2011; Reum et al., 2016). Seawater pH and DO are strongly correlated in nearshore kelp forests (Frieder et al., 2012) and in the deep sea (Alin et al., 2012; Nam et al., 2015). In addition, secular increases in nutrient concentrations and chlorophyll *a* have been observed from the same CalCOFI dataset (Bograd et al., 2015). One potential mechanism for shoaling hypoxia and changes in nutrients in the SCB include a strengthening of the CA Undercurrent, which originates from subtropical equatorial water from the south and is characterized by relatively warm, high saline, low DO, and low pH water (Bograd et al., 2015).

Koslow et al. (2011) reported striking shifts in mesopelagic and demersal larval fish community structure accompanying these decadal changes in midwater DO. Twenty four of 27 larval fish taxa collected by seasonal CalCOFI cruises demonstrated a strong relationship with midwater DO and multiple climate indices such as the Pacific Decadal Oscillation (PDO), El Niño Southern Oscillation (ENSO), and the North Pacific Gyre Oscillation (NPGO) (Koslow et al., 2011, 2015). Although the CalCOFI biological time-series provides extensive spatial and temporal coverage of pelagic species, the interactions of benthic faunal populations with climate variability along the SCB continental margin have been understudied. The phenomenon of vertical habitat compression in the ocean due to shoaling hypoxia was hypothesized to negatively affect aerobic groundfish (McClatchie et al., 2010) and mesopelagic fish (Netburn and Koslow, 2015) in southern CA and billfish in the Eastern Tropical Pacific (Prince and Goodyear, 2006; Stramma et al., 2012). However, few datasets exist to assess trends in megafauna species populations that dominant the benthos such as echinoids in the SCB (Keller et al., 2012).

Beyond the longer-term changes in oxygenation and likely pH and pCO_2, the SCB is highly dynamic on interannual, seasonal, and even diurnal and semidiurnal time scales (Nam et al., 2015; Booth et al., 2012; Send and Nam, 2012). For example, during El Niño events, elevated temperatures and reduced upwelling lead to low productivity, less respiration and biogeochemical drawdown, thus higher oxygen levels (Ito and Deutsch, 2013), while the opposite occurs during La Niña events (Nam et al., 2011). Over the last 25 years, the Multivariate ENSO Index (MEI), a composite of six key ocean-atmospheric variables: sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness (Wolter and Timlin, 2011), indicates a range of El Niño and La Niña strengths occurring in the Pacific Ocean, including one exceedingly strong El Niño in 1997–1998 (Fig. 1). Nam et al. (2011) advise caution when extrapolating their correlation results from a single El Niño-La Niña cycle to other ENSO indices, and few studies examined the direct relationship between ENSO and dissolved oxygen (see Arntz et al., 2006) despite the abundance of historical cruise data and the potentially important ecological implications (McClatchie, 2014).

Echinoderms are important benthic fauna ecologically; they are often identified as ecosystem engineers and in some cases, keystone predators or grazers (Paine, 1966). Biocalcification by echinoderms (*e.g.* sea urchins, sea stars, cucumbers, brittle stars, crinoids) contributes to globally significant carbon production rates that may rival production rates of coral reefs (Lebrato et al., 2010), and are surprisingly tolerant to low carbonate saturation states (Lebrato et al., 2016).

In the SCB, multiple deep-dwelling sea urchin species are abundant over broad depth ranges (Thompson et al., 1993) characterized by sharp gradients in oxygen, pH, and Ω (saturation state) levels that are comparable to or much lower than future ocean acidification and deoxygenation scenarios predicted for the surface ocean (Alin et al., 2012; Levin and Dayton, 2009; Nam et al., 2015). Experiments suggest that multiple life-history stages of calcifying benthic organisms, including echinoid urchins, will respond negatively to ocean acidification and hypoxia conditions (Dupont et al., 2010; Frieder, 2014; Kroeker et al., 2013). The vast majority of these studies have been conducted on shallow-water species however, and the response of deep-margin species to deoxygenation, ocean acidification, and calcium carbonate saturation ($\Omega_{CaCO_3}=1$) reduction is poorly understood (Barry et al., 2014; Hofmann et al., 2010; Taylor et al., 2014).

Detecting faunal response to long-term environmental change requires time-series sampling (Glover et al., 2010). The Southern California Coastal Water Research Project (SCCWRP) is a collaborative inter-agency environmental monitoring program that makes publicly available a time-series dataset of georeferenced benthic and epibenthic megafauna community data in southern California along the continental shelf and slope. The SCCWRP otter trawl surveys of the SCB shelf and slope benthos have occurred every 4–5 years since 1994 to water depths of 200 m, providing 5 time points in order to assess population trends in benthic fauna. In 2003 the SCCWRP *Bight* program extended their sampling depths down to 500 m, providing only 3 survey time points to the present, but extending spatial coverage into deep waters. These fishery-independent data provide a unique suite of multi-decadal samples that can be used to address questions about benthic community changes over time in the SCB.

The objective of this study was to investigate temporal changes in (1) depth distributions and (2) density estimates of five continental margin sea urchin species throughout the SCB from 1994 to 2013 to better understand echinoid response to environmental change. We hypothesized that various depth distribution parameters of deeper-occurring urchin species, which are tolerant to low oxygen, high CO_2 conditions in the upper OMZ (Helly and Levin, 2004) and OLZ (Gilly et al., 2013) would exhibit evidence of habitat expansion consistent with observed shoaling oxyclines in the region (Bograd et al., 2015; Bograd et al., 2008). This secular trend would suggest that these species have expanded their distribution into shallower waters enabled by a combination of environmental adaptation and ecological interactions. Urchin species with shallower distributions were hypothesized to be more vulnerable to expanding OMZ conditions and to have experienced habitat compression over this time period. In addition, we hypothesized that the density of shallower-occurring urchins would decrease in the upper 200 m from 1994 to 2013 due to the shoaling and intensification of hypoxic waters, and the density of deeper-occurring urchins in the upper 500 m would increase from 2003 to 2013 due to migration from deeper depths as habitat compression excludes shallower competitors. Alternatively, these trends could also be driven by environmental factors other than oxygen that may co-vary with time, such as changes in dissolved CO_2, food, temperature, and ecological interactions. Chlorophyll *a* concentration in the SCB has increased over recent decades (Bograd et al., 2015) and could lead to more food and higher densities in all species over time. In contrast, El Niño conditions, which occurred in 1997–1998 and 2002–2003 are associated with higher oxygenation and lower phytoplankton and kelp production (Ito and Deutsch, 2013), and should produce an opposite response to that expected from expanding OMZs. We