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Multi-scale responses of scattering layers to environmental variability in Monterey Bay, California

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ABSTRACT

A 38 kHz upward-facing echosounder was deployed on the seafloor at a depth of 875 m in Monterey Bay, CA, USA (36° 42.748′N, 122° 11.214′W) from 27 February 2009 to 18 August 2010. This 18-month record of acoustic backscatter was compared to oceanographic time series from a nearby data buoy to investigate the responses of animals in sound-scattering layers to oceanic variability at seasonal and sub-seasonal time scales. Pelagic animals, as measured by acoustic backscatter, moved higher in the water column and decreased in abundance during spring upwelling, attributed to avoidance of a shoaling oxycline and advection offshore. Seasonal changes were most evident in a non-migrating scattering layer near 500 m depth that disappeared in spring and reappeared in summer, building to a seasonal maximum in fall. At sub-seasonal time scales, similar responses were observed after individual upwelling events, though they were much weaker than the seasonal relationship. Correlations of acoustic backscatter with oceanographic variability also differed with depth. Backscatter in the upper water column decreased immediately following upwelling, then increased approximately 20 days later. Similar correlations existed deeper in the water column, but at increasing lags, suggesting that near-surface productivity propagated down the water column at 10–15 m d^{-1}, consistent with sinking speeds of marine snow measured in Monterey Bay. Sub-seasonal variability in backscatter was best correlated with sea-surface height, suggesting that passive physical transport was most important at these time scales.

1. Introduction

Physical variability is a fundamental feature of the ocean's pelagic habitat, and the responses of pelagic organisms to this variability play a large role in determining their distribution, abundance, and survival. As such, understanding the effects of physical change and variability on ocean life has long been recognized as a central challenge in oceanography and marine ecology. Physical variability can influence organisms at the individual or population level, and its effects can be direct (e.g. advection) or indirect (e.g production fertilized by upwelled nutrients).

"Physical-biological coupling" has most often been studied in the plankton, whose abundance and distribution are closely tied to physical variability (Platt and Denman, 1975). However, because ocean currents are variable across a wide range of spatial and temporal scales, the division between plankton and nekton (Haeckel, 1890) is somewhat arbitrary. Coupling to physical processes is thus expected to extend from zooplankton to micronekton: animals roughly 2–10 cm in length with swimming abilities in between those of drifting plankton and freely swimming nekton (Brodeur and Yamamura, 2005). These include krill, pelagic shrimps, small squids, and fishes such as myctophids.

Assemblages of micronekton are important constituents of deep scattering layers (DSLs, Dietz, 1948; Barham, 1956). DSLs are layers of elevated animal biomass, and consequently acoustic backscattering, which are found worldwide in the ocean's mesopelagic zone, ≈200 to 1000 m below the surface. Many undergo diel vertical migration (DVM) of several hundred meters to feed near the surface each night (Dietz, 1948; Hays, 2003). Micronekton, from both the meso- and epipelagic (0–200 m depth), are important food resources for a variety of larger fish, birds, and marine mammals and are important carriers of energy, both up the food chain and down the water column. Recent research suggests that the global biomass of small fishes in the DSL is on the order of 10^{10} metric tons, and that they could respire as much as 10% of primary productivity in the deep ocean (Kaartvedt et al., 2012; Irigoien et al., 2014). They are probably also influenced by physical variability, especially in dynamic environments.

The California Current is one such dynamic environment. As in other eastern-boundary systems, Ekman pumping driven by

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seasonal equatorward-flowing winds brings nutrient-rich water to the surface near the coast, fueling a highly productive ecosystem. Though limited in area, upwelling systems support a disproportionate amount of global fish landings (Pauly and Christensen, 1995), and attract large predators from great distances (Block et al., 2011). The seasonal cycle of upwelling and productivity in the California Current is generally consistent (Pennington and Chavez, 2000), but within any given year upwelling is irregular, supplying nutrients to the food web in episodic pulses. Upwelling is also spatially variable. Mesoscale (10–100 s of km) squirts, jets, eddies, and coastal waves all introduce variability into the movement of water (Keister and Strub, 2008).

The effects of oceanic variability on micronekton are only now beginning to be understood. Responses of phytoplankton to environmental variability have been well studied at interannual (McGowan et al., 2003), seasonal (Bolin and Abbot, 1963; Service et al., 1998), and sub-seasonal time scales (Service et al., 1998; Legaard and Thomas, 2007). Environmental effects on zooplankton and micronekton have also been studied, though mostly at seasonal and longer time scales (e.g. Roesler and Chelton, 1987; McGowan et al., 1996; Brinton and Townsend, 2003; Rebstock, 2003). Several recent studies have examined spatial relationships between physical features and micronekton distribution. These have regularly found changes in DSL structure and density associated with mesoscale eddies (Kloser et al., 2009; Godo et al., 2012; Fennell and Rose, 2015) and across frontal zones (Opdal et al., 2008; Irigoien et al., 2014; Boersch-Supan et al., 2015). Fewer studies have examined the temporal evolution of DSLs in relation to physical oceanography (Wang et al., 2014), and at sub-seasonal temporal scales, these effects are largely unknown.

This study used a bottom-mounted echosounder in outer Monterey Bay, CA to monitor changes in acoustic backscatter over 18 months. This sampling allowed us to characterize macrozooplankton and micronekton biomass through the entire water column at high temporal and spatial resolutions. We compared these acoustic backscatter measurements to coincident measurements of wind, temperature, and fluorescence as proxies of upwelling, and sea levels, to investigate possible links between sea-surface topography and animal biomass (e.g. Clarke and Dottori, 2008). We also examined how these responses varied as a function of depth. We expected a lagged increase in backscatter following upwelling events, due to a combination of animal aggregation, somatic growth, and population increase. A similar response to increased productivity at the surface was expected from animals at depth, but delayed and damped when compared to the response of surface animals. Finally, we estimate the relative importance of different processes in generating the observed physical-biological relationships.

2. Methods

2.1. Study location

Monterey Bay is a large, open embayment in the central California coast. The Bay's oceanographic seasons follow those of the California Current, with wind-driven upwelling in spring and early summer, a warm water “oceanic period” in the late summer and fall, and a winter downwelling or “Davidson current” period (Skogsberg et al., 1946; Pennington and Chavez, 2000). Point Año Nuevo, to the north of the Bay, is the source of a persistent upwelling plume that typically trails south across the mouth of the Bay (Rosenfeld et al., 1994, Fig. 1). Mean circulation within the bay is counterclockwise, with enhanced productivity in the “upwelling shadows” near shore (Graham et al., 1992).

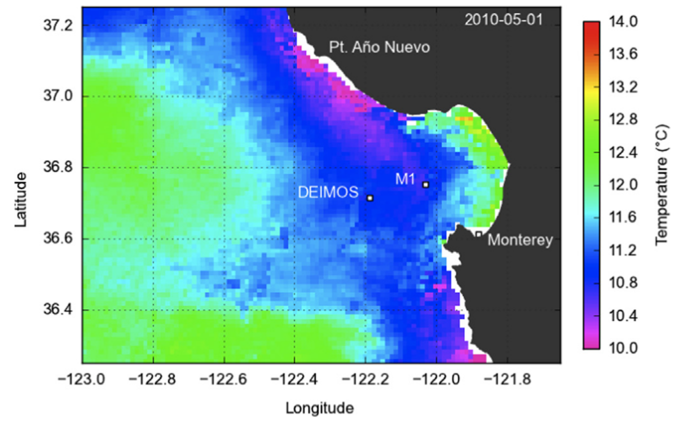

Fig. 1. Monterey Bay, showing location of the upward-facing echosounder (DEIMOS) and oceanographic data buoy (M1) used in this study, as well as a typical pattern of sea-surface temperature during the upwelling season (AVHRR 3-day composite, 1 May 2010). A band of cold, upwelled water is located along the coast, with warmer water offshore and inside the Bay. The coldest waters are near Point Año Nuevo and Point Sur.

2.2. Acoustic data

Animal density through the water column was estimated using a bottom-mounted echosounder. The Deep Echo Integrating Marine Observatory System (DEIMOS) is an acoustic package built around a 38 kHz scientific echosounder (Horne et al., 2010). It was deployed at 875 m depth from February 27, 2009 to August 18, 2010 at the Monterey Accelerated Research System (MARS), a cabled observatory node, located at 36° 42. 748′N, 122° 11. 214′W on Smooth Ridge, to the north of the Monterey Submarine Canyon. MARS is maintained and operated by the Monterey Bay Aquarium Research Institute (MBARI), and provides continuous power and communications for scientific instruments. Several multi-day gaps in the data were caused by electrical interference, software crashes, and burrowing rodents (Urmy et al., 2012). DEIMOS sampled continuously at 0.2 Hz with a 0.5 m vertical resolution through the water column. DEIMOS was calibrated *in situ* using a standard target (Foote et al., 1987) hung from a float above the transducer during the final 7 weeks of the deployment.

We were not able to take direct samples to identify scattering organisms, so acoustic volume and area backscattering coefficients (s_v and s_a, and their logarithmic forms S_v and S_a, MacLennan et al., 2002) were used as proxies of animal biomass. This is a reasonable assumption for both single species (Foote, 1983) and mixed communities (Benoit-Bird and Au, 2002).

Acoustic data were processed using Echoview software (version 4.8, Myriax Pty. Ltd. 2010). Background noise was estimated and subtracted using methods described in De Robertis and Higginbottom (2007). A backscatter threshold was applied to eliminate acoustic returns with volume-scattering strengths below −90 dB, the approximate backscattering intensity generated by one krill m^{-3} at 38 kHz (Demer and Conti, 2003). All echograms were visually inspected, and regions with external noise (e.g. ship or ROV noise) were excluded from further analysis. Also excluded were regions within 7 m of the bottom, to eliminate targets in the acoustic near field, and within 10 m of the surface, to avoid integrating bubbles from breaking waves. The mean depth of backscatter was measured using the acoustic center of mass (CM, Urmy et al., 2012).

2.3. Oceanographic data

Time series of wind velocity, sea-surface temperature (SST), and fluorescence, a proxy for chlorophyll (Kirk, 1994), were