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Changes in zooplankton habitat, behavior, and acoustic scattering characteristics across glider-resolved fronts in the Southern California Current System

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ABSTRACT

We report cross-frontal changes in the characteristics of plankton proxy variables measured by autonomous *Spray* ocean gliders operating within the Southern California Current System (SCCS). A comparison of conditions across the 154 positive frontal gradients (i.e., where density of the surface layer decreased in the offshore direction) identified from six years of continuous measurements showed that waters on the denser side of the fronts typically showed higher Chl-*a* fluorescence, shallower euphotic zones, and higher acoustic backscatter than waters on the less dense side. Transitions between these regions were relatively abrupt. For positive fronts the amplitude of Diel Vertical Migration (DVM), inferred from a 3-beam 750 kHz acoustic Doppler profiler, increased offshore of fronts and covaried with optical transparency of the water column. Average interbeam variability in acoustic backscatter also changed across many positive fronts within 3 depth strata (0–150 m, 150–400 m, and 400–500 m), revealing a front-related change in the acoustic scattering characteristics of the assemblages. The extent of vertical stratification of distinct scattering assemblages was also more pronounced offshore of positive fronts. Depth-stratified zooplankton samples collected by Mocness nets corroborated the autonomous measurements, showing copepod-dominated assemblages and decreased zooplankton body sizes offshore and euphausiid-dominated assemblages with larger median body sizes inshore of major frontal features.

Introduction

Ocean fronts separate waters with different temperature, salinity and nutrient profiles. Consequently, the floral and faunal assemblages on either side of a front can diverge. Fronts, therefore, have long been thought to play an important role in spatially structuring biomass and species distributions (Lefevre, 1986; Sournia, 1994). Much of the research into the ecology of fronts, however, has focused on fronts that are either relatively persistent in time and space, such as those that occur at large-scale ocean convergences (Polovina et al., 2001), or occur predictably due to their association with continental shelf breaks (Munk et al., 2003), tides (Pingree et al., 1975), nearshore upwelling (Smith et al., 1986), or estuarine mixing (Eggleston et al., 1998). Here we assess the roles of recurrent mesoscale (O(30–300 km)) and submesoscale (O(1–10 km)) fronts in structuring marine zooplankton assemblages and habitats in deeper waters of an eastern boundary current ecosystem.

The California Current is an eastern boundary current flowing along the west coast of North America from Vancouver to Baja California (Hickey, 1979). Within the California Current System (CCS) there are three major interacting currents that transport four distinct water types. The California Current (CC) proper is an equatorward flowing surface current; the Inshore Counter Current (ICC) transports warm subtropical surface waters poleward in the nearshore region, and is strongest during the fall and winter months; and the subsurface (200–500 m), poleward California Undercurrent (CUC) transports relatively warm, high-salinity, high nutrient waters from more southern sources (Simpson, 1984; Gay and Chereskin, 2009; Todd et al., 2011). The CCS is notable for its complex and vigorous mesoscale flows, which are primarily forced by seasonal upwelling-favorable winds along the coast (Marchesiello et al., 2003). These upwelling favorable winds, and consequent Ekman transport of surface waters offshore, are also responsible for transporting subsurface cold, salty, and nutrient-rich waters into surface waters.

The CCS is therefore a patchwork of different water masses that are horizontally stirred by eddies and jets, brought in close proximity to each other, and separated by ocean fronts. This mesoscale horizontal stirring can create a mosaic of potential habitats (Martin, 2003). Within the CCS, satellite SST and ocean color imagery suggest that, over a time scale of days to weeks, phytoplankton

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can be considered nonconservative tracers of the flows in which they are embedded (Denman and Abbott, 1994). A dominant phytoplankton assemblage may be selected by the specific conditions in a water parcel (d'Ovidio et al., 2010). A predictable transition often occurs from waters with low surface chlorophyll (with an offshore-type assemblage) to high-surface chlorophyll (with an inshore assemblage) across the inshore edge of the low-salinity core of the California Current, approximately 100–150 km offshore (Venrick, 2009).

The zooplankton assemblages that exist in association with the varying phytoplankton assemblages might likewise differ, even though the assemblages within adjacent water parcels may be separated by a narrow front. Ship-based studies of ocean fronts in the CCS have demonstrated that zooplankton biomass and abundance can change rapidly across fronts. Mackas et al. (1991) found a 3–4-fold increase in zooplankton biomass across a cold-water filament extending offshore from Point Arena, California, with a shift from a more doliolid-dominated assemblage on the warm side of the filament to a crustacean-dominated assemblage within the filament and extending to its cold side. In the Ensenada Front within the southern CCS (SCCS), Haury et al. (1993) noted a 3-fold change in primary productivity and 3–4-fold change in zooplankton displacement volume over a distance of less than 15 km across the front. In another front in the same region (the A-Front), Ohman et al. (2012) found that abundances of calanoid copepods were elevated within the front, and detected a shift from a herbivorous, particle-grazing zooplankton assemblage on the cool side of the front to a more carnivorous-dominated assemblage on the warm side. Smith and Lane (1991) found that *Eucalanus californicus* within the Point Arena cold filament were able to maintain increased egg production without drawing down their lipid reserves, due to the increased food availability within the filament. In the A-Front study, Ohman et al. (2012) also noted an increased abundance of copepod nauplii within the front, suggesting that secondary production was elevated there. Balancing this potential for increased secondary production is the potential for increased predation risk. Fronts have long been known to attract mobile zooplanktivores, including fish (Humston et al., 2000), seabirds (Ainley et al., 2009), baleen whales (Munger et al., 2009), and turtles (Polovina et al., 2004). Increased abundances of carnivorous zooplankton such as narcomedusae can also occur at fronts (McClatchie et al., 2012).

Zooplankton within the SCCS show some general cross-shore trends in zooplankton biomass. Ohman and Wilkinson (1989) found that the ash-free dry mass of zooplankton decreased offshore along cross-shore transects within the CalCOFI survey region. Other studies have found a long-term local maximum in zooplankton displacement volume located approximately 100 km offshore, which is maintained either by advection of zooplankton-enriched waters from the north (Chelton et al., 1982), or possibly by increased secondary production fostered by wind-stress curl driven upwelling offshore (Chelton, 1982; Rykaczewski and Checkley, 2008). Johnston and Rudnick (2014) demonstrate topographically-related increased mixing at the western boundary of the Southern California Bight, which potentially could be related to increased nutrient fluxes and food web responses in the region. Offshore of the local maxima, however, average zooplankton displacement volumes decreases monotonically (Chelton, 1982; Ohman and Wilkinson, 1989). In addition to the noted biomass trends, size compositions of zooplankton assemblages also change when moving offshore, with an increasing fraction of biomass coming from smaller-bodied zooplankters (Rykaczewski and Checkley, 2008).

Our understanding of the ecological changes occurring across ocean fronts comes mostly from limited duration ship-based studies of individual fronts. To quantify the ecological changes observed across fronts within a region, it is necessary to sample a representative distribution of such features through extended studies encompassing a variety of frontal conditions over a multi-year period. The advent of autonomous ocean gliders has opened new opportunities for continuous *in situ* measurements across (sub)mesoscale features in the California Current System (Davis et al., 2008; Ohman et al., 2013). Within the SCCS, *Spray* ocean gliders revealed that horizontal gradients in physical properties (e.g., temperature, salinity, and density) co-varied with horizontal gradients in Chl-*a* fluorescence and acoustic backscatter measured at 750 kHz (Powell and Ohman, 2015). Frontal regions were more likely to be zones of elevated acoustic backscatter compared to non-frontal regions, suggesting that fronts act as zooplankton accumulation zones. In the biotic and hydrographic gradient regions, Powell and Ohman (2015) estimated that large mobile planktivorous predators were up to three-times more likely to encounter favorable foraging conditions by traveling up local density gradients rather than down those gradients.

In the present analysis, we analyze differences that occur on either side of frontal regions in the SCCS. These differences include cross-frontal changes in concentrations and the vertical distribution of phytoplankton Chl-*a*, and in acoustic characteristics, body size, taxonomic composition, and Diel Vertical Migration behavior of zooplankton assemblages. We address three questions related to glider-detected fronts in the SCCS: (1) Do the depth of the chlorophyll maximum and the depth of the euphotic zone change across fronts? (2) Does the amplitude of Diel Vertical Migration behavior change at frontal boundaries? (3) Does the size structure of zooplankton and micronekton assemblages changes across frontal transitions?

Material and methods

Study area and duration

Spray ocean gliders were deployed nearly continuously along lines 80 and 90 of the California Current Ecosystem Long-Term Ecological Research (CCE-LTER) and CalCOFI sampling area (Fig. 1) between October 2006 and July 2011. The gliders traveled autonomously along the two lines from about 20 km offshore of the coast to a maximum 370 km (line 80) and 585 km (line 90)

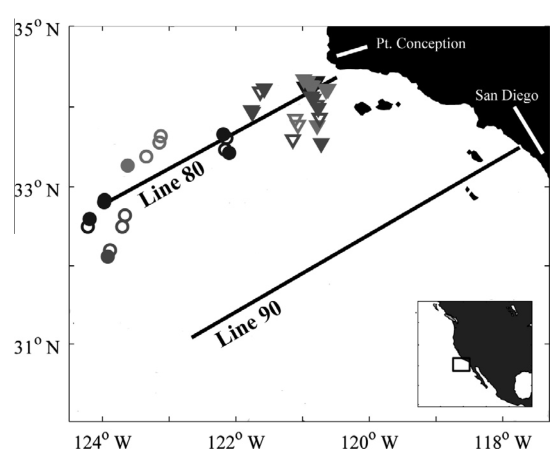

Fig. 1. CCE-LTER *Spray* glider transect lines 80 and 90, off the Southern California coast. Inset shows location off North America. Symbols depict location of Mocness tows conducted during three cruises: P0605 (black), P0704 (light gray), and P0810 (dark gray). Circles and triangles indicate tows occurring offshore and inshore, respectively, of a contemporaneous major frontal feature along line 80. Open (solid) symbols indicate daytime (nighttime) tows.