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Distributions of invertebrate larvae and phytoplankton in a coastal upwelling system retention zone and peripheral front

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ABSTRACT

Near-coastal retention of larvae affects the ecology of many marine species. In coastal upwelling ecosystems having strong offshore transport, larval ecology is greatly influenced by nearshore retention in bays and in the lee of headlands. Further, frontal dynamics along the periphery of retention zones can drive larval accumulation and transport. The purpose of this study is to examine larval distributions and associated processes across a retention zone and its peripheral front in the coastal upwelling environment of Monterey Bay, California, USA. During fall 2009 an autonomous underwater vehicle (AUV) was used to observe environmental variability at high resolution and acquire targeted water samples. Invertebrate larvae in samples were subsequently identified and quantified using molecular methods. To infer ecological processes we examine larval distributions in relation to environmental processes revealed by the AUV data and the greater regional observing system. As a window into biological–physical interactions that may concentrate motile larvae in convergence zones, we examine more extensive in situ and remote sensing observations that describe distribution patterns of motile phytoplankton. During the 10-day study intensification of upwelling caused flow of cold water into the bay and formation of an upwelling front. Drifter and satellite observations showed retention of near-surface water within the bay inshore of the front, where a bloom of motile phytoplankton intensified. Larval distributions were related to processes inferred at a range of scales. At the scale of the retention zone, dense phytoplankton accumulations indicated concentration of motile plankton in a convergence zone created by flow toward the coast, as well as nutritional support for larvae. At the scale of the front, velocity and water property measurements indicated convergence between cold deep-shelf water transported shoreward along shoaling bathymetry and the overlying warm surface water, influencing plankton accumulation and vertical transport. At the finest scales resolved, aerial photography revealed banded accumulations of dense phytoplankton bloom patches and narrow foam lines, common indicators of small-scale convergence zones and consistent with internal wave processes. Exceptionally high larval concentrations were detected in samples from locations affected by frontal and internal wave dynamics. This study illustrates how autonomous feature recognition and targeted sampling with an AUV, applied within the greater context of multidisciplinary observation across regional to small scales, can advance plankton ecology research.

1. Introduction

As agents of population persistence and connectivity, larvae are essential to the structure and function of coastal marine ecosystems (Carson, 2010; Cowen et al., 2006; Mace and Morgan, 2006). Advancing the understanding of larval ecology is thus essential to effective ecosystem based management (Davoren et al., 2007; Sponaugle, 2009). Only through understanding processes of larval ecology – and the associated forcing, scales, and interactions – can we design marine reserves to effectively sustain the biodiversity and resilience of marine communities (Fenberg et al., 2012; Gaines et al., 2010; Palumbi, 2003). However, difficult research challenges are presented by the small size of larvae relative to the scales of ocean dynamics, as well as the inherent complexity, patchiness and variability of both coastal marine ecosystems and larval populations. These challenges hinder our ability to understand the survival and transport of larvae and the cascading effects on ecosystems. This study presents results from novel methods designed to overcome some of these challenges. These methods integrate high-resolution multidisciplinary sensing and adaptively targeted sampling conducted simultaneously by an autonomous underwater vehicle (AUV), providing effective observation and sampling of plankton patchiness and its ecological context.

The study region, Monterey Bay (Fig. 1), resides in the dynamic California Current upwelling system. In coastal upwelling systems, an immense supply of nutrients to the photic zone supports tremendous productivity – from phytoplankton through zooplankton, fish, mammals

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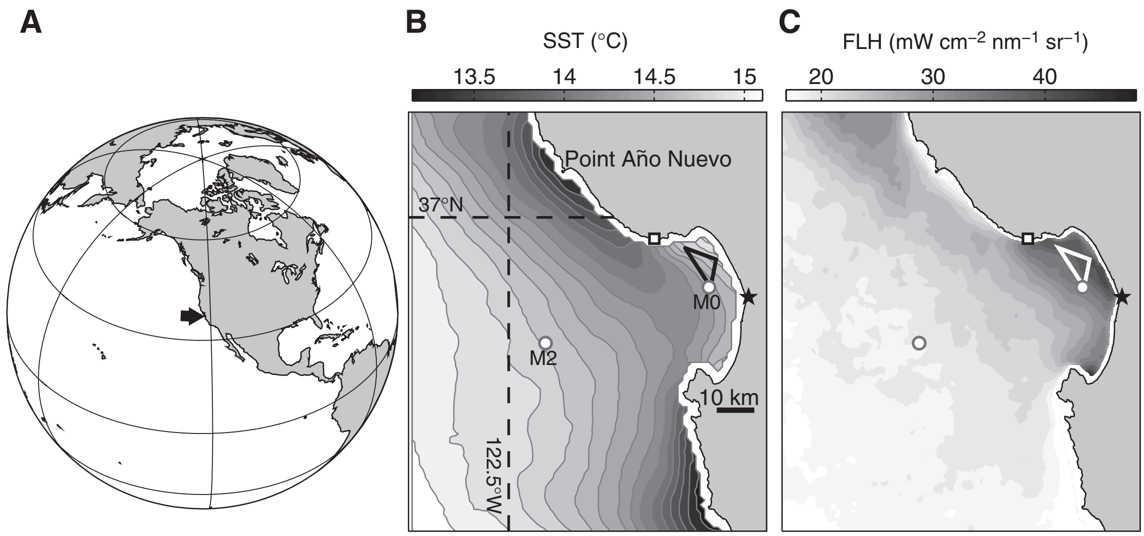

Fig. 1. Environmental setting and study design. (A) Geographic position of the study region along the northeastern Pacific margin. Fall climatological averages of (B) sea surface temperature (SST) and (C) chlorophyll fluorescence line height (FLH) from the MODIS Aqua satellite sensor are based on data from 2004 to 2008. The triangle over northern Monterey Bay represents the surface track of repeated AUV surveys conducted between 29 September and 8 October 2009. Moorings M0 and M2 provided continuous hourly measurements during the study (Figs. 2, 7). The star and square symbols indicate the locations for which predicted tidal height and zonal wind data, respectively, are examined relative to variation in water column conditions and circulation (Section 3.4).

and birds (Barber and Smith, 1981). While high primary productivity enhances larval food supply, strong offshore transport of surface water that drives coastal upwelling threatens larvae that must remain near shore for successful recruitment to adult habitats. In this context, bays and areas in the lee of coastal headlands, described as retention centers or upwelling shadows, are crucial (Graham et al., 1992; Morgan et al., 2011; Roughan et al., 2005).

Northern Monterey Bay contains a large retentive upwelling shadow (Graham et al., 1992). Physical distinction of this feature is evident as the warmest long-term averaged sea surface temperature (SST, Fig. 1B), while biological distinction at the level of phytoplankton is evident in the corresponding average of chlorophyll fluorescence (Fig. 1C). The spatial patterns of these distinctions represent regional atmospheric and oceanic circulation patterns, as shaped by coastal geomorphology (Breaker and Broenkow, 1994; Graham and Largier, 1997; Rosenfeld et al., 1994). Upwelled water typically approaches the bay as an along-coast flow from the north, originating around Point Año Nuevo (Fig. 1B). Eastward turning of the coastline at the northern end of the bay results in separation of upwelling flow from the coast, and a cyclonic gyre typically forms in the northern bay. The Santa Cruz Mountains along the bay's northern coast buffer northwesterly wind stress, thereby reducing wind-forced vertical mixing and enabling stratification. These geomorphological influences locally enhance residence time and thermal stratification in the upwelling shadow. Elevated chlorophyll concentrations in the upwelling shadow (Fig. 1C) reflect the blooming of phytoplankton within the relatively warm and stratified environment into which nutrients are episodically transported (Ryan et al., 2008, 2009, 2011). These conditions lead to comparatively great abundance and diversity of zooplankton within the upwelling shadow, the biological attribute essential to original distinction of the upwelling shadow as an ecological phenomenon (Graham et al., 1992).

The significance of retention centers and their peripheral fronts to larval ecology off northern California has been studied. Larval settlement and recruitment are greater in the sheltered lee of coastal headlands south of Point Reyes and Bodega Head than along the exposed coastline at Bodega Head (Mace and Morgan, 2006; Wing et al., 2003). Larvae of multiple taxa in all stages of development can be entrained and accumulated in a recirculation feature in the lee of Bodega Head (Morgan et al., 2011). Accumulation within retention zones during upwelling has been hypothesized as a mechanism of larval supply to more exposed and recruitment-limited sites when regional wind relaxation causes poleward transport around the coastal headland of the retention zone (Mace and Morgan, 2006; Wing et al., 2003). Integration of satellite remote sensing and in situ measurements of larval recruitment off California reveal that coastal upwelling fronts, including those that form along the periphery of retention centers, organize recruitment patterns of both community-building invertebrates in intertidal habitats and fishes in nearshore rocky reef habitats (Woodson et al., 2012). Hypothesized mechanisms include convergent flow at the front, which can drive accumulation of swimming larvae, and along-front transport toward the coast, which can funnel larvae to nearshore recruitment sites (Woodson et al., 2009). While these mechanisms have a sound theoretical basis, larval accumulation in the Monterey Bay upwelling shadow front has not been observed directly.

The importance of retentive zones and fronts to larval ecology motivates development and application of better methods to observe processes and sample populations. In this study we employ an AUV developed to respond to feature recognition based on real-time analysis of environmental data, and to acquire precisely located water samples. Larvae in samples are identified and quantified by molecular methods. These high-resolution observations are placed in a regional ecological context with multidisciplinary observations of a greater ocean observing system, to infer processes of importance to larval ecology. Our objectives are to describe ecological processes across horizontal scales of ~10^2 to 10^4 meters and to relate observed distributions of invertebrate larvae and phytoplankton to these processes.

2. Materials and methods

2.1. AUV surveys

The primary platform for observation and sampling was the *Dorado* AUV. *Dorado* has been applied to study a variety of complex coastal ocean processes in the Monterey Bay region, including zooplankton ecology (Harvey et al., 2012; Ryan et al., 2010a), phytoplankton ecology (Ryan et al., 2008, 2010b, 2014), upwelling dynamics (Fitzwater et al., 2003; Ryan et al., 2011), nutrient-based primary productivity rates (Johnson and Needoba, 2008), frontal processes (Ryan et al., 2010c), and internal wave dynamics (Cazenave et al., 2011). Toward effective plankton ecology research, the focus of the present study, the *Dorado* AUV provides key enabling capabilities: (1) a multidisciplinary sensor suite for measuring physical, chemical and optical properties, (2) fast