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Spatial differences in larval abundance within the coastal boundary layer impact supply to shoreline habitats

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ABSTRACT: Explorations of the dynamics of nearshore regions of the coastal zone are missing from many efforts to understand larval transport and delivery to suitable habitats. Larval distributions in the coastal ocean are variable and depend on physical processes and larval behaviors, leading to biophysical interactions that may increase larval retention nearshore and bolster their return to natal sites. While recent evidence suggests that many larvae are retained within a few kilometers from shore, few studies incorporate measurements sufficiently close to shore to plausibly assess supply to the shoreline benthos. We measured cross-shore distributions of larvae of benthic crustaceans between 250 and 1100 m from shore (i.e. just beyond the surf zone) within the coastal boundary layer (CBL)—a region of reduced alongshore flow—and simultaneously quantified a suite of physical factors that may influence larval distributions. We found high larval abundance within the CBL, with a peak at 850 m from shore, and a decrease in abundance along the shoreward edge of the sampled transect. We also found distinctly different larval assemblages at outer stations within the CBL, as compared to inner stations that are more influenced by shoreline dynamics. These patterns persisted across sample dates, suggesting that the spatial structure of nearshore larval assemblages is at least somewhat robust to temporal changes in physical conditions. Thus, while larval abundance appears to be high within the CBL, larvae appear to be sparse within the narrow band of water adjacent to the surf zone. Low larval supply adjacent to suitable habitats has important implications for the coupling of supply and recruitment, and resulting dynamics of shoreline populations.

KEY WORDS: Dispersal · Invertebrate larvae · Retention · Nearshore · Transport

INTRODUCTION

A central goal of ecology is to understand patterns of abundance and distribution of organisms. Determining the key factors that drive population dynamics requires knowledge of demographic inputs (birth and immigration) and losses (death and emigration). In marine systems, the process of larval dispersal adds additional complexity to quantifying population inputs as many marine organisms release dispersive larvae that act as the primary agents coupling birth at one site to immigration at another. Therefore, larval recruitment to coastal populations relies not only on reproductive output of parent populations and post-settlement processes, but also on oceanographic factors that affect the dispersal and delivery of settlers

(Cowen 1985, Gaines et al. 1985, Roughgarden et al. 1988, Gaylord & Gaines 2000, Morgan 2001, Underwood & Keough 2001, Largier 2003, Prairie et al. 2012). While larval recruitment is a critical determinant of population structure (Gaines & Roughgarden 1985, Underwood & Fairweather 1989, Menge et al. 2004) and larval delivery has long been recognized for its role in driving population dynamics (Thorson 1946), larval transport pathways and connectivity are difficult to quantify due to the small size of larvae and the difficulty of tracking them (Levin 2006). These difficulties are exacerbated by a lack of understanding of how larval supply varies over time and space.

Relatively few studies have measured larval supply and settlement concurrently in such a way as to explicitly link them. Those that have done so have reached mixed conclusions: some found supply and settlement to be coupled (e.g. Gaines et al. 1985, Bertness et al. 1992, Gaines & Bertness 1992, Dudas et al. 2009) while others did not (e.g. Yoshioka 1982, McCulloch & Shanks 2003, Rilov et al. 2008). Such differences may be due to the magnitude of recruitment, with larval supply acting as a strong predictor of adult dynamics in regions where recruitment is limited (Connell 1985), but less so in areas where recruitment is high. Connections between supply and settlement or recruitment may be easier to assess in other systems; for instance those involving dispersal of macroalgal spores (see, e.g. Reed et al. 1988, Gaylord et al. 2002, 2004, 2006, 2012, Reed et al. 2006).

Much of the west coast of North America is recruitment-limited to one degree or another, such that larval supply is a critical determinant of population dynamics in many species. This feature derives from the fact that the west coast sits within a major upwelling region. During times of strong equatorward winds, the predominant currents flow equatorward and surface waters move offshore. The potential for upwelling waters to move larvae offshore has been widely recognized (Yoshioka 1982, Roughgarden et al. 1988, Botsford et al. 1994), and is consistent with observations that larval settlement and supply in persistent upwelling regions is higher during relaxation events when wind speeds decrease or reverse directions (Farrell et al. 1991, Botsford 2001). Increases in settlement and supply during relaxation events can also result from poleward advection of larvae (Wing et al. 1995a,b). More recent work has shown the persistence of sequential larval stages in nearshore plankton during upwelling conditions, indicating that many taxa are not swept offshore in upwelling regions (Morgan et al. 2009b, Shanks & Shearman 2009). Larvae appear to be able to at least

partially avoid offshore transport associated with upwelling through physical and behavioral mechanisms. Nearshore retention zones arising from topographic effects on coastal circulation have been observed (Graham & Largier 1997, Wing et al. 1998, Roughan et al. 2005), and are associated with higher larval abundances and settlement (Mace & Morgan 2006, Morgan et al. 2009a, 2011, 2012). Avoidance of surface waters by larvae can favor retention and decrease offshore transport (Morgan et al. 2009b,c, Shanks & Shearman 2009, Morgan & Fisher 2010, Morgan et al. 2012) and there is mounting evidence that larval concentrations are high close to shore, even in areas of strong upwelling that are traditionally viewed as being recruitment-limited. Here we investigate this phenomenon closer to shore to see if high abundances extend over the inner shelf and inward to the shoreline.

Nearshore processes play an important role in larval ecology, and may be relevant for a significant portion of pelagic larval durations. A number of recent studies measured larval abundance in cross-shore transects and found increases in abundance closer to shore in a range of invertebrates and fishes (Borges et al. 2007, Tapia & Pineda 2007, Morgan et al. 2009b,c, Shanks & Shearman 2009). For example, Morgan et al. (2009b) measured larval abundance of benthic crustaceans from 1 km from shore out to the shelf break (30 km offshore) along the open coast of northern California and found that the highest larval abundances were within 3 km from shore. The combination of larval behaviors (e.g. swimming and vertical migration) and nearshore processes may increase retention of larvae close to shore and to their natal site. Such retention is consistent with evidence from a range of species and systems that shows self-recruitment is higher and dispersal distances smaller than previously thought (Swearer et al. 2002, Levin 2006, Shanks 2009), and further emphasizes the importance of understanding the role of nearshore processes in larval supply and population dynamics.

A number of nearshore processes may reduce scales of dispersal. Adjacent to the shore within the surf zone, rip tides can create recirculation zones (MacMahan et al. 2010) and onshore wave transport can lead to accumulation of water-borne material (Monismith 2004, McPhee-Shaw et al. 2011). There is also a region termed the coastal boundary layer (CBL) that extends beyond the surf zone and is characterized by reduced speeds (Nickols et al. 2012). In particular, average alongshore velocities in the CBL are an order of magnitude larger than cross-shore velocities (Lentz et al. 1999, Gaylord et al. 2007), and

alongshore velocities increase strongly with distance from shore until reaching a 'free-stream' value offshore (Nickols et al. 2012). Such decreased velocities provide another potential mechanism for reducing scales of dispersal in coastal populations (Nickols et al. 2012, Nickols et al. unpubl. data), but require that larvae spend sufficient time within the CBL for reduced flow to influence net transport. Because previous studies of coastal larval distributions did not extend into the CBL or only just entered the CBL (McQuaid & Phillips 2000, Morgan et al. 2009b,c, Shanks & Shearman 2009), or sampled over an insufficient temporal scale to fully characterize patterns (Tapia & Pineda 2007), the general role of the CBL in influencing patterns of larval transport and supply remains unknown.

The goals of this study were therefore to address the following questions: (1) what is the spatial pattern of larval abundance within the CBL, (2) are there differences in larval assemblages close to shore (i.e. are different larvae found inshore versus offshore within the CBL), and (3) do time-dependent or space-dependent physical processes tend to dictate variability in larval abundance? We recognize in targeting these goals that it is not possible to definitively ascribe particular mechanisms to observed patterns; rather, our aim is to present the first description of the spatio-temporal distribution of larval assemblages within the CBL, which is critical for understanding the potential for nearshore transport processes to impact larval supply to shoreline habitats. We additionally hope that this study will also inform the methodological question of where supply should be measured to best address relationships between settlement and supply when exploring questions about marine population dynamics, particularly for recruitment-limited regions.

MATERIALS AND METHODS

Study system and species

This study was conducted along the open coast in northern California, USA, near Bodega Head, California (Fig. 1), a region characterized by strong seasonal upwelling during spring and summer that drives prevailing currents equatorward and pushes surface waters offshore (Winant et al. 1987, Largier et al. 1993). When the winds weaken or reverse direction (inducing a 'relaxation' event), currents move poleward, often responding within a day or less in very nearshore regions (Send et al. 1987). Inner shelf
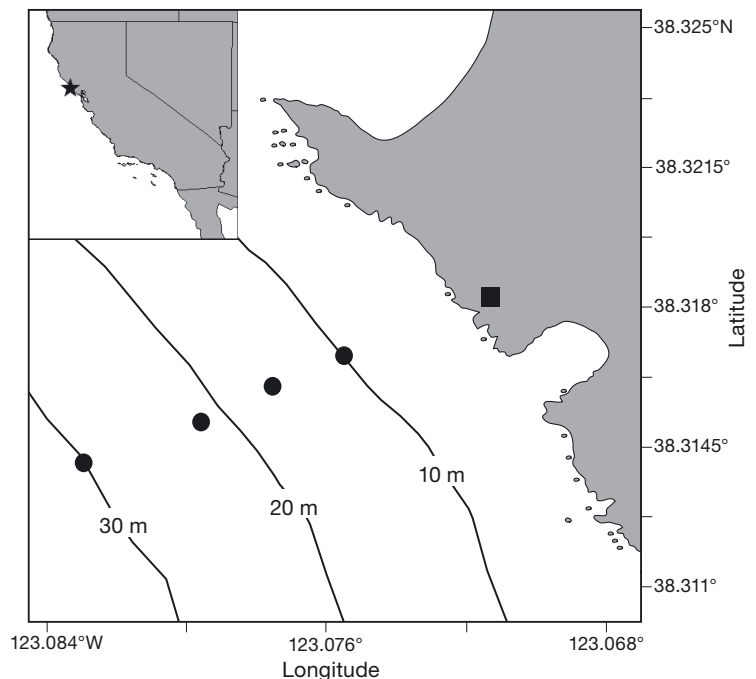

Fig. 1. Map of the study region showing the cross-shelf transect located off Bodega Head in northern California, USA. Circles indicate locations of moorings where plankton tows and CTD casts began. The moorings on the 10, 15, and 22 m isobaths included bottom mounted ADCPs and thermistors. The mooring on the 15 m isobath contained a thermistor string measuring temperature at depths of 4, 7, 10, and 14 m. Wind velocity was measured via an anemometer located on-shore at the Bodega Marine Laboratory, indicated by the square

currents, observed previously on the scale of kilometers, are slower than currents farther offshore, have a higher tendency to move poleward (Kaplan et al. 2005), and are associated with increases in invertebrate settlement (Wing et al. 1995a,b). Benthic crustacean larvae can be present during both relaxation and upwelling conditions within areas of topographic retention and along the open coast, and many can be retained in areas within 1 to 3 km of the shore via a combination of physical and behavioral mechanisms (Morgan et al. 2009b, Morgan & Fisher 2010, Morgan et al. 2012). The present study focused on waters within 1 km of the shore.

Our efforts focused on larvae of benthic crustaceans (primarily barnacles and crabs), which are the best-studied meroplankton in this region. From prior work, it is known that larval abundance of benthic crustaceans peaks during the spring and summer, coinciding with the upwelling season. Barnacles molt through 6 larval stages (nauplii) and a postlarval stage (cyprid) and spend about 2 to 4 wk in the water

column (Strathmann 1987). Barnacle larval release generally begins in spring (Gaines et al. 1985, Strathmann 1987) and is continuous through the summer months (Shanks & Eckert 2005). Barnacle species from both subtidal (*Balanus crenatus*, *B. nubilus*) and intertidal (*B. glandula*, *Chthamalus* spp., and *Pollicipes polymerus*) habitats are common in this region (Morgan & Fisher 2010). Crab larvae spend weeks to months in the plankton, and peak recruitment for most species in this region is during the spring and summer (Shanks & Eckert 2005, Mace & Morgan 2006). The most common taxa include members of the families Pinnotheridae, Porcellanidae, Cancridae, and Majidae.

Larval samples

Cross-shore distributions of nearshore larvae were sampled during 6 daytime cruises using a 0.5 m diameter, 200 μm mesh net equipped with a mechanical flow meter (Model 2030, General Oceanics). The net was modified with a sled to accommodate towing along the bottom. Cruise dates spanned 3 mo during the upwelling season, from May through July 2010, and occurred approximately every 10 d (Fig. 2) under a variety of oceanographic conditions. We sampled 4 stations in a cross-shore transect along the 10, 15, 22, and 30 m isobaths, corresponding to approximately 250, 425, 850, and 1100 m from shore (Fig. 1). We refer to the 10 and 15 m isobath stations as 'inner CBL stations', and the 22 and 30 m isobath stations as 'outer CBL stations'. We conducted a single 10 min oblique tow at each station, which sampled from the bottom to the surface of the water column. Larvae were sorted and identified to species, or the lowest taxonomic group possible, and developmental stage. Larval abundances were calculated per m^3 to standardize across stations.

Physical data

To provide physical context during our study, we measured currents, temperature, salinity, and winds. Current speed and direction were measured throughout the water column using moored acoustic Doppler current profilers (Workhorse Sentinel ADCP, 1200 kHz; Teledyne RD Instruments). Instruments were located on the 10, 15, and 22 m isobaths near the starting position for plankton tows. The ADCPs collected 1 min bursts of 0.75 Hz velocity data every 2

min in 1 m vertical bins that typically extended from ~1.5 m above the bottom to ~1.5 m below the surface. The velocity record at the 10 m station ended early on 10 June 2012 when its anchor was dislodged. To quantify general velocity patterns, the raw velocity time series were depth-averaged, rotated onto their principal axes, and low-pass filtered with a 33 h cutoff to remove dominant tidal motions (Rosenfeld 1983). The major principal axes aligned parallel to shore and along-isobath, corresponding to an angle of 300°.

Bottom temperature was recorded at the ADCP mooring sites every minute over the duration of the study at the 10, 15, and 22 m stations, and temperatures at depths of 4, 7, 10, and 14 m were recorded at the 15 m station (SBE 37 and SBE 39, Sea-Bird Electronics). During cruises, temperature, salinity, and density were profiled at each station throughout the water column using a conductivity, temperature, and depth profiler (SBE 19-Plus, Sea-Bird Electronics), with the exception of the cruise on 25 June.

Wind data during this study were available from an anemometer located on the shore at the Bodega Marine Laboratory, within 1 km of the study locations, at a height of 20 m (38° 19′ 3.35″ N, 123° 4′ 17.20″ W; RM Young 05103 Wind Monitor; data available online http://bml.ucdavis.edu/boon/).

Data analysis

We performed multivariate analyses to determine if larval abundance and larval assemblages varied with distance from shore and with time. We examined patterns of cross-shore abundance for all taxa, for crab and barnacle larvae separately, and according to larval stage. All statistical analyses were conducted using the multivariate statistical software package PRIMER v. 6.1.10 (Clarke & Gorley 2006). We determined whether larval assemblages changed with distance from shore and with sampling date using nonparametric analysis of similarity (ANOSIM) and hierarchical cluster analysis and ordination. Data were fourth-root transformed to reduce the heterogeneity of variance among samples and assembled into a Bray-Curtis dissimilarity matrix with a dummy variable of 1. The resultant dendrogram was tested for group differences using a similarity profile test (SIMPROF), and the percentage contribution (SIMPER) of each species and stage to the significant clusters was assessed to classify species-stage combinations by their cross-shore distributions and sampling date. We used non-metric multidimensional scaling
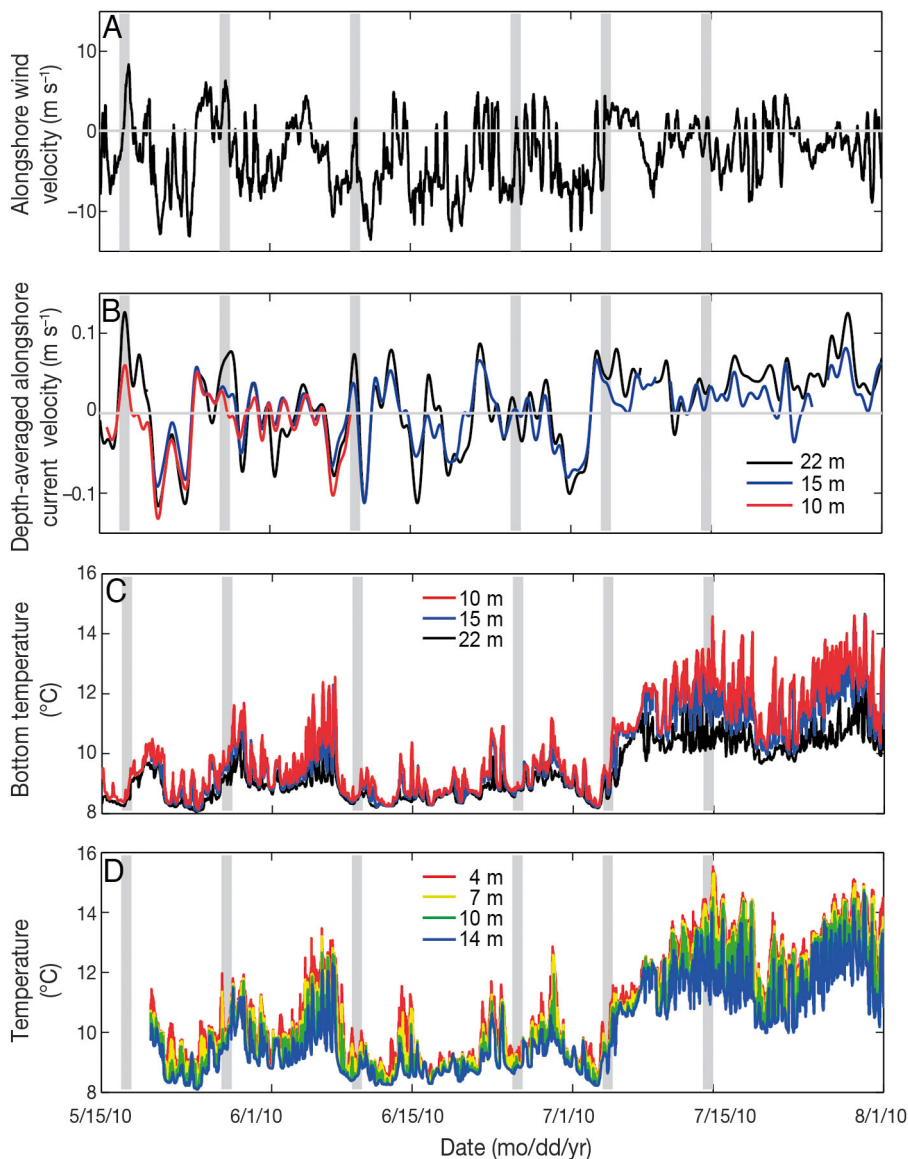
Fig. 2. (A) Alongshore wind velocity measured at Bodega Marine Laboratory. (B) Alongshore depth-averaged and 33 h low-pass filtered current velocity measured by bottom-moored ADCPs at the 10, 15, and 22 m isobaths. Positive alongshore velocity is poleward and negative alongshore velocity is equatorward. (C) Bottom temperature measured on the ADCP moorings at the 10, 15, and 22 m isobaths. (D) Temperature at depths of 4, 7, 10, and 14 m measured at the 15 m isobath. Vertical gray bars indicate when sampling occurred

RESULTS

Physical conditions

During the study period, we captured a variety of oceanographic conditions, including upwelling, relaxation, and post-relaxation (Fig. 2). However, our larval sampling dates generally occurred during low-wind conditions due to logistical constraints on field operations. Daily-averaged alongshore wind speeds during each sampling date ranged from −8 m s^{-1}, indicative of northwesterly winds, to 8 m s^{-1}, indicative of southeasterly winds, but winds were predominantly upwelling favorable over the study period (Fig. 2A). While depth-averaged alongshore currents are known to alternate between equatorward and poleward in this region (Largier et al. 1993, Roughan et al. 2005, Kaplan & Largier 2006, Morgan et al. 2012), on all sampling days of our study the alongshore current was poleward (Fig. 2B). In general, depth-averaged alongshore velocities measured at inner CBL locations (10 and 15 m isobaths) were slower than velocities measured at the outer CBL instrument on the 22 m isobath (Fig. 2B), characteristic of a coastal boundary layer. Exceptions occurred during onset of strong upwelling winds on 20 May and 6 June and during flow reversals.

Water column properties during larval sampling dates ranged from well-mixed to stratified (Figs. 2 & 3). The 17 May, 9 June, and 25 June sampling events represented upwelling conditions, with a cold homogeneous water column across stations: temperatures below 10°C and salinities similarly uniform, with the exception of some low-salinity water on the surface near the outer station on 17 May (Figs. 2, 3A & 3C). Alongshore wind speeds on the day preceding these sampling dates were from the northwest and reached up to 10 m s^{-1}, characteristic of strong upwelling conditions and accounting for the presence of cold isothermal conditions over the inner shelf. On 27 May and 4 July, the

(NMDS) to examine separation of assemblages according to sample date and distance from shore. To assess if community composition was structured in space or time, we repeated each of these analyses on untransformed data that were standardized by total sample abundance. For all analyses, when there was significant structure among samples we then determined which species and stages contributed to the patterns.
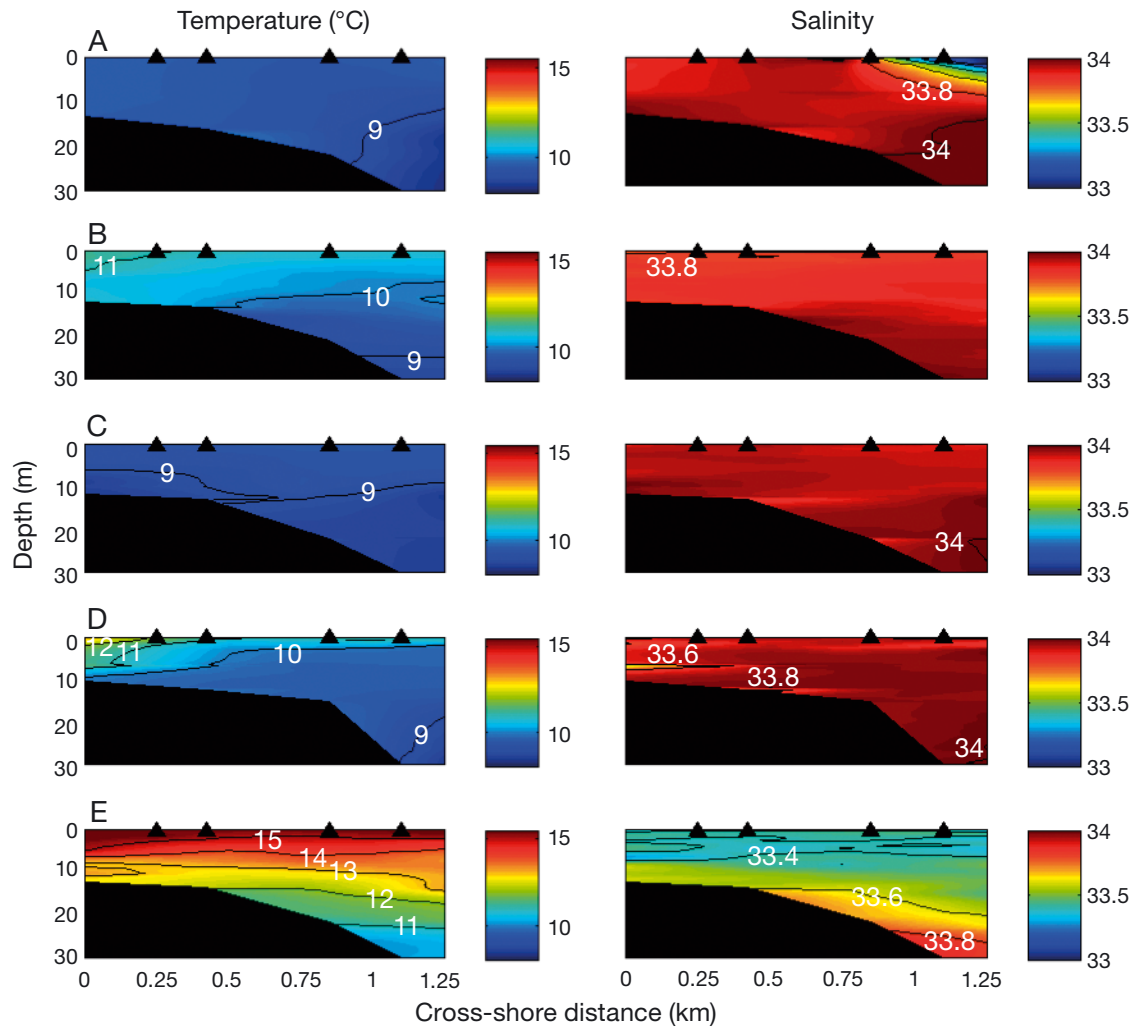
Fig. 3. Contours of temperature (left) and salinity (right) at the beginning of larval tows along the 10, 15, 22, and 30 m isobaths on (A) 17 May 2010, (B) 27 May 2010, (C) 9 June 2010, (D) 4 July 2010, and (E) 14 July 2010. Sample locations are indicated by triangles

water column was stratified at the 2 inner CBL stations (Figs. 2, 3B & 3D), following a day of southeasterly or weak winds. After 4 July temperatures increased substantially, and the water column was stratified at all stations on the 14 July sampling day (Fig. 2C). Winds during this period were substantially weaker than previous sampling events (Figs. 2C, 2D & 3E).

Larval abundance

We identified larvae of 22 crustacean species during our study (Table 1). The outer CBL station, along the 30 m isobath, had the highest number of species, with 10 species on average as compared to 6 to 7 spe-

cies at the other stations. Throughout the study, larvae were most abundant along the 22 m isobath, 850 m from shore (Fig. 4A). This pattern was driven by high abundances of barnacle larvae (Fig. 4B). Early, middle and late stage barnacle larvae were present at all stations with the highest abundance along the 22 m isobath (Fig. 5A). Barnacle postlarvae (cyprids) were found in similar abundance across stations. Crab larvae were most abundant near the 30 m isobath, 1100 m from shore (Fig. 4C). All larval crab stages were most abundant at the 2 outer CBL stations, although early stage crab larvae dominated the samples and abundance decreased with increasing stage (Fig. 5B). Very few crab larvae were found at the inner CBL stations, and the majority of those were early stage larvae.

Table 1. Crustacean larvae identified in the study

Family	Taxon
Cirripedia	*Balanus crenatus*
	Balanus glandula
	Balanus nubilus
	Chthamalus dalli
	Lepas spp.
	Pollicipes polymerus
Cancridae	*Cancer antennarius*
	Cancer magister
	Cancer productus
	Carcinus maenas
Grapsidae	*Hemigrapsus oregonensis*
Hippidae	*Emerita analoga*
Majidae	*Mimulus foliatus*
	Pugettia producta
	Pugettia richii
	Scyra acutifrons
Paguroidae	Pagurid spp.
Pinnotheridae	Pinnotheridae
Porcellanidae	*Pachycheles* spp.
	Petrolisthes cinctipes
Thalassinidae	*Neotrypaea californiensis*
Xanthidae	*Lophopanopeus bellus*

Larval assemblages

Considering all taxa, larval assemblages within the CBL differed among stations (2-way ANOSIM ρ_{av} = 0.322, p = 0.017) and were similar among dates. Because overall larval assemblages were not structured by date we performed a 1-way ANOSIM to detect spatial differences among assemblages at the different stations. The innermost station drove differences between assemblages, and it differed from the 2 outer stations (1-way ANOSIM pairwise test: for 10 m vs. 30 m stations: R = 0.463, p < 0.01; for 10 m vs. 22 m stations: R = 0.609, p < 0.01). These differences were echoed in the dendrogram from cluster analysis, and the NMDS ordination, which both revealed spatial structure with 2 main clusters: one defined by low numbers of larvae, with samples primarily from inner CBL stations, and the second defined by high numbers of larvae, with samples primarily from the outer CBL stations (Fig. 6).

Partitioning the analysis by taxa, we found that patterns of barnacles and crabs differed. Crab larval assemblages by themselves did not differ by station or date, but barnacle larval assemblages did differ by station and sampling date (2-way ANOSIM: station ρ_{av} = 0.322, p = 0.02; date ρ_{av} = 0.35, p < 0.01). The dendrogram from cluster analysis and the NMDS ordination revealed 2 main clusters of barnacle samples. One cluster occurred early in the season and mostly offshore, and it was composed of samples from all stations during 17 May and samples from the outer CBL stations during June and July. The other cluster occurred late in the season (June through July) and consisted primarily of samples from the inner CBL stations (Fig. 7). In the early-season, outer CBL assemblage, barnacle larval abundances were as high as 7200 larvae m^{-3}, whereas in the late-season, inner CBL assemblage, barnacle concentrations were less than 500 larvae m^{-3}.

We also analyzed changes in the composition of the larval assemblage. We divided our larval counts (both species and stage) by the total number of larvae in each sample, providing a fraction of the total sample for each species and stage, to standardize the data for differences in larval abundance across time. Larval community composition within the CBL differed mostly among stations, but also by date (2-way ANOSIM station ρ_{av} = 0.394, p < 0.01; date ρ_{av} = 0.282, p = 0.026). As noted previously, date was not significant when abundance was considered in the analysis of larval assemblages. In this analysis of composition,
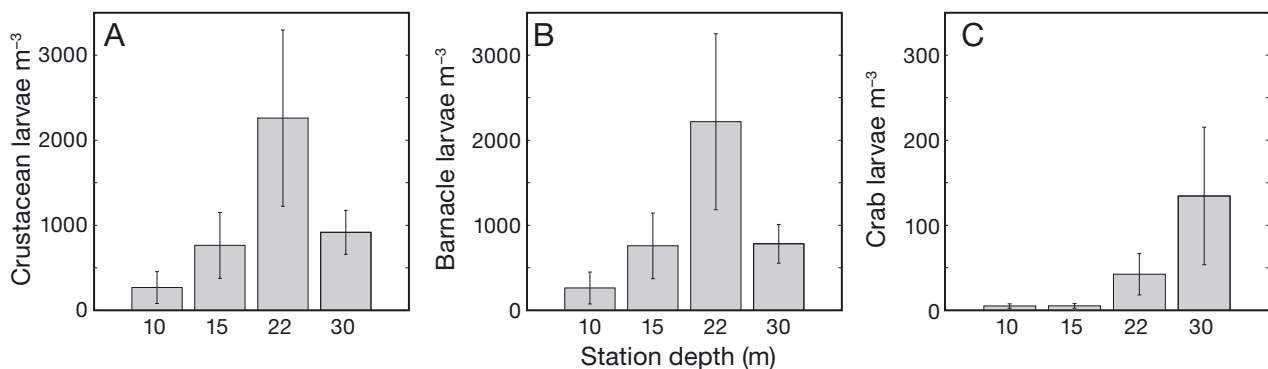

Fig. 4. Average larval abundance and standard error across date by station for (A) all benthic crustaceans, (B) barnacles, and (C) crabs. Note that the y-axis of (C) is an order of magnitude smaller than (A) and (B)
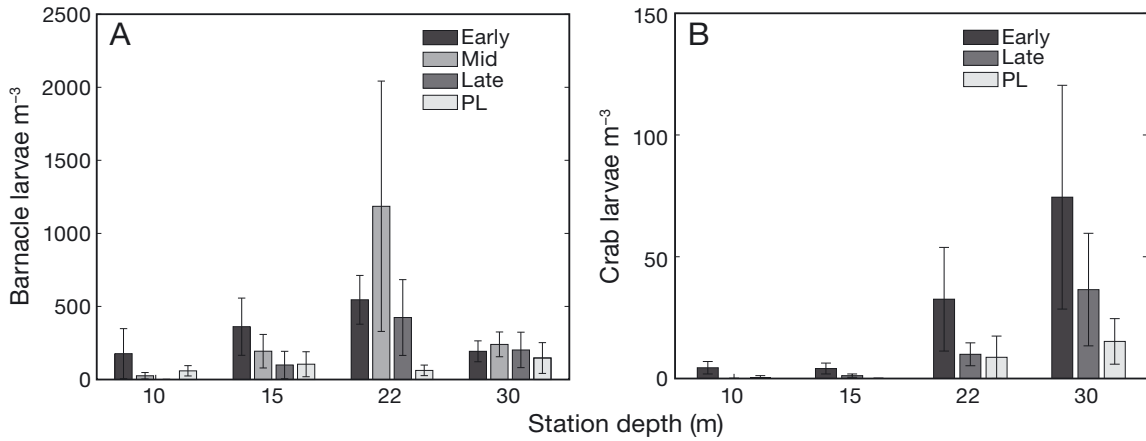
Fig. 5. Average larval abundance and standard error across date by station for (A) barnacles according to early, mid, late, and postlarval (PL) stage and (B) crabs according to early, late, and PL stage
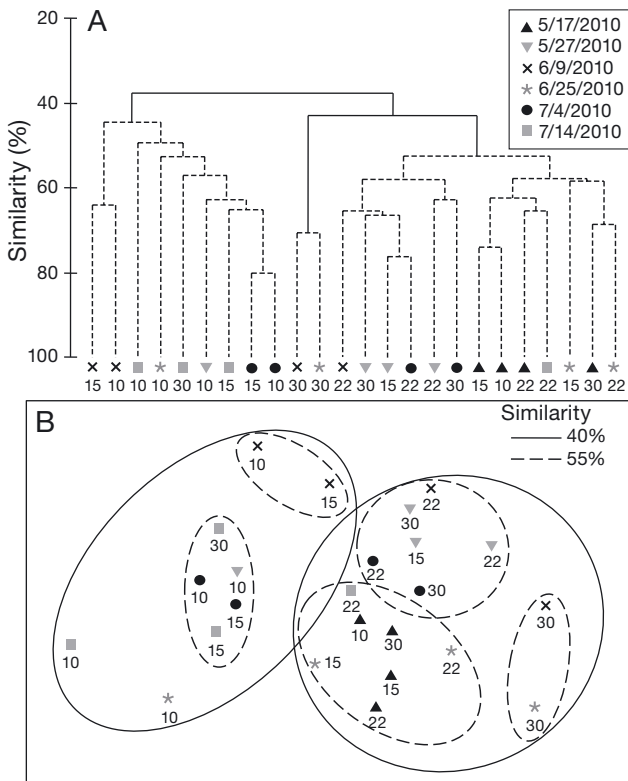

Fig. 6. (A) Hierarchical clustering dendrogram (using group-average linking) of larval assemblages of benthic crustaceans from 24 samples taken over 6 d (indicated by symbols and legend entry) at 4 sampling stations across the coastal boundary layer (along the 10, 15, 22, and 30 m isobaths, indicated by numbers adjacent to symbols), using transformed data. Solid black lines indicate significant group structure at the 5% level. Dashed lines represent nonsignificant group structure. Sample station isobaths are reported beneath each symbol. (B) Non-metric multidimensional scaling plot (2D stress, 0.15; 3D stress, 0.09) from the 24 samples with superimposed significant clusters at similarity levels of 40% (solid lines) and 55% (dashed lines). Symbols and numbers as in (A)
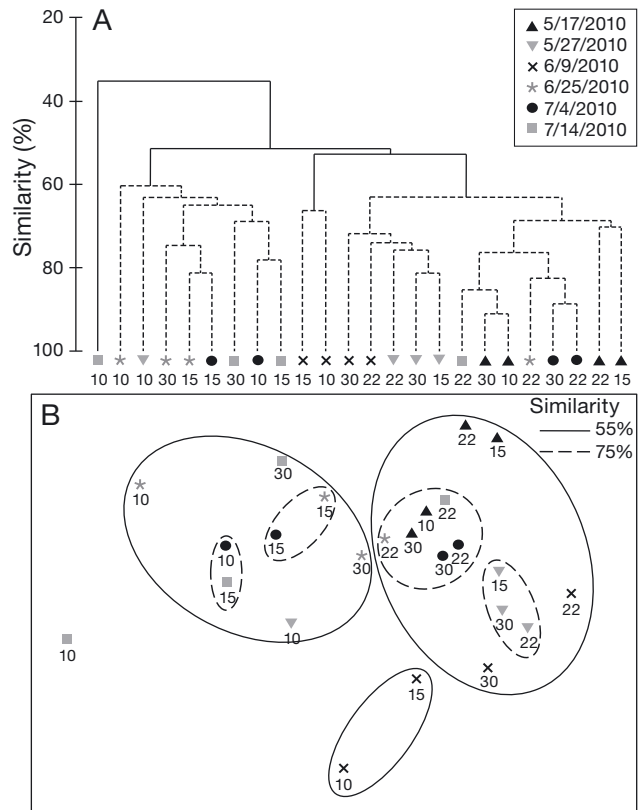
Fig. 7. (A) Hierarchical clustering dendrogram (using group-average linking) of barnacle larval assemblages from 24 samples taken over 6 d (indicated by symbols and legend entry) at 4 sampling stations across the coastal boundary layer (along the 10, 15, 22, and 30 m isobaths, indicated by numbers adjacent to symbols). Solid black lines indicate significant group structure at the 5% level. Dashed lines represent non-significant group structure. Sample station isobaths are reported beneath each symbol. (B) Non-metric multidimensional scaling plot (2D stress, 0.12; 3D stress, 0.07) from the 24 samples with superimposed significant clusters at similarity levels of 55% (solid lines) and 75% (dashed lines). Symbols and numbers as in (A)
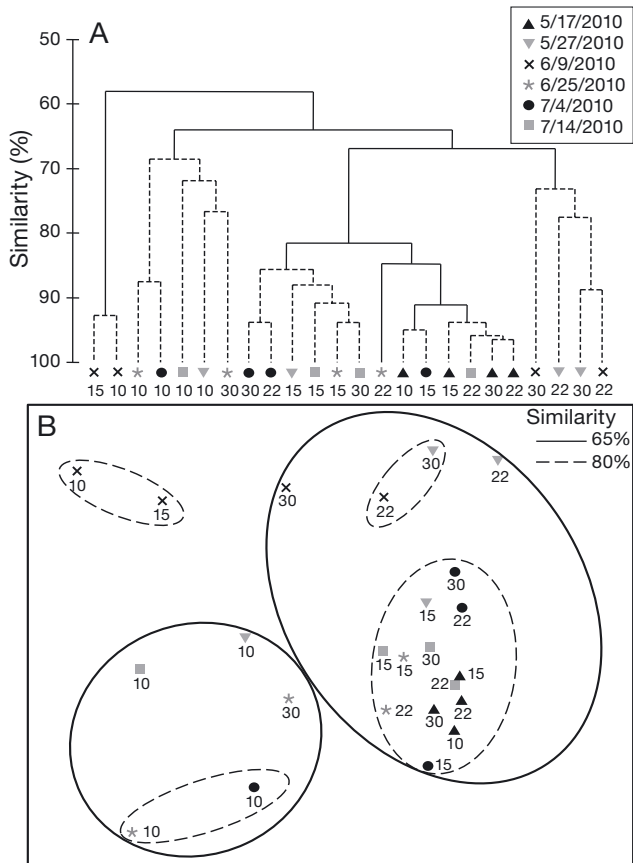
Fig. 8. (A) Hierarchical clustering dendrogram (using group-average linking) of assemblage composition from 24 samples taken over 6 d (indicated by symbols and legend entry) at 4 sampling stations across the coastal boundary layer (along the 10, 15, 22, and 30 m isobaths, indicated by numbers adjacent to symbols), using standardized data. Solid black lines indicate significant group structure at the 5% level. Dashed lines represent non-significant group structure. Sample station isobaths are reported beneath each symbol. (B) Non-metric multidimensional scaling plot (2D stress, 0.09; 3D stress, 0.06) from the 24 samples with superimposed significant clusters at similarity levels of 65% (solid lines) and 80% (dashed lines). Symbols and numbers as in (A)

the effect of date was driven by one particular sampling event on 9 June, when there was a distinct inner CBL assemblage (10 and 15 m stations; 92% similarity). The dendrogram from cluster analysis and the NMDS ordination showed 2 additional assemblages (Fig. 8): an inner CBL assemblage (68% similarity) and a main CBL assemblage containing nearly all of the other samples from the CBL, the 2 outer CBL stations as well as the 15 m station (67% similarity).

The barnacles *Balanus crenatus* and *B. nubilus* larvae dominated the composition of the assemblage and drove differences between clusters. The assemblage at the inner CBL stations on 9 June (Fig. 8) was composed of >75% *B. crenatus* cyprids. All other

samples were composed of 30% or less *B. crenatus* cyprids. In addition, the 9 June inner CBL assemblage contained <16% *B. crenatus* nauplii (early, middle, and late stage), compared to the assemblage from the majority of the CBL stations which was composed of 39 to 99% *B. crenatus* nauplii. The larger cluster of inner CBL assemblages also had low percentages of *B. crenatus* nauplii, ranging from 3 to 37%, as well as a high proportion of *B. nubilus* cyprids, which ranged from 11 to 74%, as opposed to the main CBL assemblage, which was composed of <1 to 10% *B. nubilus* cyprids. Crab larvae were in nearly all samples, but they did not generally make up a large percentage of the assemblage, except in the larger inner CBL cluster, which was composed of 21% crab larvae (compared to an average of <0.1% crab larvae in the 9 June inner CBL assemblage and 4% crab larvae in the main CBL assemblage).

DISCUSSION

Larval supply and retention within the CBL

Consistent with previous work in this study region (Morgan et al. 2009b,c, Morgan & Fisher 2010, Morgan et al. 2011, 2012), we found high abundances of benthic crustacean larvae in nearshore regions across sampling days under different oceanographic conditions. However, in contrast to previous work, we found a striking and persistent pattern of decreased larval abundance at locations closest to shore just outside the surf zone (<500 m from shore). While there were differences among taxa in cross-shore distributions of larvae, with barnacle abundance peaking at 850 m from shore and crab abundance highest 1100 m from shore, all benthic crustaceans were at their lowest abundance at the innermost station within the CBL (250 m from shore). We are unable to assess whether larvae were transported out of these innermost CBL waters (i.e. whether an intrusion of low larvae abundance waters was confined to this area), whether larvae were avoiding this region through active behavior, or whether an appreciable fraction of larvae were settling rapidly or being eaten and therefore exiting the plankton. Although we did not sample during strong southward currents, the consistency of low larval abundance across sampling days and oceanographic conditions suggests that larvae avoid the innermost waters in the CBL regardless of background transport conditions. These patterns are similar to that measured in southern California, a region of weak upwelling. Tapia & Pine-

da (2007) measured larval concentrations of *Balanus glandula* and *Chthamalus* spp. at 3 cross-shore stations within 1100 m from shore over a period of 7 d. While concentrations of most larval stages of *B. glandula* were similar among stations, concentrations of third through sixth stage *Chthamalus* nauplii were lower at the innermost station, 300 m from shore (Tapia & Pineda 2007). Even over a short temporal period, barnacle concentrations exhibited spatial structure and nauplii may potentially have avoided very nearshore waters.

Despite low concentrations of larvae in the innermost waters of the CBL, the high concentrations of all larval stages of barnacles in the CBL along the 15, 22, and 30 m isobaths suggest that many barnacle larvae may be retained within the CBL and develop in waters within 1100 m from shore. All larval stages of crabs occurred at the 2 outer CBL stations, suggesting that they may also complete development within the CBL. These findings are consistent with other studies in both weak and strong upwelling regions where high abundances of all larval stages occurred within a few kilometers from shore (Tapia & Pineda 2007, Morgan et al. 2009b,c, Shanks & Shearman 2009, Morgan & Fisher 2010, Morgan et al. 2011, 2012). Benthic crustacean larvae exhibit depth preferences that can aid nearshore retention for most species in upwelling regions (Miller & Morgan 2013). By remaining near the bottom, larvae can take advantage of slower velocities in the bottom boundary layer (in both the along- and cross-shore directions), as well as avoid offshore transport in the surface Ekman layer (Morgan et al. 2009b, Shanks & Shearman 2009, Morgan & Fisher 2010, Morgan et al. 2012).

Inshore and offshore assemblages within the CBL

A distinct larval assemblage occurred closest to shore within the CBL. Although some features of larval assemblages changed with time, these assemblages were predominantly defined by space: not only was there spatial structure in larval abundance, there was spatial structure in the composition of the assemblage. This spatial structure occurred even though physical conditions were variable among sampling dates (flow velocity, water temperature, stratification) and on many days there was no clear difference in physical parameters between the innermost station and those within the rest of the CBL (Figs. 2 & 3).

The spatial boundary between assemblages of inner and outer stations within the CBL is dynamic.

Larval assemblages on half of the sampling dates at the 15 m station were most similar to the 10 m station, and on the other half were more similar to the 22 m station. There is no clear physical difference between these groupings of days apparent from our data, as they spanned oceanographic conditions. For example, on 9 June, 4 July, and 14 July the 15 m station matched most closely with the 10 m station, yet the water column profiles from each of these days are quite distinct (Fig. 3C–E). One possible physical factor we did not explore that could influence the demarcation of the inshore community is the width of the surf zone and associated rip current zone, which is itself a dynamic boundary, dependent on the significant wave height and tidal elevation (Lentz et al. 1999, Brown et al. 2009). Surf zone characteristics appear to impact shoreline settlement of invertebrates, with low settlement observed at reflective beaches — which are characterized by high beach slopes and standing waves and are thought to have reduced cross-shore exchange (Shanks et al. 2010). Rocky shores are hypothesized to be similar to reflective beaches, and if so, the associated reduction in cross-shore exchange might explain low settlement at some locations and low abundances of larvae in surf zone waters (Shanks et al. 2010). Our study found low larval concentrations in waters just beyond the surf zone, but at distances that could be influenced by surf zone processes through the action of rip currents. Specifically, off Horseshoe Cove (Fig. 1, just downcoast of station locations), wave-driven circulation has been observed to extend as a macro-rip up to distances ~250 m offshore (J. L. Largier, unpubl. drifter data), comparable with the distance to our inner CBL station along the 10 m isobath. This suggests that the influence of wave-driven processes on larval transport may extend offshore (contrary to the idea of reduced exchange off rocky shores, as suggested by Shanks et al. 2010).

In addition to potential physical differences between the habitat of the inshore and offshore assemblages, predation may be higher within the narrow band of inner CBL water than farther offshore. Habitat along the 10 m isobath at our study site features rocky substrate with some areas supporting stands of the bull kelp, *Nereocystis luetkeana*. In central California, larval abundances were found to be negatively correlated with kelp density, and lower larval abundances on the inshore edges of kelp forests were attributed to predation (Gaines & Roughgarden 1987). Although the kelp in our region is much more sparse than the giant kelp *Macrocystis pyrifera* beds in central California, predation is still a

possible explanation for decreased abundance at the most inshore station of our study.

Implications of cross-shelf larval structure within the CBL

Larvae are clearly spending time within the coastal boundary layer; some may even complete their entire development within the CBL, which could impact estimates of population connectivity. During their time in the CBL, larvae are exposed to slower moving alongshore flows than farther offshore, which will have an impact on overall dispersal distance (Nickols et al. 2012, Nickols et al. unpubl. data). Although we did not have current velocity measurements throughout the water column beyond the 22 m isobath, concurrent measurements of surface currents by high-frequency radar showed that current velocities were faster farther offshore (data not shown). The radar domain begins 2 km offshore, and generally has high agreement with measurements from ADCPs (Kaplan et al. 2005). This gradient is also observed in a cross-shore array of moorings deployed during WEST (Wind Events and Shelf Transport; Largier et al. 2006) and in other unpublished data from BML. Estimates of dispersal distance in this region should therefore consider current velocities within 1 km or less from shore, as this is where the majority of larvae appear to be concentrated. Such consideration may improve estimates of dispersal distance derived from pelagic larval durations, which are often larger than dispersal distances estimated from genetics, tagging, and natural tracers (Palumbi 2004, Jones et al. 2009, Shanks 2009, López-Duarte et al. 2012). Refining our understanding of dispersal distances will improve our ability to accurately model population dynamics and assess population persistence (Botsford et al. 2009, White et al. 2010, Burgess et al. in press).

The coast of northern California generally has lower recruitment than other regions along the west coast of North America (Connolly et al. 2001), and a longstanding question has been whether or not this pattern is linked to larval supply. Although it was proposed that larval supply is diminished when larvae are forced offshore by strong upwelling (e.g. Roughgarden et al. 1988), numerous studies now suggest strongly that many larvae of multiple species are retained nearshore during both upwelling and relaxation conditions (Tapia & Pineda 2007, Morgan et al. 2009b,c, Shanks & Shearman 2009, Morgan & Fisher 2010, Morgan et al. 2011). Our study also found high abundance of larvae close to the shore,

and extended closer to shore than previous work in this region of strong upwelling.

An important finding of our study is the observation of low larval concentrations and a different larval assemblage in the innermost waters of the CBL, indicating a potential disconnect between high larval abundance in the CBL and larval supply to shoreline recruitment habitat. Further, this disconnect appears to occur in waters beyond the surf zone, in contrast to recent work by Shanks et al. (2010) that suggests that surf zone processes may disrupt the supply of nearshore planktonic larvae to shoreline habitats. While these results are from a single location, they represent a diversity of oceanographic conditions and the observed mismatch raises important questions about how general this result may be. Our study also focuses attention on the need to understand the mechanisms that control transport of larvae to shoreline habitats, while highlighting methodological concerns of studies that explore links between supply and settlement. As we endeavor to better understand the links between larval dispersal and population dynamics, it is essential that the nearshore zone be studied in greater detail and that we work to address the spatial pattern of recruitment limitation in coastal systems.

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