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Depths, migration rates and environmental associations of acoustic scattering layers in the Gulf of California

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ABSTRACT

The ecology in the Gulf of California has undergone dramatic changes over the past century, including the emergence of Humboldt squid (*Dosidicus gigas*) as a dominant predator. In the face of these changes, we compare the ubiquitous and ecologically important concentrations of mid-water organisms that comprise acoustic scattering layers to published results, describing their occurrence in detail and showing that they remain similar to features described 50 years previously. To classify scattering layers in the region, we applied an automatic detection algorithm to shipboard echosounder data from four cruises. We consistently detected a broad (>200 m) background layer with a mean daytime bottom boundary depth of 463 ± 56 m (night: 434 ± 66 m), a near-surface layer with mean daytime bottom depth of 43 ± 40 m (night: 61 ± 38 m), and a main migrating layer with mean bottom depth of 333 ± 76 m (night: 54 ± 27 m). Diel vertical migration rates for dusk ascents reached a maximum, on average, of 8.6 ± 3.1 cm s^{-1}, and dawn descents averaged a maximum of 6.9 ± 2.4 cm s^{-1}. Deep scattering layers were often found concurrent with regions of severe hypoxia and we used environmental data to test for the association of scattering layer boundaries with environmental parameter values. Although results were inconsistent, we found scattering layer depths to be more highly associated with temperature and density than with oxygen. These results suggest that the recent success of *D. gigas* in the Gulf of California is not likely to be attributable to the effects of shoaling oxygen minimum zones on acoustic scattering layers.

1. Introduction

In every ocean horizontally-extensive, continuous mid-water features known as acoustic scattering layers have been identified using echosounders (Tont, 1976; O'Brien, 1987). Composed of densely concentrated planktonic and nektonic organisms whose echoes cannot be individually resolved (Barham, 1966; Tont, 1976), scattering layers are found throughout the entire water column from surface layers down to at least 2000 m (Burd et al., 1992; Opdal et al., 2008). Most commonly, the organisms detecting in scattering layers are krill, shrimp, small squid, and mesopelagic fish species like myctophids (Butler and Pearcy, 1972; Simard and Mackas, 1989; Benoit-Bird and Au, 2002). A single layer can be on the order of meters to tens of meters thick (Sameoto, 1976; Thomson et al., 1992), and can be hundreds of kilometers in extent (Chapman and Marshall, 1966). It is no surprise, therefore, that the mesopelagic organisms detected in these features are keystone components of pelagic ecosystems (McGehee et al., 1998; Fock et al., 2002; Hays, 2003) and contain an estimated 10 billion tons of mesopelagic fish worldwide, likely representing the bulk of fish biomass in the oceans (Irigoien et al., 2014).

In the Gulf of California, the primary study on scattering layer characteristics was completed nearly fifty years ago (Dunlap, 1968). This region, however, has gone through extensive ecological changes in that time period and there have been substantial changes in the degree of human influence in the region both locally, where the population and associated pressures of just the peninsula side increased nearly 30-fold between 1940 and 2010 (Instituto Nacional de Estadística y Geografía, 2014), and regionally due to climate change, increased agricultural runoff and the diversion of nearly all of the freshwater input from the Colorado River (Rodriguez et al., 2001). As a result, the biota in the region has undergone striking changes. In a recent study, Sagarin et al. (2008) found dramatic losses of intertidal species abundance and diversity and substantial decreases in pelagic species abundance in the region relative to descriptions provided by Steinbeck and Ricketts (1941).

Abbreviations: CI, confidence interval; CTD, conductivity, temperature and depth sensor; DSL, deep scattering layer; DVM, diel vertical migration; OMZ, oxygen minimum zone; PAR, photosynthetically active radiation; SOR, standardized odds ratio

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A significant change in the biota noted by Sagarin et al. (2008) is the appearance, likely in the 1970s, of one of the region's most important predators, the Humboldt squid (*Dosidicus gigas)* (Rosas-Luis et al., 2008). Humboldt squid are voracious predators whose diet is dominated by scattering layer organisms, primarily the myctophids *Benthosema panamense* and *Triphoturus mexicanus* and the small squid, *Pterygioteuthis giardi* (Markaida et al., 2008). Indeed, studies of squid diet and behavior have been a primary source of insight into the composition and distribution of mid-water fishes in the Gulf (Markaida et al., 2008). Since *Dosidicus* is well-adapted to low-O_2 environments (Rosa and Seibel, 2010), and because their abundance in other regions has been correlated with prey abundance (Stewart et al., 2014), it has been proposed that squid are successful in the Gulf because of the proximity of deep scattering layers to a shallow, extensive oxygen minimum zone (OMZ) (Robison, 1972; Markaida et al., 2008).

The OMZ in the Gulf of California is extensive, with hypoxic waters (<0.5 mL $L^{-1} \approx 1.7$ kPa) extending from 200 m to 1200 m depth on average, and is overlain with a narrow oxygen limited zone (0.5 mL $L^{-1} \approx 1.7$ kPa $< O_2 < 1.5$ mL $L^{-1} \approx 5.1$ kPa) that overlaps with the euphotic zone (Gilly et al., 2013). What is not known is to what degree the depth of the OMZ controls the depth of scattering layers. If the features are linked, as suggested by Gilly et al. (2013), then *Dosidicus* may have greater success when OMZs shoal because their food sources are squeezed into a smaller portion of the water column. If the two features are not linked, however, then a shallow OMZ may influence the success of *Dosidicus* by bringing an environmental habitat to which they are well-adapted within range of prime feeding grounds, and their prey would be increasingly exposed to low-oxygen water in which they typically reduce their activity (Childress and Seibel, 1998). It has been shown that El Niño Southern Oscillation (ENSO) events strongly influence squid distribution in the Gulf (Rosas-Luis et al., 2008; Hoving et al., 2013) and the relationship of environmental conditions to scattering layer distribution may help explain some of this habitat shift. The questions of what factor or factors control scattering layer depth, and how scattering layer characteristics have changed from fifty years ago are thus of importance to the ecology and management of this important fishery species.

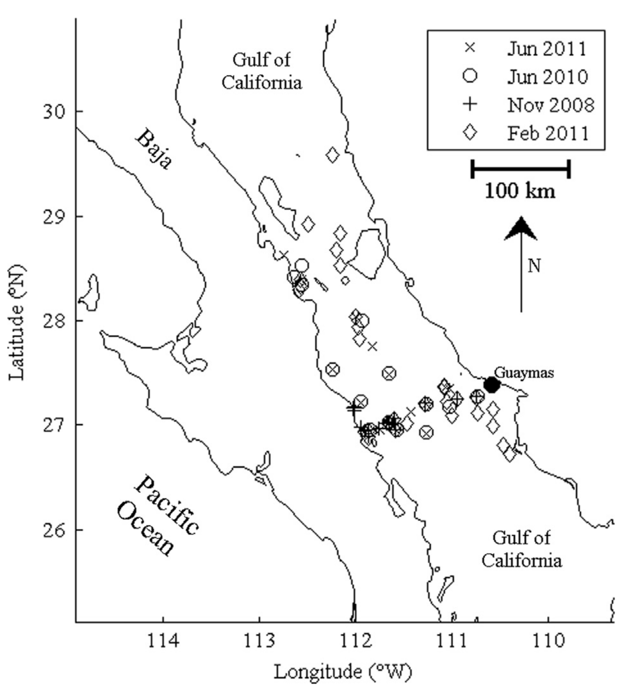

Fig. 1. Map of the research area in the Guaymas Basin in the Gulf of California (CEC, 2009). Symbols indicate CTD profile collection locations for all four cruises.

In other regions, along with oxygen (Devol, 1981; Bertrand et al., 2010) additional environmental factors have been linked with the depths of scattering layers including light (Clarke, 1970), density layering (Herdman, 1953; Weston, 1958), thermocline depths (Kumar et al., 2005), low-salinity water (Forward, 1976), and pressure (Forward and Wellins, 1989). Under various conditions, each of these environmental variables has been shown to play a role in controlling organisms' depth after a nightly surface feeding foray. This process, known as diel vertical migration (DVM), is commonly observed in scattering layers and has important implications for turbulent mixing, biogeochemical cycling, the transport of nutrients and gases, and the life cycles and behavior of scattering layer organisms and their predators (Longhurst et al., 1990; Steinberg et al., 2000; Kunze et al., 2006; Bianchi et al., 2013).

The gaps in our understanding of scattering layer behavior in the Gulf of California, the broad ecological implications of changes in this behavior, and the potential links between environmental conditions and scattering layers have inspired our study's two goals: (1) to describe general features of acoustic scattering layers in the Gulf of California, including rates of DVM, and (2) to understand the environmental forces in the region that determine the depths of these layers. As Childress and Seibel (1998) point out, "within a given geographic area, [environmental parameters] are almost hopelessly confounded and it is difficult, if not impossible, to demonstrate an adaptive response to one" of the variables. Using acoustic data from four research cruises, we described layer features and attempt a comprehensive analysis that would untangle the influence of environmental variables on the vertical positions of these mixed assemblages.

2. Methods

2.1. Summary of approach

Data for this study were collected on four multi-week cruises in the Guaymas Basin region of the Gulf of California (Fig. 1) in November 2008, June of 2010, February of 2011, and June of 2011. Conductivity, temperature, depth (CTD), oxygen and light profiles were collected a total of 103 times, and acoustic data were recorded continuously. Scattering layers within acoustic echograms were identified by applying an automatic layer detection algorithm to all data, enabling each layer's depth and migration speed to be tracked. The scattering layers surrounding the CTD profile sites were subsequently examined and three statistical approaches were used to study the environmental context in which the layers appear.

2.2. Field site and data collection

The Gulf of California is a 1000 km long, 160 km wide subtropical body of water characterized as a series of troughs, ridges and basins that range in depth from 100 to 3600 m (Rusnak et al., 1964). The water masses making up the Gulf are strongly affected by Pacific Ocean fluctuations including El Niño, with surface temperatures ranging from 16 °C in winter to 31 °C in summer and a surface salinity typically above 35 (Robles and Marinone, 1987) that decreases with depth.

Acoustic data from the two June cruises aboard the RV New Horizon were collected with Simrad EK60 split-beam, pole-mounted echosounders at 38, 70, 120 and 200 kHz with 512 μs pulse lengths. The 38 kHz transducer had a 12° beam-width and the others had 7° beam widths. For the November and February cruises, acoustic data collection was from the RV BIP XII with a