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Nearshore larval retention in a region of strong upwelling and recruitment limitation

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Abstract. The ability of miniscule larvae to control their fate and replenish populations in dynamic marine environments has been a long-running topic of debate of central importance for managing resources and understanding the ecology and evolution of life in the sea. Larvae are considered to be highly susceptible to offshore transport in productive upwelling regions, thereby increasing dispersal, limiting onshore recruitment, and reducing the intensity of community interactions. We show that 45 species of nearshore crustaceans were not transported far offshore in a recruitment-limited region characterized by strong upwelling. To the contrary, 92% of these larvae remained within 6 km from shore in high densities throughout development along two transects sampled four times during the peak upwelling season. Larvae of most species remained nearshore by remaining below a shallow Ekman layer of seaward-flowing surface waters throughout development. Larvae of other species migrated farther offshore by occurring closer to the surface early in development. Postlarvae evidently returned to nearshore adult habitats either by descending to shoreward-flowing upwelled waters or rising to the sea surface where they can be transported shoreward by wind relaxation events or internal waves. Thus wind-driven offshore transport should not limit recruitment, even in strong upwelling regions, and larvae are more likely to recruit closer to natal populations than is widely believed. This study poses a new challenge to determine the true cause and extent of recruitment limitation for a more diverse array of species along upwelling coasts, and thus to further advance our understanding of the connectivity, dynamics, and structure of coastal populations.

Key words: California, USA; dispersal; Ekman transport; larval behavior; larval recruitment; larval transport; marine larvae; recruitment limitation; upwelling.

INTRODUCTION

The vast majority of marine species produce tiny larvae that develop for weeks or months in the open ocean, where large spatial and temporal variation in dispersal and survival are key determinants of the dynamics and structure of adult populations and communities and adaptation across species ranges (Morgan 2001, Underwood and Keough 2001, Strathmann et al. 2002, Morgan and Anastasia 2008). This critical distinction between marine and terrestrial life has important consequences not only for ecological and evolutionary theory but also for the management of commercial species, the design of reserve networks, and the spread of invasive species, and for adaptation or extinction in the midst of global climate change (Strathmann et al. 2002, Carr et al. 2003). The sheer numbers of larvae produced, their poor swimming capabilities, and episodic settlement events have led to

the widespread belief that advection by currents and other sources of mortality often overwhelm larvae, carrying them far from natal populations, resulting in unpredictable recruitment in time and space (Thorson 1950, Scheltema 1975, Caley et al. 1996). However, it has become increasingly apparent that larvae may regulate transport by exploiting circulation patterns, and recruit closer to natal habitats than is widely expected (Swearer et al. 2002, Warner and Cowen 2002, Cowen et al. 2006). This would have important consequences for the dynamics and structure of marine communities if it applies to highly advective upwelling regions along the western margins of continents where much of the theoretical framework of marine ecology has been developed (Morgan 2001, Underwood and Keough 2001).

Larvae in upwelling regions are considered to be especially susceptible to offshore transport, limiting the number of recruits to coastal communities and subsequent interactions among them (Parrish et al. 1981, Yoshioka 1982, Gaines and Roughgarden 1985, Roughgarden et al. 1988). Strong winds and the Coriolis effect drive persistent offshore transport of near-surface waters (Ekman transport), thereby lowering sea level at the coast and forcing upwelling of cold, nutrient-rich

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bottom waters that generate high productivity and some of the world's most important fisheries (Kirincich et al. 2005). An "upwelling front" can form between cold upwelled water nearshore and warmer water offshore, and it was proposed that its distance from shore is a good indicator of recruitment in time and space (Shkedy and Roughgarden 1997, Roughgarden et al. 1998). Recruitment occurs infrequently and episodically when upwelling winds relax or reverse, delivering larvae either onshore (Farrell et al. 1991, Roughgarden et al. 1992) or alongshore from retention hotspots in the lee of capes (Wing et al. 1995, 2003). The evidence of recruitment-limited populations was influential in explaining why postsettlement competition and other density-dependent processes might not play a key role in regulating adult populations and structuring communities in some regions of the world. This stimulated a resurgence of interest in the larval phase and oceanographic conditions in establishing the dynamics and structure of marine communities (Young 1990). Recent studies have supported the recruitment-limitation hypothesis by documenting a relationship between variation in recruitment and adult densities of intertidal barnacles and mussels relative to the strength of upwelling along the west coast of the United States (Connolly et al. 2001, Menge et al. 2004) and in upwelling regions elsewhere (Broitman et al. 2001, Menge et al. 2003, Rilov and Schiel 2006).

It remains uncertain why larvae are often unable to replenish adult populations in upwelling regions. Characteristic circulation of upwelling regions enables zooplankton to limit cross-shelf and alongshore transport by regulating depth in opposing stratified currents (Peterson 1998, Shanks and Eckert 2005, Papastephanou et al. 2006), as has been well documented for larvae and other zooplankton in non-upwelling regions of the world (Young 1990, Epifanio and Garvine 2001, Queiroga and Blanton 2005, Morgan 2006). Some species of copepods remain close to shore throughout their lives by remaining below a shallow Ekman layer or only rising into productive surface waters to forage at night when offshore flow is weakest (Peterson et al. 1979, Peterson 1998, Batchelder et al. 2002). Larvae and copepods that avoid being carried to the surface in upwelled waters are trapped in an onshore flow convergence near the coast (Genin et al. 2005, Shanks and Brink 2005). Other species of copepods migrate farther onto the shelf by undertaking a classic ontogenetic vertical migration in which they spend more time in the Ekman layer early in development and return onshore by occurring deeper in the water column late in development (Peterson et al. 1979, Peterson 1998, Papastephanou et al. 2006). Late-stage larvae also can return to shore by undertaking a reverse ontogenetic vertical migration by rising high in the water column, where internal waves or infrequent wind relaxations transport them shoreward (Hobbs et al. 1991, Shanks 1995, Pineda 1999, Poulin et al. 2002). Determining the

extent of larval control over advection by strong currents is vital to understanding the connectivity, dynamics, and structure of populations in coastal regions throughout the world.

We tested the hypothesis that larvae are swept far offshore by Ekman transport in a region that is considered to be recruitment limited. The null hypothesis is that larvae passively diffuse so that concentrations progressively diminish seaward during development. The alternate hypothesis is that some species remain close to shore throughout larval development by avoiding the Ekman layer while larvae of other species are transported offshore early in development by ascending to the surface layer. To provide a robust test of these hypotheses, we examined 45 species of crustacean larvae that were collected from the strongest upwelling region along the west coast of the United States (Koracin et al. 2004, Dorman et al. 2005). The study was conducted during the peak upwelling season, when offshore transport should be greatest and most nearshore species develop in the plankton (Shanks and Eckert 2005, Mace and Morgan 2006a).

MATERIALS AND METHODS

Study system

The study was conducted between Point Reyes and a perennial upwelling center at Point Arena in northern California, USA (Fig. 1a), which is consistently the windiest region on the west coast of North America (Koracin et al. 2004, Dorman et al. 2005). Strong, upwelling-favorable winds persist for weeks during the peak upwelling season, which occurs during spring and summer in the northern hemisphere, and near-surface waters (<50 m) across the entire shelf flow equatorward and offshore (Hickey 1998, Roughan et al. 2006). Prevailing northwesterly winds weaken (relax) or reverse for several days about every four to 10 days (Hickey 1998, Koracin et al. 2004). Flow slows over the outer shelf and moves northward and onshore in less than a day over the inner shelf (Send et al. 1987, Largier et al. 1993, Roughan et al. 2006).

The coastline topography and shallow depths reduce offshore Ekman transport and slow alongshore currents in a coastal boundary layer that occurs <10 km from shore (Lentz and Chapman 1989, Largier et al. 1993, Kaplan et al. 2005, Roughan et al. 2006). The boundary layer broadens south of Bodega Bay as equatorward flow interacts with Point Reyes headland and is deflected offshore (Vander Woude et al. 2006). An upwelling shadow forms in the lee of the headland, trapping upwelled waters, phytoplankton, and larvae until alongshore flows reverse, transporting larvae poleward (Send et al. 1987, Wing et al. 1995, Vander Woude et al. 2006). Mean alongshore transport is near zero due to reversing flows (Largier et al. 1993, Kaplan et al. 2005). An upwelling front is often observed over the outer shelf (between 100- and 200-m isobaths), separating newly upwelled inshore waters from warmer offshore waters,

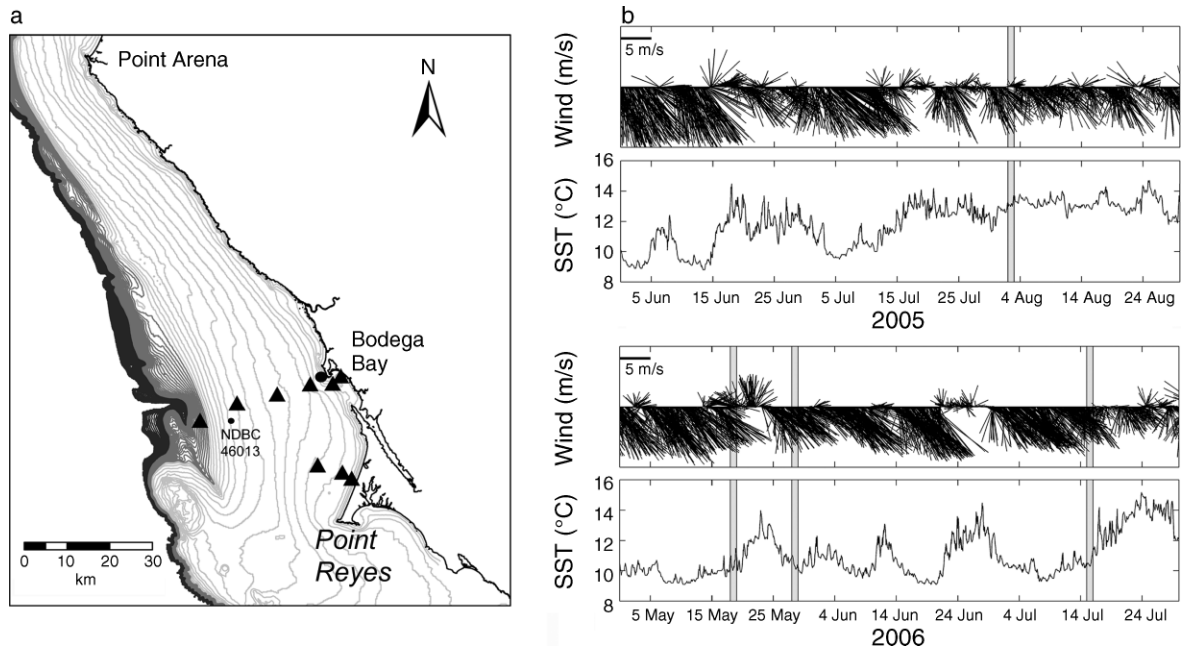


FIG. 1. (a) Map of the study region showing cross-shelf transects located off Bodega Bay and Point Reyes in northern California, USA. Location of moored acoustic Doppler current profiler (ADCP) (large solid circle) and National Data Buoy Center (NDBC) 46013 wind buoy are shown. Sample locations along transects are indicated by solid triangles. (b) The timing of four cruises (vertical bars) relative to hourly wind vectors (m/s) and sea surface temperature (SST; °C) from NDBC 46013 for June through August 2005 (top) and May through July 2006 (bottom). Upwelling-favorable northwesterly winds (negative vectors >5 m/s) and cold temperatures ($<10^{\circ}\text{C}$) were punctuated by brief relaxation or reversal events.

and different plankton assemblages occur along each side of the front, despite occasionally breaking down and reforming (Kudela et al. 2006, Papastephanou et al. 2006).

Approach

An ideal approach to test the proposed hypotheses would be to frequently sample the horizontal and vertical distributions of larvae throughout upwelling–relaxation cycles at multiple stations across the continental shelf and at several locations across the study region. This approach requires an extraordinary effort that is rarely attempted and difficult to accomplish in the rough seas during the peak upwelling season. We used a more modest version of this approach, sampling multiple stations across the shelf and at two locations along the coast during prolonged upwelling events when larvae are expected to occur far offshore. We targeted widely spaced upwelling events in this dynamic environment to sample different larval pools. We also conducted a complementary study, sampling frequently during upwelling–relaxation cycles along transects paralleling the shore to determine the stability of the larval pool (S. G. Morgan and J. L. Fisher, *unpublished data*).

Cross-shelf and vertical distributions of larvae were determined on four cruises that were conducted during the daytime off Bodega Bay and Point Reyes (Fig. 1a). We sampled five stations to 20 km from shore of Bodega Bay in 2005 and six stations to the edge of the shelf, 30

km offshore, in 2006. Stations were located 1, 3, 6, 13, 22, and 30 km from shore. The first station was located in Bodega Bay, and the remaining stations were located 1, 4, 11, 20, and 28 km from the exposed coast of Bodega Head in ~20, 25, 80, 90, and 120 m of water, respectively. The second transect off Point Reyes was sampled 1, 5, and 10 km from shore during the first two cruises of 2006. This transect extended diagonally rather than perpendicularly across the shelf due to differences in the orientation of the shoreline at the two locales. The depth of the water column increased more gradually than off Bodega Bay, and larvae were predicted to occur farther along this transect while remaining closer to shore in shallower waters.

Cruises were planned to occur during upwelling conditions, based on marine weather predictions and conditions monitored offshore at the National Data Buoy Center 46013 ($38^{\circ}13'30''$ N, $123^{\circ}19'00''$ W; data *available online*).⁴ Upwelling was considered to occur when winds blew from the northwest at >5 m/s and water temperatures were decreasing or $<10^{\circ}\text{C}$. One cruise was conducted on 3 August 2005 following three days of upwelling and within hours of the onset of a relaxation event (Fig. 1b). Three cruises were conducted during prolonged periods of upwelling in 2006. The first cruise occurred on 19 May after 24 days of upwelling

⁴ (<http://www.ndbc.noaa.gov>)

and one day before the onset of poleward, downwelling-favorable winds. The second cruise occurred on 29 May, after five days of upwelling, during prolonged upwelling. The third cruise occurred on 16 July after 16 days of upwelling and three days before relaxation.

Plankton were collected using an electronically tripped Tucker Trawl, a standard plankton-sampling device (0.5- or 1-m² mouth), that was equipped with five 335- μ m mesh nets and a temperature and depth sensor to interactively sample relative to the thermocline. The water column was partitioned into four depth bins. When the thermocline was deeper than 10 m, two tows were taken above and two below it. A single tow was taken above the thermocline and three tows were taken below it when the thermocline was <3 m deep. A net (0.5-m² mouth) sampled the surface of the water column (neuston). Temperature and salinity were profiled throughout the water column at each station using a conductivity, temperature, and depth profiler (Seabird 19-Plus, Sea-Bird Electronics, Bellevue, Washington, USA).

Current speed and direction were measured through the water column by a moored acoustic Doppler current profiler (ADCP, 300 kHz; Teledyne RD Instruments, Poway, California, USA), which was located near the second station \sim 1 km off Bodega Head at the 30-m isobath (Fig. 1a). Surface circulation throughout the study area was mapped hourly with high-frequency (HF) radar during the study.

Profiles of water column properties and HF radar maps were examined for each of the four sampling dates and the week preceding them to place larval distributions in the context of circulation patterns. Representative temperature and salinity profiles and HF radar surface vectors are displayed for one cruise (29 May 2006) along the Bodega transect, which was sampled most often and extended farthest offshore. A progressive vector diagram was generated for water column velocity profiles from the Bodega Head mooring for 14 June to 25 July 2006, as there was a data gap from May to early June. To place the strength of upwelling during our study in context with earlier studies on recruitment limitation (Gaines and Roughgarden 1985, Roughgarden et al. 1988), we obtained mean daily values of the Bakun Coastal Upwelling Index for our region (39° N, 125° W) and central California (36° N, 122° W) during the three weeks preceding cruises from the Pacific Fisheries Environmental Laboratory (data available online).⁵

We plotted the cross-shelf distributions of early-, mid-, and late-stage larvae and postlarvae for each species along both transects to determine whether larvae are swept offshore during upwelling conditions. Larval concentrations were calculated per m² to standardize for the increasing depth of the water column with distance from shore, and species exhibiting similar cross-

shelf distributions were combined for presentation. Cross-shelf larval distributions were similar among cruises and also were combined for presentation.

We explored the possibility that larval behavior might regulate cross-shelf transport for the 34 most-abundant species of crustacean larvae. We determined whether the larval assemblage changed across the shelf and among depths for the four cruises using nonparametric analysis of similarity (ANOSIM) followed by hierarchical cluster analysis and ordination (Appendix). We first tested for cross-shelf differences in the larval assemblage among sampling dates after depths were averaged for each station. The larval distributions did not differ significantly among sampling dates (ANOSIM $R = 0.013$, $P = 0.39$), so subsequent analyses on cross-shelf distributions and depth were conducted on date-averaged data. 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 objectively classify species-stage combinations by their cross-shelf and depth distributions (Appendix). Non-metric multidimensional scaling (NMDS) was used to examine the distance offshore and depth separation among larval assemblages (Appendix). Contour plots of depth distributions of species and stages relative to the distance from shore display potential suites of larval behaviors that may contribute to the different cross-shelf distributions. The mean depth center of mass (ZCM) and standard error were calculated for each group for comparison.

RESULTS

Temperature and salinity profiles across the shelf were indicative of upwelling conditions in our region. Isotherms and isohalines typically were inclined toward the surface onshore with a shallow thermocline slightly deepening from <3 m to 10 m deep seaward of the upwelling front that was located \sim 20 km from shore (Fig. 2a). Mean surface currents recorded by high-frequency (HF) radar across the study region showed that the weakest equatorward flow occurred <10 km from shore (Fig. 2b). The progressive vector diagram of acoustic Doppler current profiler (ADCP) data revealed offshore and equatorward transport near the surface (5–10 m; Fig. 2c) during upwelling periods (indicated by winds and temperature in Fig. 1b), but weaker flow at depth, and onshore and poleward net transport throughout the water column for this nearshore site over the six-week period. The upper 10 m of the water column was most subject to wind relaxations and reversals, and larvae that remained deep in the water column traveled the shortest distance. The upwelling index was consistently greater in our study region (100–200 m³·s⁻¹·100 m⁻¹ coastline) than in central California (60–120 m³·s⁻¹·100 m⁻¹ coastline) during the three weeks preceding our four cruises, and it was greater than the three weeks preceding the cruises conducted off

⁵ (<http://www.pfeg.noaa.gov>)

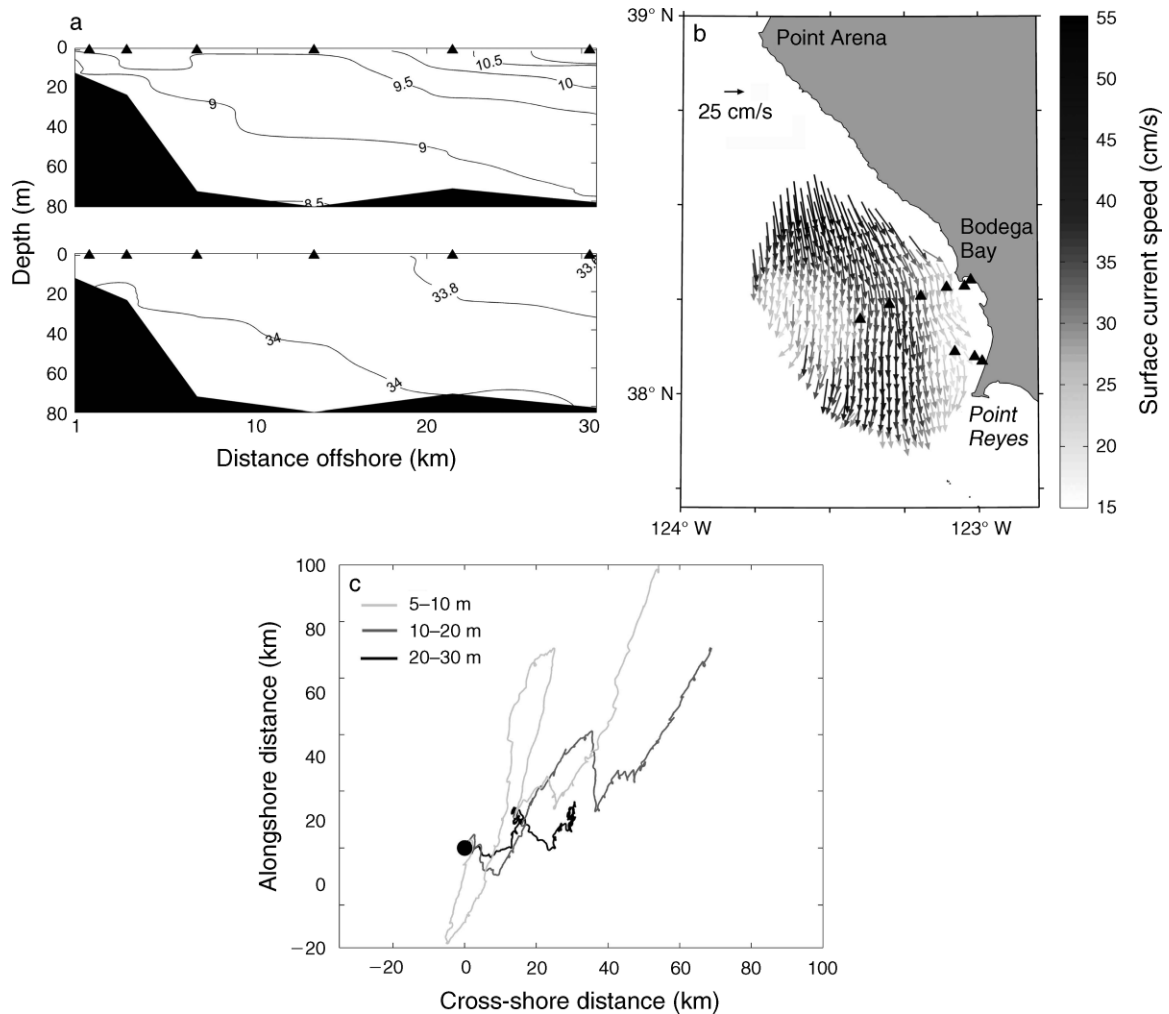


FIG. 2. (a) Contours of temperature ($^{\circ}\text{C}$; top) and salinity profiles (in practical salinity units; bottom) at six stations along the transect off Bodega Bay on 29 May 2006. Sample locations along transects are indicated by solid triangles. (b) Mean surface current velocity (cm/s) recorded by high-frequency radar across the study region during the 29 May 2006 cruise. (c) Progressive vector diagram of alongshore and cross-shore transport in near-surface, mid, and near-bottom currents at a 30 m deep site located ~ 1 km offshore on the Bodega Bay transect. Current velocity was measured by a bottom-moored ADCP (large solid circle) from 14 June to 25 July 2006. Positive and negative alongshore distances are poleward (to the north) and equatorward (to the south), respectively. Positive and negative cross-shore distances are toward shore and away from shore, respectively.

central California in the 1970s and 1980s (exceeding $85 \text{ m}^3 \cdot \text{s}^{-1} \cdot 100 \text{ m}^{-1}$ coastline only once during seven years).

Larvae of 45 species of crustaceans largely occurred (92%) < 6 km from shore along both transects. Early larval stages of all species were most abundant close to shore where adults typically release larvae (Fig. 3). Along the Bodega Bay transect, all larval stages of 23 species were collected almost entirely (98%) < 6 km from shore (Fig. 3a), indicating that they completed development there. All larval stages of seven more species were collected primarily (82%) < 6 km from shore, and late larval stages ranged farther onto the continental shelf with almost all larvae (95%) being collected < 13 km from shore (Fig. 3b). Ten more species occurred < 13 km from shore early in development (80%) and > 13 km

from shore as late-stage larvae and postlarvae (70%; Fig. 3c). The five remaining species also occurred very close to shore, but the extent of their cross-shelf distributions could not be determined reliably due to incomplete collection of larval stages. Larvae of all species again were maximal inshore along the Point Reyes transect, with species showing the same cross-shelf distributions as off Bodega Bay (Fig. 3d–f). Although larvae appeared to occur farther from shore off Point Reyes, they remained in shallower water because the short transect angled diagonally rather than perpendicularly across the shelf, and the bottom slope was gradual (Fig. 1a). Thus larvae of most species remained nearshore or on the inner shelf throughout development, while others occurred on the outer shelf late in development.

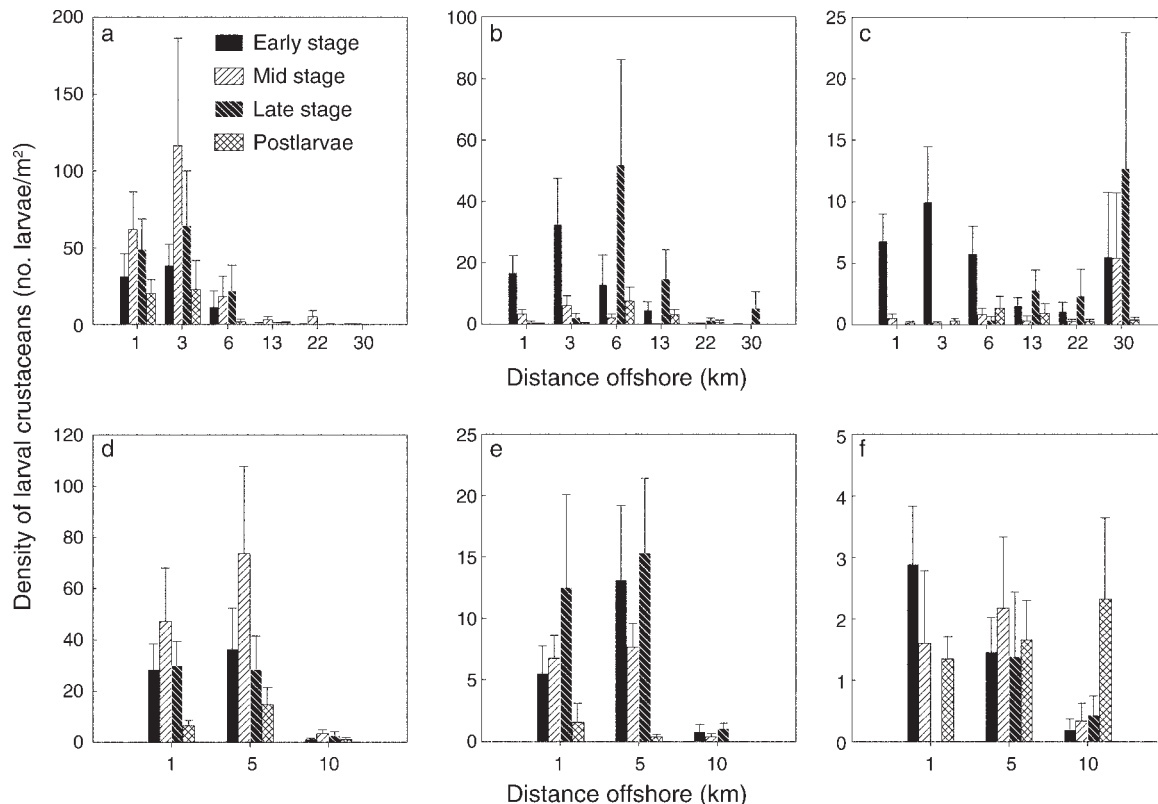


FIG. 3. Densities (mean \pm SE) of larval stages of 40 species of crustaceans relative to distance from shore for all depths and cruises combined. Off Bodega Bay, (a) 23 nearshore species remained <6 km throughout development, (b) seven midshelf species primarily occurred <13 km late in development, and (c) 10 outer-shelf species occurred >13 km from shore late in development. Off Point Reyes, all larval stages of (d) 19 nearshore species and (e) seven midshelf species primarily occurred <5 km from shore, and all larval stages of (f) six outer-shelf species occurred <10 km from shore. Note x- and y-axis scale differences.

Larval assemblages of the 34 most-abundant species and stages along the Bodega Bay transect differed mostly among stations (ANOSIM $R = 0.58$, $P = 0.001$) but also differed among depths (ANOSIM $R = 0.32$, $P = 0.002$), raising the possibility that depth preferences and ontogenetic vertical migrations contribute to interspecific differences in cross-shelf transport. Indeed, the dendrogram from the cluster analysis and the nonmetric multidimensional scaling (NMDS) ordination both revealed a high degree of spatial structure in the larval assemblage, based on differences in distance offshore and depth (Fig. 4). The percentage contribution of each species and stage to the clusters grouped taxa into five categories.

Two clusters were composed of all larval stages of 20 species and primarily occurred <3 km from shore (<1 km from Bodega Head; Figs. 4 and 5). All stages of seven species belonging to two taxa that comprised 11% of all larvae collected and contributed 25% of the similarity to the first nearshore cluster (Figs. 4 and 5a). These larvae occurred highest in the water column overall, with postlarvae occurring closer to the surface (depth center of mass [ZCM] = 4.5 ± 1.7 m [mean \pm SE]) than larvae (ZCM = 9.0 ± 1.5 m). All stages of 13

species of four taxa comprised 65% of all larvae collected and contributed 61% of the similarity to the second nearshore cluster (Figs. 4 and 5b). Larvae of these species collectively occurred several meters higher in the water column early (ZCM = 11.9 ± 1.3) rather than later in development (ZCM = 15.7 ± 3.8).

Two clusters were composed of all larval stages of six species, mostly occurring <13 km offshore of Bodega Bay (11 km from Bodega Head; Figs. 4 and 6). Early-stage larvae of the six species contributed 32% to the nearshore shallow cluster, while the mid and late stages contributed 86% to the midshelf cluster, indicating that early-stage larvae occurred higher in the water column nearshore and deeper offshore. Each midshelf cluster consisted of three species. The three species in the first cluster contributed 5% of all larvae collected. The early larval stages and postlarvae of these species contributed 14% to the nearshore shallow cluster and 46% to this midshelf cluster. The first and second larval stages of these species occurred higher in the water column (ZCM = 17.5 ± 3.1 m) than the last three larval stages (ZCM = 38.3 ± 9.1 m), and postlarvae occurred closest to the surface (ZCM = 12.7 ± 3.7 m; Fig. 6a). The three species in the second midshelf group contributed 14% of all

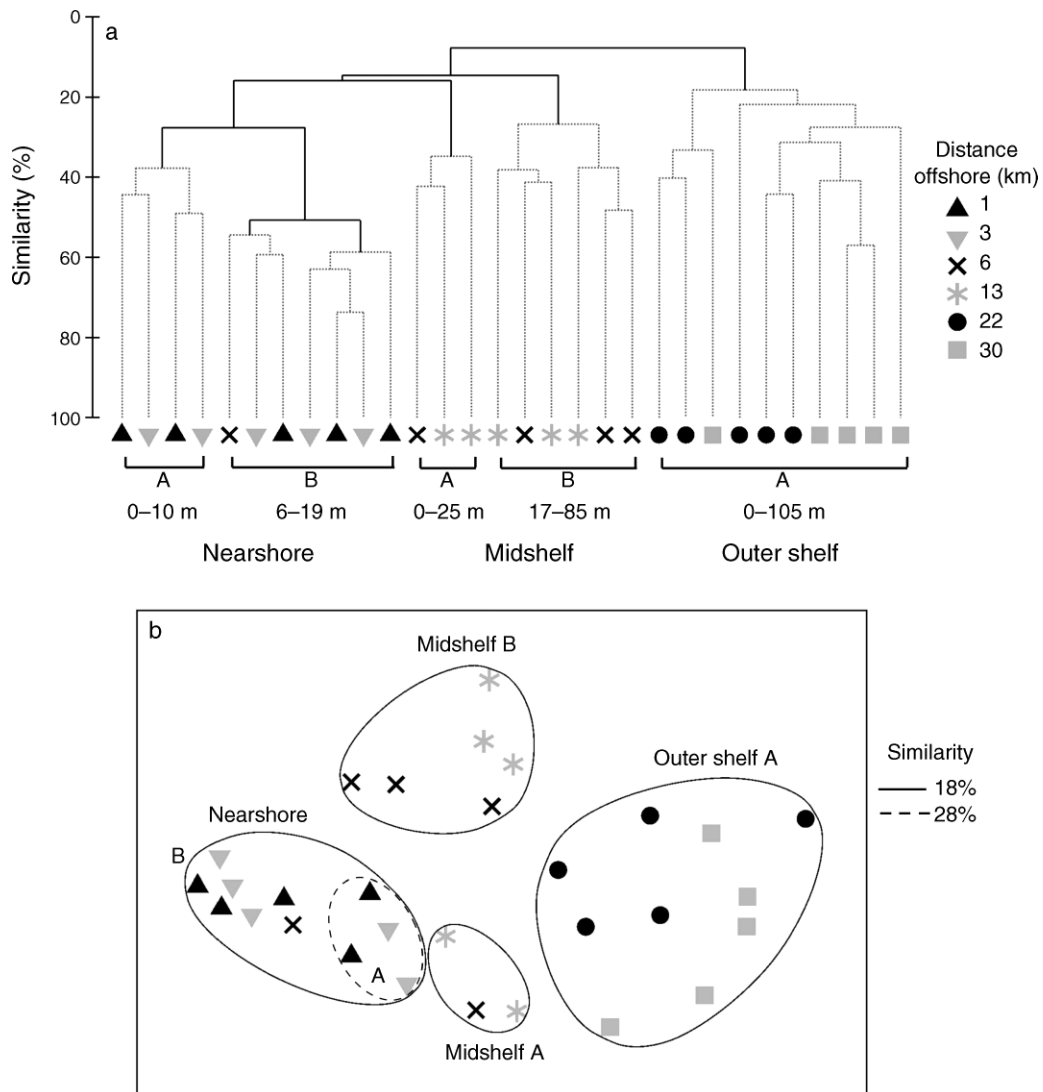


FIG. 4. (a) Hierarchical clustering dendrogram (using group-average linking) of 30 samples taken from five depths at six sampling stations across the continental shelf (1, 3, 6, 13, 22, and 30 km from shore). Samples were categorized based on 18% and 28% similarities. Solid black lines indicate significant group structure at the 1% level. Sample depths are reported beneath each group. The gray lines represent nonsignificant group structure >1%. (b) Nonmetric multidimensional scaling plot (2-D stress, 0.14; 3-D stress, 0.09) from the 30 samples with superimposed significant clusters at similarity levels of 18% (solid lines) and 28% (dashed lines).

larvae collected. Mid- and late larval stages of this group contributed 78% to this cluster. Larvae in this group occurred shallower close to shore through midlarval stages (ZCM = 16.1 ± 1.3 m) and farther from shore during late stages (ZCM = 32.5 ± 8.7 m; Fig. 6b). Early larval stages of all six species mostly occurred <6 km from shore, later larval stages 3–22 km from shore, and postlarvae <13 km from shore (Fig. 6).

The fifth cluster was composed of larvae of eight species that were common on the outer shelf 30 km from shore (Figs. 4 and 7). These larvae contributed 71% of the similarity to the cluster (Fig. 4) and collectively occurred several meters higher in the water column than midshelf species (ZCM = 21.6 ± 7.2 m; Fig. 7). Early

larval stages occurred close to shore, and later stages occurred farther from shore for all species (Fig. 7). Late developmental stages of all species occurred closer to shore and shallower in May than July 2006.

DISCUSSION

Contrary to prevailing theory, we found few larvae of 45 species of nearshore crustaceans offshore at two locations, even though we sampled four times during or immediately following upwelling conditions when they were expected to occur far from shore. We instead found a striking and general pattern of high densities of larvae close to shore where nets often were filled with crustacean larvae. Overall, 92% of all larvae were

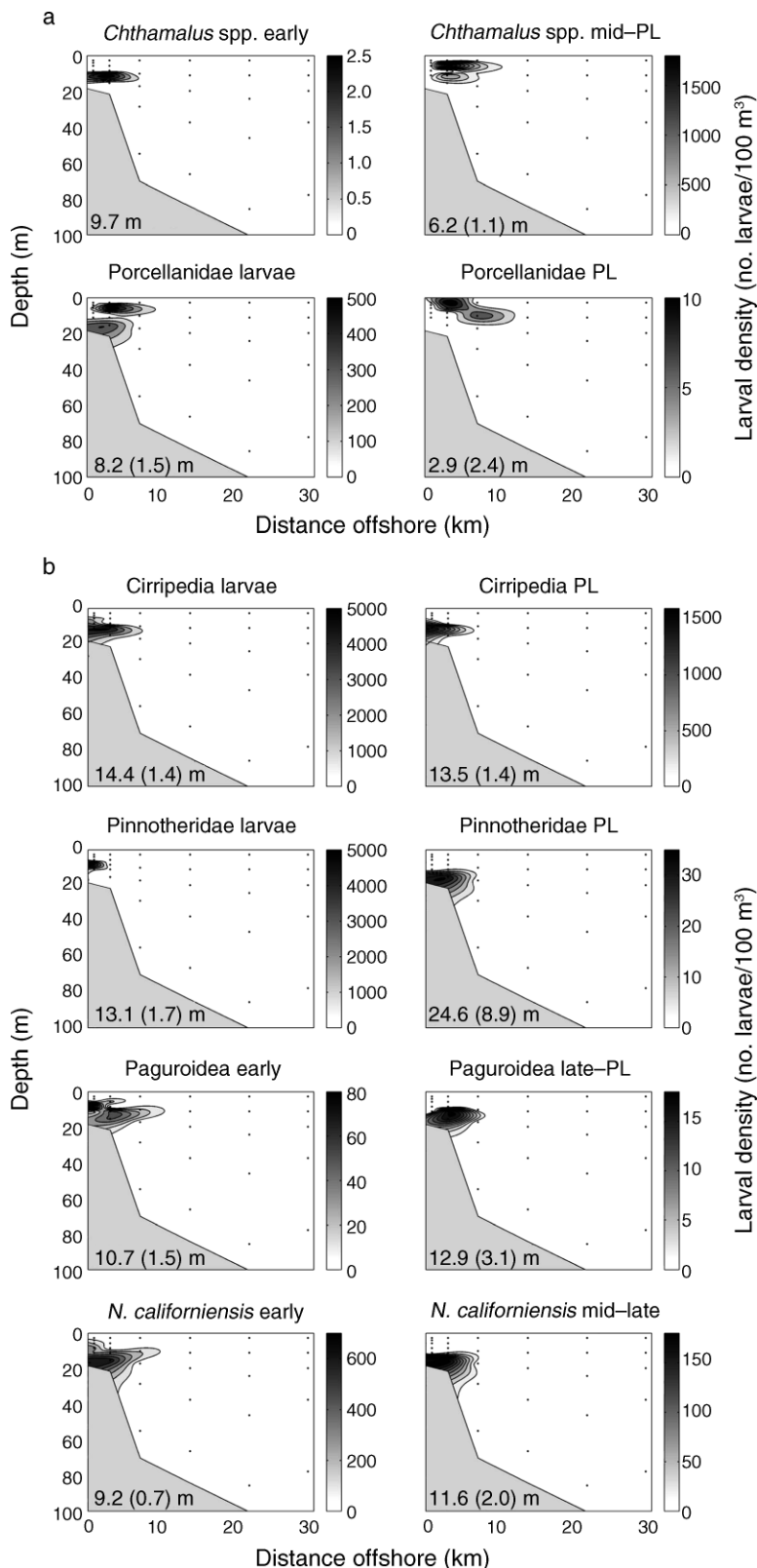


FIG. 5. Nearshore larval development of 20 species in relation to depth and distance offshore. The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. (a) Two species of barnacles (*Chthamalus dallifissus*) and five species of porcelain crabs (*Petrolisthes cinctipes*, *Pet. erimerus*, *Pet. manimaculus*, *Pachycheles rudis*, *Pac. pubescens*) completed

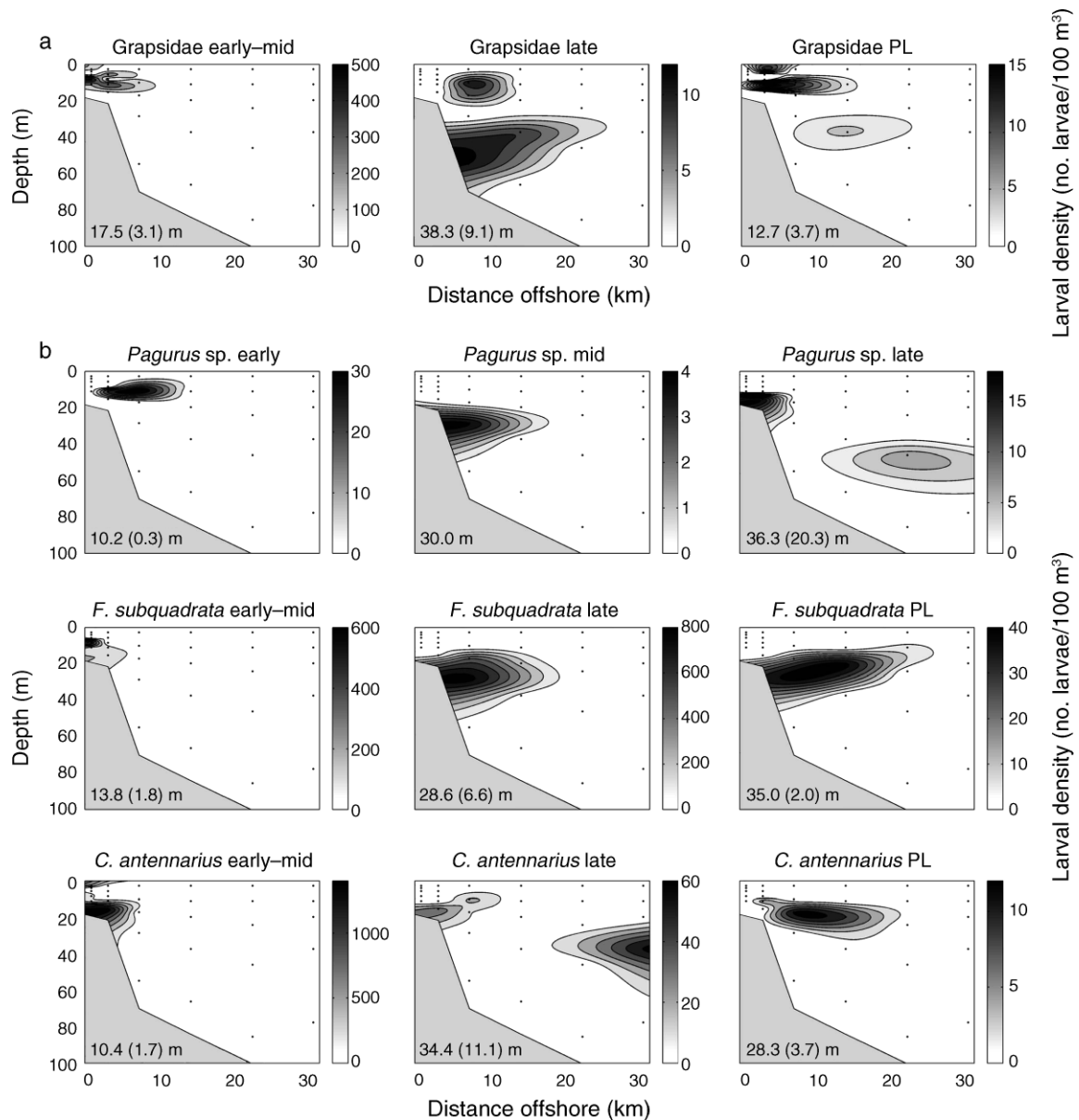


FIG. 6. Midshelf development of six species in relation to depth and distance offshore. The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. Larvae mostly occurred <13 km from Bodega Bay, with early larval stages being abundant close to shore and later stages occurring farther from shore. (a) Three species of grapsid crabs (*Pachygrapsus crassipes*, *Hemigrapsus nudus*, *H. oregonensis*) ranged from 5 to 80 m deep in the water column. These species occurred with a combined depth center of mass (ZCM; mean \pm SE) of 17.5 ± 3.1 m in a shallow water column as early-stage larvae, descending in a deepening water column as late-stage larvae, and ascending closest to the surface as postlarvae. (b) An unidentified species of hermit crab, a pea crab (*Fabia subquadrata*), and a rock crab (*Cancer antennarius*) primarily occurred from 5 m deep to the middle of the water column (~ 50 m) with a ZCM of 25.2 ± 4.3 m. They occurred higher in the water column (21.2 ± 4.3 m) during the first two larval stages than in later stages (33.2 ± 8.7 m). The two groups of *C. antennarius* and grapsid late-stage larvae and postlarvae were collected during different cruises. ZCM with no variation shown in parentheses indicates species collected during a single cruise.

←

larval development <6 km from shore by occurring at a ZCM of 6.7 ± 1.6 m overall, with postlarvae (PL) occurring closer to the surface (4.5 ± 1.7 m) than larvae (9.0 ± 1.5 m). Mean depth with no variation shown in parentheses indicates species collected during a single cruise. (b) Three species of barnacles (*Balanus glandula*, *B. crenatus*, *Semibalanus cariosus*), six species of pea crabs (*Pinnixa faba*, *P. tubicola*, *Pinnotheres pugettensis*, *Scleroplax granulata*, two unidentified species), three species of hermit crabs (*Pagurus samuelis*, *P. hirsutiussculus*, *P. granosimanus*), and a mud shrimp (*Neotrypaea californiensis*) were most abundant <3 km from shore and were uncommon 6 km from shore. Larvae primarily occurred 5–20 m deep with a ZCM of 13.8 ± 2.6 m.

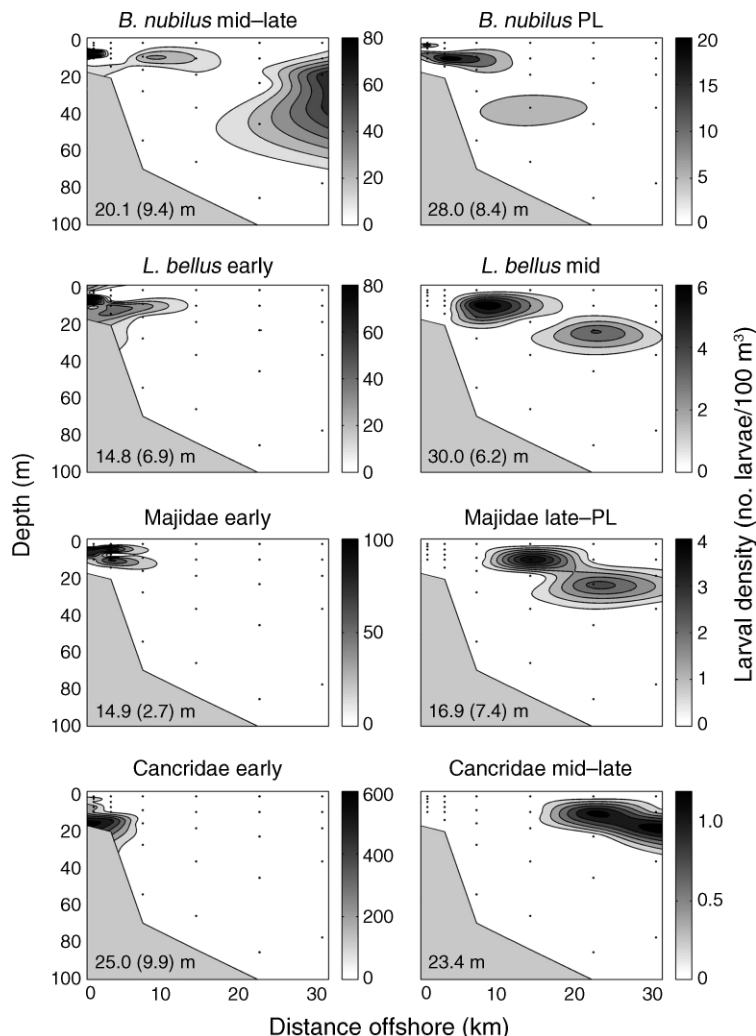


FIG. 7. Outer-shelf development of eight species in relation to depth and distance offshore. The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. Results are shown for larvae of the barnacle *Balanus nubilus*, the xanthid crab *Lophopanopeus bellus*, three species of spider crabs (Majidae: *Pugettia producta*, *P. richii*, *Scyra acutifrons*), and three species of cancrid crabs (Cancridae: *Cancer productus*, *C. oregonensis*, *C. magister*). These species occurred close to shore early in development and on the outer continental shelf later during development in low densities. They ranged from 0 to 50 m deep, with most larvae and postlarvae (PL) occurring <30 m deep. Later-stage larvae and postlarvae occurred farther offshore and deeper in July than in May 2006, as indicated by the separate groups of larvae within panels. ZCM values with no variation shown in parentheses indicate species collected during a single cruise.

collected <6 km from shore along both transects, and 23 species completed development there, rarely occurring farther from shore. The pattern of high nearshore concentrations was repeated in time and space, providing strong evidence that larvae typically remain close to shore throughout development. Larvae were concentrated in the coastal boundary layer of reduced offshore Ekman transport and slow alongshore currents <10 km from shore (Lentz and Chapman 1989, Largier et al. 1993, Kaplan et al. 2005, Kirincich et al. 2005, Roughan et al. 2006). This characteristic feature of shoreline circulation (Pettigrew and Murray 1986, Shanks 1995, Largier 2002, 2003) was observed throughout our study in high-frequency (HF) radar maps of surface currents

(Fig. 2) and likely contributes to the retention of diverse crustacean larvae close to shore in our region as well as the weaker upwelling conditions along the coasts of Oregon (Peterson et al. 1979) and central and southern California (Grantham 1997, Tapia and Pineda 2007).

The remaining species occurred nearshore early in development and >6 km from shore later in development. Seven species completed development <13 km from shore, primarily within the coastal boundary layer. The seaward limit of these species was ~7 km, which is inshore of the upwelling front where larvae displaced by Ekman transport are expected to accumulate (Roughgarden et al. 1988, 1992). Maximal densities of the early larval stages of the 10 remaining species also occurred

close to shore where adults typically release larvae, later larval stages occurred on the outer shelf, and postlarvae occurred all across the shelf as they recruit shoreward to adult habitats. Similar cross-shelf distributions of crustacean larvae were reported in the weaker upwelling conditions off the coast of Oregon (Lough 1974), indicating that these interspecific differences are maintained across regions.

The three patterns of cross-shelf distribution were associated with distinctive vertical distributions of larval stages that may contribute to the maintenance of these patterns. The nearshore and midshelf groups were divided by multivariate analysis into two subgroups, suggesting that the maintenance of cross-shelf distributions may be accomplished in two ways per group. Larvae of 65% of taxa in the nearshore group remained deep in a shallow water column throughout development or occurred deeper in the water column late in development, perhaps undertaking classic ontogenetic vertical migrations. The deep vertical distributions of these larvae in onshore and weak alongshore flow recorded by the acoustic Doppler current profiler (ADCP) during our study (Fig. 2) and observed during previous studies in our region (Largier et al. 1993, Dever et al. 2006, Roughan et al. 2006) likely facilitated nearshore retention (Peterson 1998, Batchelder et al. 2002, Shanks and Brink 2005, Papastephanou et al. 2006). Barnacle larvae typically remain deep in the water column, whereas crab larvae typically ascend closer to the surface at night (S. G. Morgan and J. L. Fisher, unpublished data) when winds are weakest and often onshore, minimizing advection (Peterson et al. 1979, 1998, Batchelder et al. 2002). The second subgroup consisted of 35% of nearshore taxa and occurred closest to the sea surface late in development, apparently undertaking reverse vertical migrations. These larvae could be transported shoreward by winds and internal waves, which are prevalent in our region (Pineda 1994, Shanks 1995, Pringle 1999). Postlarvae of one genus of barnacle (*Chthamalus* spp.) collected near the surface during this study previously have been reported to occur in the neuston and recruit onshore during spring tides (Pineda 1994, 1999, Shanks 1995), and recruitment of other species peaks biweekly relative to the tidal amplitude (spring-neap) cycle along the open coast (Pineda 1994, Shanks 2006).

The remaining species are transported farther onto the shelf by spending more time in the Ekman layer early in development, as observed for copepods (Peterson et al. 1979, Peterson 1998, Batchelder et al. 2002, Papastephanou et al. 2006). Later-stage larvae of six species descended into deeper onshore flow late in development and completed development <13 km from shore. Seaward transport early in development may be offset by landward transport late in development, thereby limiting cross-shelf displacement. Postlarvae of half of these species remained deep in onshore flow, apparently enabling them to return to adult habitats

nearshore (Peterson et al. 1979, Grantham 1997, Peterson 1998, Papastephanou et al. 2006), whereas postlarvae of the other half of the midshelf group (grapsids) ascended to surface waters where they could be transported shoreward by winds and internal waves. Postlarvae of at least one of these grapsids (*Pachygrapsus crassipes*) previously have been reported to occur in the neuston and be transported onshore by internal waves (Shanks 2006). Multivariate analysis did not detect different types of ontogenetic vertical migrations among the eight species that were transported to the outer shelf late in development. These species were transported farthest offshore by primarily occurring <30 m deep throughout development. Postlarvae of several of these species occur in the neuston in surface convergences (*Lophopanopeus bellus*, *Pugettia* spp.) or <5 m deep (*Cancer productus*, *C. oregonensis*, *C. magister*), where they can be transported onshore by winds and internal waves (Shenker 1988, Hobbs et al. 1991, Shanks 2006).

Passive larval advection and diffusion alone cannot account for the interspecific differences in cross-shelf distributions. Larvae of these species all hatch nearshore and develop concurrently, being subject to the same physical processes. Moreover, larval behavior must mediate cross-shelf transport because different stages of the same species are being transported in opposite directions at the same time; larvae are transported from shore while postlarvae return to shore. Interspecific differences in cross-shelf distributions of postlarvae are not due to differences in larval durations, because species that develop offshore pass through as few as two stages, while those developing nearshore molt through as many larval stages (five) as those developing on the outer shelf (Morris et al. 1980). Natural selection may have favored simple larval behaviors that exploit conservative circulation patterns, enabling larvae of different species to remain nearshore or be transported various distances offshore while limiting alongshore displacement across species ranges (Strathmann et al. 2002, Shanks and Eckert 2005, Morgan 2006, Morgan and Anastasia 2008). Circulation in upwelling regions is fundamentally similar worldwide, which may enable zooplankton to minimize losses from advection (Peterson 1998).

Other explanations for the high concentration of larvae nearshore are unlikely. First, high larval concentrations after hatching were not diluted by vertical mixing as the water column deepened offshore because larval densities were adjusted for increasing cross-shelf depth. Further, larval concentrations of later larval stages of some taxa remained similar or increased on the middle and outer shelf rather than diminishing offshore. Second, the high concentrations of larvae did not result from being retained in Bodega Bay, because they were as abundant in open waters 1 km from shore as they were in the bay. Upwelling is active in this wind-exposed bay, and newly upwelled surface waters move as rapidly

offshore and equatorward as on the open coast (Roughan et al. 2005). Third, the high concentrations of larvae probably did not originate primarily from Bodega Bay. Adults producing the diverse array of larvae collected during our study are distributed along the open coast rather than being restricted to Bodega Bay, and many of the larvae found nearshore could have originated to the north or south of the study area. Moreover, nearshore retention also occurred off Point Reyes, 25 km from Bodega Bay. Fourth, larvae were not transported poleward along the coast from a retention area in the lee of the Point Reyes headland, as this flow only happens during infrequent relaxation events. It takes several days for water and larvae from the lee of Point Reyes to reach our study area once the prevailing upwelling wind relaxes, and we sampled during upwelling or just at the onset of relaxation (Wing et al. 1995). Fifth, retentive eddies do not occur nearshore off Bodega Bay during prolonged upwelling conditions (Kaplan et al. 2005) and were not present in HF radar maps of surface currents during our study (Fig. 2b). Lastly, nearshore retention of crustacean larvae also has been documented in weaker upwelling regions (Lough 1974, Grantham 1997, Tapia and Pineda 2007). We conclude that larval retention may be more common in upwelling regions than is widely believed. As a consequence, larvae are more likely to recruit closer to natal populations and in higher abundance than is generally realized, which has profound implications for the ecology, evolution, and management of species inhabiting upwelling coasts (Strathmann et al. 2002, Sotka et al. 2004, Shanks and Eckert 2005, Pfeiffer-Herbert et al. 2007).

Balamus glandula larvae were thought to be advected far offshore during strong upwelling (Roughgarden et al. 1988). In contrast, we found that nearly all *B. glandula* larvae (99.6%) were collected <6 km from shore and were much more abundant than during the previous study, even though the stronger Ekman transport in our region should have transported them farther offshore (Koracin et al. 2004). The discrepancy between the two studies likely arose because samples were not taken <8 km from shore in the previous one (Roughgarden et al. 1988). All larval stages of *B. glandula* also occurred close to shore in the weak upwelling off southern California (Tapia and Pineda 2007).

Our study raises a question of fundamental importance to our understanding of the dynamics and structure of marine populations. If the vast majority of larvae remain close to shore in areas of strong upwelling, then why are these populations limited by the number of recruiting postlarvae? Larvae still may occur too far from shore to recruit without being aided by infrequent relaxation events or internal waves, which propagate in a stratified water column (Shanks 2006). Larval recruitment also may increase when winds relax, because lighter winds form smaller waves and less turbulence

that make it easier for larvae to settle on the substrate (Crimaldi et al. 2002). It also is possible that larvae have difficulty crossing the surf zone (Rilov et al. 2008). Regardless of the explanation, it is important to realize that offshore advection of larvae during periods of strong upwelling probably is not the cause of recruitment limitation, even for the select few species on which the hypothesis was based. This explanation is even less tenable for other species that commonly recruit during upwelling conditions or by internal tides rather than during infrequent relaxations (Mace and Morgan 2006b, Shanks 2006).

The recruitment-limitation hypothesis has shaped our understanding of marine population dynamics, but two tenets do not appear to hold. Larval recruitment of most species studied is not limited to infrequent relaxation events (Mace and Morgan 2006b, Shanks 2006), and now we show that larvae of most species remain close to shore even during strong upwelling. Although conventional wisdom suggests that larval retention in upwelling regions is restricted to bays and upwelling shadows in the lee of headlands (Wing et al. 1995, Graham and Largier 1997, Roughan et al. 2005), it is increasingly evident that larval retention occurs along the open coast (Marliave 1986, Poulin et al. 2002, Tapia and Pineda 2007). New comprehensive studies are needed to investigate the coupling of larval abundance in the plankton with settlement and postsettlement mortality on the shore for diverse taxa and locations across upwelling coasts to determine the underlying mechanisms responsible for the observed spatial and temporal patterns of recruitment. This is an essential step in further advancing our understanding of processes that regulate marine populations and communities as well as the evolution of life in the sea (Strathmann et al. 2002, Carr et al. 2003, Shanks and Eckert 2005).

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APPENDIX

Multivariate analysis of cross-shelf and vertical distributions of 34 species of crustacean larvae (*Ecological Archives* E090-243-A1).