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Limited recruitment during relaxation events: Larval advection and behavior in an upwelling system

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Abstract

We capitalized on a long-term record of larval recruitment and a distinctive oceanographic signature to reveal how changes in ocean conditions affect larval advection, behavior, and recruitment in a region of strong, persistent upwelling and recruitment limitation. We repeatedly sampled the vertical and horizontal distribution of a larval assemblage and ocean conditions during infrequent relaxations of prevailing upwelling winds near Bodega Bay, California. During prolonged relaxation events, a poleward, coastal, boundary current imported low-salinity surface waters that were devoid of larvae to the study area. The resident larval assemblage was restricted to cold, saline, bottom waters and pushed offshore while diel vertical migrations were suppressed. Hence, changes in oceanographic conditions strongly affected behaviorally mediated larval distributions, revealing the reason that few species recruit during relaxation events in this region. During relaxation events in upwelling regions, poleward coastal boundary currents will force larvae offshore throughout the water column at small headlands and in seaward-flowing bottom currents at straight coastlines, but recruitment may decrease markedly only near estuaries where few larvae will arrive in low-salinity surface waters. Targeted profiling of larval assemblages complements widespread monitoring of recruitment from shore and is necessary to determine how changing ocean conditions affect larval distributions, recruitment dynamics, and the connectivity of populations.

Complex life cycles in a dynamic ocean make it especially challenging to establish processes that regulate marine populations and communities (Morgan 2001; Strathmann et al. 2002). The sheer numbers of larvae produced, their poor swimming capabilities and the episodic nature of settlement events have led to the widespread belief that high larval mortality results in unpredictable recruitment in time and space (Thorson 1950; Caley et al. 1996). This view was based on logical inference and data from experimental designs that were limited in their ability to determine the fate of long-lived microscopic larvae in ocean currents. Tracking large fluctuations in the numbers of recruits at a focal study area cannot resolve whether most larvae died or were transported to neighboring locales beyond this area of inference (Morgan 1995). In contrast, sampling over large spatial and long temporal scales has demonstrated that larval production and recruitment can be coupled (Robertson et al. 1988; Hughes et al. 2000) and oceanographic patterns can result in predictable spatial changes in populations and communities (Yoshioka 1982; Broitman et al. 2008; Shanks et al. 2010).

Monitoring larval recruitment at appropriate scales is most feasible from shore for intertidal and shallow subtidal communities, but surveying larval distributions at sea is needed to provide a deeper understanding of the processes behind the observed patterns. A long history of surveying ontogenetic changes in the cross-shelf abundances of larvae of nearshore species has shown that exploitation of circulation patterns enables larvae to either remain nearby or expedite transport from natal populations (Queiroga and Blanton 2005; Morgan 2006; Morgan and Anastasia 2008). The extent of cross-shelf migrations and the timing of recruitment onshore largely are determined by the vertical distributions of larvae in a stratified water column (Queiroga and Blanton 2005; Morgan et al. 2009*a,c*). However, these surveys cannot resolve alongshore transport, because larvae could have originated from many possible locations.

A long-term recruitment study by our colleagues and us exemplifies the reason that complementary profiling of larvae and ocean conditions across oceanographic events is necessary to determine the extent of larval advection and control in regulating alongshore transport and recruitment to coastal populations and communities. Although larval recruitment has been monitored for 13 yr in a region of strong, persistent upwelling on the west coast of the USA, processes responsible for inter-annual variation in recruitment to coastal populations and communities are still not resolved (Wing et al. 2003; Mace and Morgan 2006*a*; Morgan et al. 2009*a*). Prevailing northwesterly winds force surface waters offshore due to the Coriolis effect (Ekman transport), lowering sea level at the coast and forcing upwelling of bottom waters and southward alongshore transport (Largier et al. 1993). Larvae in surface waters may be passively advected southward and offshore except in the lee of headlands, where eddies may entrain them during prevailing upwelling conditions (Wing et al. 1998; Lagos et al. 2005; Morgan et al. 2011). When winds infrequently weaken (relax) or reverse, larvae that have accumulated in the lee of a large headland (Point Reyes) during upwelling conditions are transported poleward by a coastal boundary current, which is both characterized and enhanced by warm, low-salinity surface waters originating in the large estuary of San Francisco Bay, which is located

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~ 50 km to the south (Largier et al. 1993, 2006; Wing et al. 2003). Only larvae of the Dungeness crab (*Cancer magister*) appear to be transported poleward long distances and primarily when relaxation events lasting several days occur during the recruitment season in this region (Wing et al. 2003; Morgan et al. 2009*a*).

The objective of our present study was to provide a fuller mechanistic understanding of the dynamic interplay between larval behavior and ocean conditions on recruitment over upwelling-relaxation cycles. We tested the hypothesis that larvae are transported poleward by the coastal boundary current from the larval retention zone in the lee of Point Reyes during relaxation events, increasing larval supply to recruitment-limited populations (Wing et al. 2003). If so, then larvae should be more abundant in poleward-flowing, warm, low-salinity, surface waters during relaxation events than in cold, saline waters during prevailing upwelling conditions. Larvae must remain within the surface boundary current to be transported poleward, but it is unknown whether larvae residing beneath the surface intrusion will ascend into the warm, low-salinity waters, especially during diel vertical migrations to the surface at night (Morgan and Fisher 2010). To test these hypotheses, we repeatedly profiled the vertical and horizontal distributions of nearly the entire larval assemblage of nearshore benthic crustaceans relative to ocean conditions for 2 months during the peak upwelling season, over alternating upwelling and relaxation conditions and diel cycles. We sampled a small embayment where larvae are entrained during upwelling (Roughan et al. 2005; Mace and Morgan 2006*b*; Morgan et al. 2011), as well as in the open waters of the adjacent continental shelf, to determine the effect of the boundary current on larval distributions throughout nearshore coastal waters along topographically complex coastlines in upwelling regions.

Methods

Sampling—The study was conducted in the windiest region on the west coast of North America, where equatorward winds persist during the spring and summer (Dorman et al. 2006). To determine whether the vertical and horizontal distributions of larvae changed across the study area over upwelling-relaxation cycles, we surveyed the assemblage of crustacean larvae in Bodega Bay (in the lee of Bodega Head) and along the open coast about 1 km offshore of Bodega Head from 07 June to 05 August 2005. Eight surveys were conducted along three replicate transects inside the bay and three more replicate transects outside the bay (Fig. 1). Sampling was conducted during the daytime, and it also was conducted at night on two consecutive dates (04–05 Aug). Larvae were collected using an electronically tripped Tucker Trawl (0.5 m² mouth) that was equipped with 335-μm mesh nets and real-time temperature and depth sensors that allowed samples to be collected relative to the thermocline. The water column was partitioned into two depth bins that were sampled equally. In addition, a neuston net (0.5-m² mouth) sampled the surface of the water column. Each net was towed for 5 min. A flowmeter (General Oceanics model 2030) was fitted to
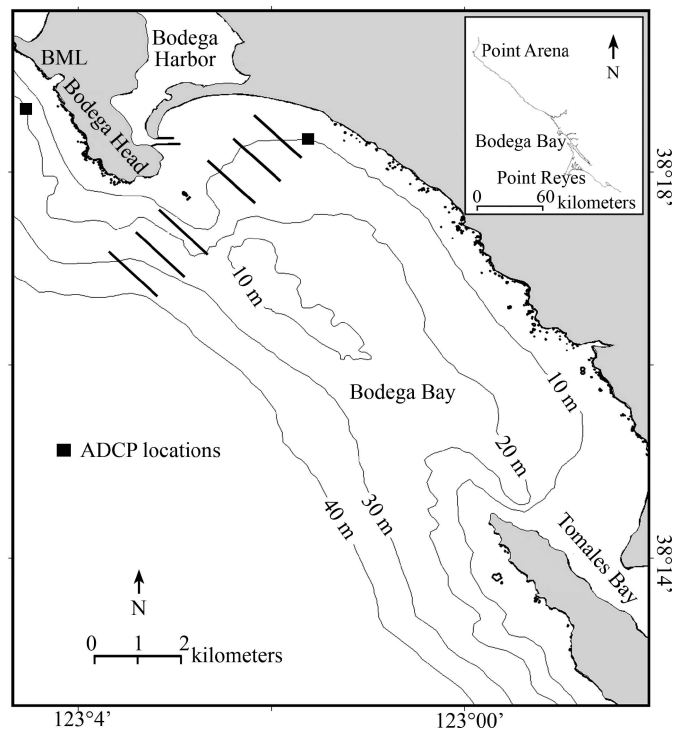

Fig. 1.   Locations of three replicate transects sampled in Bodega Bay, California, USA, and three replicate transects sampled in the open coastal waters flowing past Bodega Head. Sampling occurred during 7 weeks from 07 June to 10 August 2005. Solid squares depict the locations of the acoustic Doppler current profilers (ADCP) located in Bodega Bay and off Bodega Head. Salinity was measured continuously at the Bodega Marine Laboratory (BML).

the mouth of each net to determine the volume of water sampled.

A concurrent study determined whether larval densities increased in Bodega Bay upon the arrival of the coastal boundary current. We sampled along the three bay transects on alternate days from 07 June to 10 August 2005, resulting in a time-series of 33 sets of replicate samples (Fig. 1). We collected larvae throughout the water column (10–15 m) with a sled-mounted 0.5-m-diameter ring net fitted with 335-μm mesh and a flow meter.

During all cruises, profiles of water-column properties were taken at the beginning and end of each plankton tow to place larval distributions in the context of hydrographic patterns. Temperature, salinity, fluorescence, and turbidity data were collected using a profiling conductivity–temperature–depth (CTD) package (Seabird Electronics SBE-19 Plus and WETLabs WETStar fluorometer, and WETLabs transmissometer).

Salinity was measured continuously at the seawater intake of the Bodega Marine Laboratory (Seabird Electronics SBE-16 Plus). In addition, moorings obtained time-series of temperature and current velocity: one mooring was located at a depth of 10 m in Bodega Bay and a second mooring was located in 30 m of depth offshore of Bodega Head (Fig. 1). Temperature (T, ± 0.2°C) was recorded every 6 min using Optic StowAway® TidbiT thermistors.

The thermistors were attached to the mooring 1 m above the bottom and 1 m below the surface in Bodega Bay and 1 m, 9 m, 16 m, 23 m, and 30 m above the bottom offshore of Bodega Head. Decreasing temperature values indicate the arrival of upwelled water in response to increased (negative) equatorward wind stress, and increasing temperature values indicate relaxation conditions. Current velocity was measured continuously using bottom-mounted acoustic Doppler current profilers in Bodega Bay (RDI 1200 kHz) and offshore of Bodega Head (RDI 300 kHz): data were collected in 1-m- and 2-m-depth bins and 3-min and 10-min ensembles, respectively. Velocity ensembles were averaged hourly at both sites and rotated to the alongshore direction of 332.5° inside the bay and 300.4° along the open coast, as defined by the depth-averaged principal axis at each site. Each site was characterized by potential along- and cross-shore transport that was calculated from time-integrated, depth-averaged water velocities (progressive vector diagrams) over the upper 30%, middle 30%, and bottom 30% of the water column (data from the top 10% were omitted due to high errors associated with side-lobe reflection from the surface).

We also mapped surface circulation offshore of the study site hourly with high-frequency (HF) radar. Pseudo-Lagrangian particle trajectories were calculated to determine origins of waters in the study region. Water origins were determined following prolonged upwelling and relaxation conditions (quasi-steady scenarios).

Continuous wind data were obtained from a meteorological buoy, which is located 28 km offshore of Bodega Bay and serves as an index of wind forcing in our region (National Data Buoy Center buoy 46013, 38°13′30″N, 123°19′00″W; http://las.pfeg.noaa.gov/las6_5/servlets/dataset?catitem=1708). Upwelling was considered to occur when 36-h, low-pass filtered, northwesterly winds were ≥ 5 m s^{-1} and water temperatures were decreasing or $< 10°$C. Relaxation occurred when northwesterly wind speeds were < 3 m s^{-1}, and downwelling occurred when southerly winds exceeded 5 m s^{-1}.

Data analysis—All crustacean larvae and postlarvae were identified to species and stage, and counts were standardized by the volume of water sampled. Larvae of most of the 21 taxa collected were combined into five broad taxonomic categories (barnacles, grapsids, pinnotherids, porcellanids, other anomurans) for presentation after determining that the vertical and horizontal distributions of species were similar over upwelling-relaxation cycles. Three species are reported individually either because larval distributions differed between congeners (*Cancer antennarius*, *C. magister*) or only one species was collected within a family (*Lophopanopeus bellus*). Remaining taxa were not abundant and larval distribution patterns were similar to the other representative taxa.

We determined how larval distributions for the eight cruises conducted along the three transects inside and three transects outside the bay differed for the 21 taxa during discrete upwelling and relaxation events using nonmetric multidimensional scaling (NMDS) and nonparametric analysis of similarity (ANOSIM). Analyses were conducted using PRIMER software (version 6.1.10; Plymouth Routines in Multivariate Ecological Research). For these analyses, temperature and salinity from CTD profiles and larval concentration were averaged among depths and sites for each sampling date. Before analysis, the physical variables were normalized (the mean was subtracted from each sample and divided by the standard deviation) and larval concentrations were square-root transformed to deemphasize the contribution of very abundant species. NMDS was conducted on Euclidean distance and Bray–Curtis similarity matrices for the physical and biological data, respectively. ANOSIM tests (999 maximum permutations) determined whether temperature and salinity and the larval assemblages changed with wind condition. The ANOSIM test statistic (R) is a useful measure of separation between factors, with zero indicating no separation and one indicating complete separation. A RELATE test was conducted on the physical and biological resemblance matrices to determine how closely the physical and biological multivariate patterns matched.

Results

Water-column structure and current flow during upwelling-relaxation cycles—The eight cruises spanned upwelling-relaxation cycles over 7 weeks (Fig. 2A), and the water column responded to the fluctuating winds in a similar fashion throughout the study area (Fig. 2B,C). Two cruises (15 Jun, 07 Jul) occurred during upwelling conditions; they followed prolonged northwesterly winds > 5 m s^{-1} (Fig. 2A), when the water column typically was cold and well-mixed inside and outside of the bay (Fig. 2B,C). A third upwelling cruise (23 Jun) was conducted following a brief relaxation period (Fig. 2A), when the water column was still well-mixed and water temperatures were $\sim 10°$C, although winds were briefly from the south at this time (Fig. 2B,C). This cruise was categorized as occurring in upwelling because water-column properties were similar to upwelling conditions immediately before the cruise. However, the surface currents in the bay during this time were not directed equatorward, as they were during the other two upwelling cruises (Fig. 2D).

Two more cruises (27 Jun, 29 Jun) followed short periods of weak, northwesterly winds (Fig. 2A) when the water column was beginning to warm and stratify (Fig. 2B,C). Sampling in August occurred following weeks of relaxation with only brief bouts of weak, northwesterly winds (Fig. 2A), and the water column was stratified and warm ($\sim 13°$C; Fig. 2B,C). Three cruises were conducted during this period: (1) following 2 d of weak, northerly winds (02 Aug), (2) following a period of brief poleward winds while the water column was well-stratified (04 Aug), and (3) during weak equatorward winds while the water column was more mixed (05 Aug). Warming during relaxation is due to both solar heating and advection of warmer offshore waters into the area (Wing et al. 2003). During brief periods of northwesterly winds, waters cool due to upwelling and mixing, which also reduces stratification.

The topographic complexity of the shoreline resulted in different circulation in the bay than on the open coast.
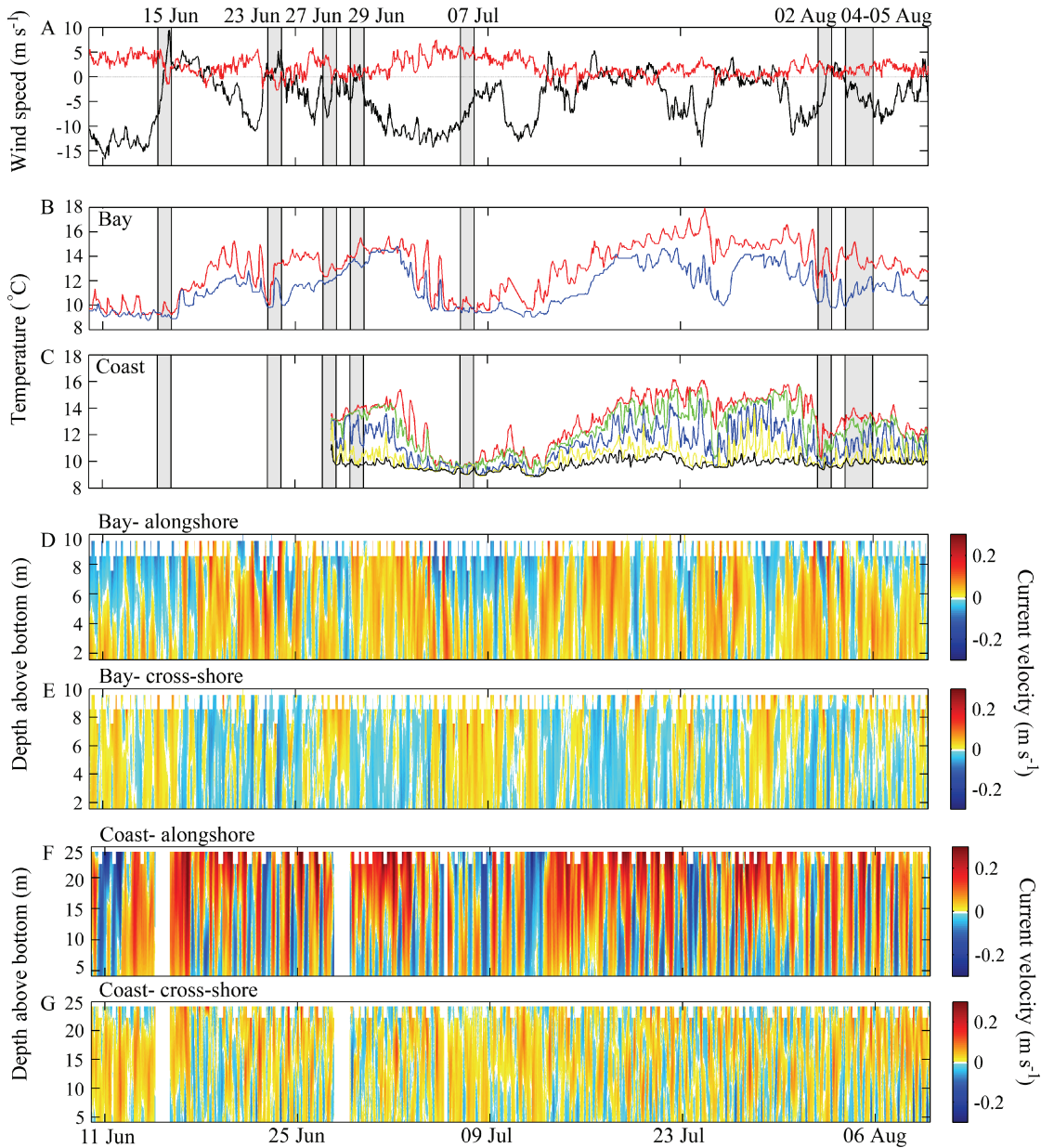
Fig. 2. Time-series of physical data sampled in Bodega Bay and off Bodega Head from 07 June to 10 August 2005. (A) Wind (m s^{-1}) at National Data Buoy Center 46013—alongshore wind (black) and cross-shore wind (red); gray bars indicate cruise dates; (B) temperature (°C) at 1 m above the bottom (blue) and 1 m below the surface (red) at a mooring on the 10-m isobath inside Bodega Bay; (C) temperature at 1 m (red), 9 m (green), 16 m (blue), 23 m (yellow), and 30 m (black) above the bottom at a mooring on the 30-m isobath off Bodega Head; (D) alongshore current velocity (m s^{-1}) at the mooring in Bodega Bay—positive values indicate poleward flow; (E) cross-shore current velocity (m s^{-1}) at the mooring in Bodega Bay—positive values indicate onshore flow; (F) alongshore current velocity (m s^{-1}) at the mooring off Bodega Head—positive values indicate poleward flow; and (G) cross-shore current velocity (m s^{-1}) at the mooring off Bodega Head—positive values indicate onshore flow. Current velocity data were omitted for 10% of the water column near the surface.

Near-surface circulation in the bay was typical of wind-driven coastal upwelling regions. During upwelling-favorable conditions, currents were equatorward (Fig. 2D) and weakly seaward (Fig. 2E) throughout much of the water column. When winds relaxed, currents flowed poleward (Fig. 2D) and weakly shoreward (Fig. 2E), particularly in the upper water column. Near-bottom currents in the bay were influenced by subsurface recirculation flow, as

previously described by Roughan et al. (2005) and Morgan et al. (2011).

In open waters outside the bay, currents were stronger, but near-surface currents again followed typical patterns of offshore and equatorward flow during upwelling winds (Fig. 2F,G). During relaxation, currents typically were poleward, sometimes extending throughout the water column while remaining stronger near the surface, as
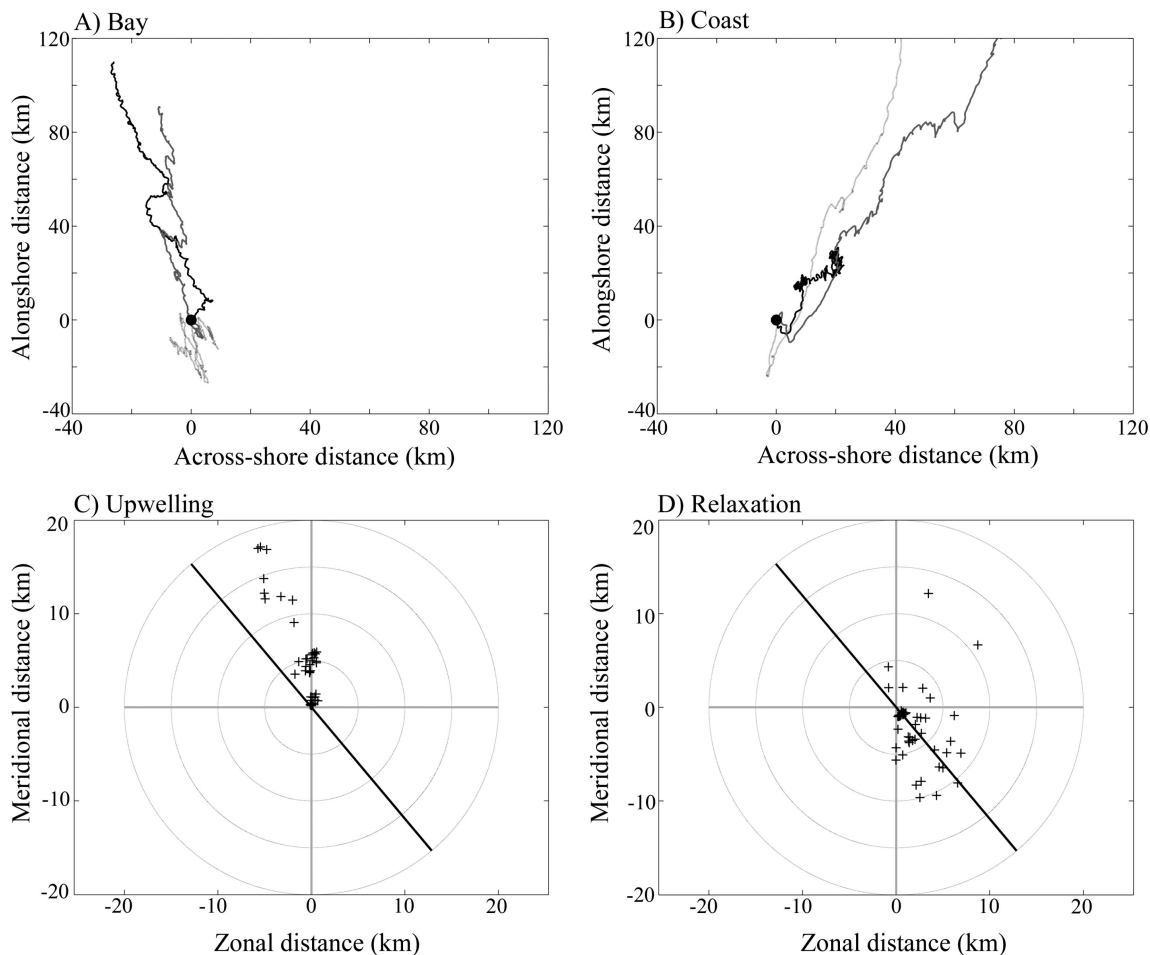
Fig. 3. Progressive vector diagrams of currents in (A) in Bodega Bay, and (B) open coastal waters off Bodega Head in 2005. Each line represents the time-integrated velocity from 10 June (5 d before sampling began) to 10 August (5 d after sampling ended). The black line represents velocity averaged over the bottom 30% of the water column, whereas the dark gray and light gray lines represent average velocities for the middle and upper 30% of the water column. Data from the uppermost 10% of the water column were unreliable and omitted. Origins of surface-water parcels calculated from HF-radar data within 5–15 km of Bodega Head on (C) 07 July following a week of upwelling-favorable winds and (D) on 29 June following a few days of weak, relaxation-favorable winds. Crosses represent the origins of surface waters reaching gridded locations along a cross-shelf transect. The gridded locations are reset to a common origin of (0,0) for comparing the direction of flow. The heavy black line represents the orientation of the coast. Due to the limited spatial extent of the HF-radar data, parcels were only 'back-tracked' for 2–3 d.

previously described by Largier et al. (1993, 2006). Strong tidal and diurnal signals were present. Cross-shelf currents were weaker with a tendency for near-bottom offshore flow during relaxation periods, as seen previously in this area (Largier et al. 1993; Wing et al. 2003; Dever et al. 2006).

On average, alongshore transport inside and outside the bay during the summer of 2005 was poleward, with maxima near the bottom in the bay and near the surface in open waters outside the bay (Fig. 3A,B). Cross-shore transport also differed inside and outside the bay. Inside the bay, transport alternated between shoreward and seaward near the surface, and it was seaward in the mid- and lower water column (Fig. 3A) due to the persistent, deep, recirculation feature (Roughan et al. 2005; Morgan et al. 2011). Along the open coast, net transport was largely poleward and slightly onshore in the upper water column, with little net transport at the bottom (Fig. 3B). Following prolonged upwelling-favorable winds, surface currents outside the bay typically originated from the northwest (Fig. 3C); during relaxation, surface waters originated from the southeast (Fig. 3D), as previously described (Largier et al. 1993, 2006; Wing et al. 2003).

Changes in larval assemblages and distributions during upwelling-relaxation cycles—Few larvae occurred in relatively warm, low-salinity water during the eight cruises that were conducted both inside and outside of the bay, and most of them occurred in cold, saline water during both relaxation and upwelling conditions (Fig. 4). Very few larvae were collected in waters warmer than 14°C and fresher than a salinity of 33.4, which typically occurred during relaxation. Larval abundance of the eight representative taxa in Bodega Bay decreased during two drops in salinity in June (with the exception of porcellanids on 21
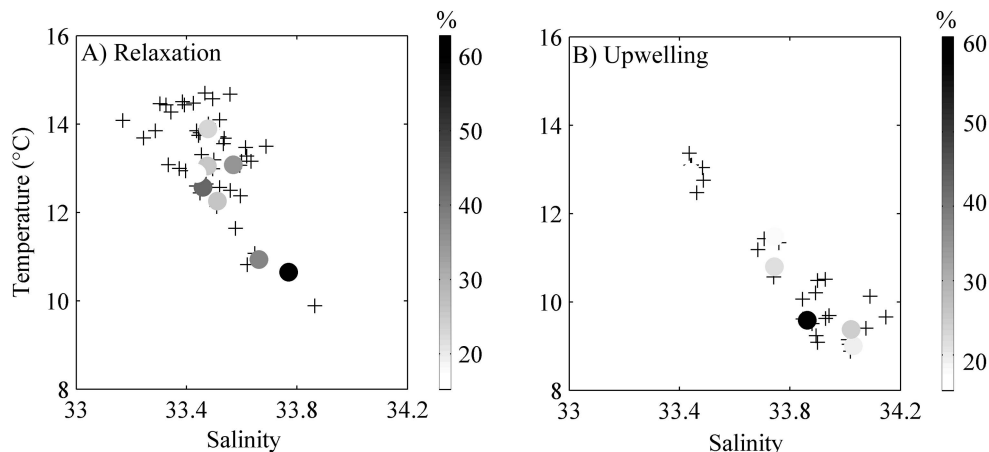
Fig. 4.   Percentage of larvae collected per tow on eight cruises inside and outside Bodega Bay relative to water temperature and salinity during (A) relaxation and (B) upwelling. Samples were collected from surface and bottom waters along the six transects. Neuston samples were omitted because few larvae occurred there during the daytime, and our objective was to compare larval abundance in different water masses over upwelling-relaxation cycles. Crosses represent tows in which $\leq 15\%$ of larvae from a survey were collected in one tow.

Jun) and again during a prolonged decrease in salinity on 30 July (Fig. 5).

The NMDS analysis of temperature and salinity across sites and depths revealed distinct differences among the eight cruises that were conducted both inside and outside of the bay (Fig. 6A; 2-dimensional stress = 0). These differences were separated strongly based on wind forcing (ANOSIM $R = 0.90$, $p = 0.018$). The two cruises that followed prolonged and strong upwelling winds (15 Jun, 07 Jul) and the cruise conducted after a few days of strong northwesterly winds (23 Jun) were most separated from the dates that were sampled during relaxation conditions. The two relaxation dates with the least water-column structure (27 Jun, 05 Aug) were more closely related than the three remaining dates that followed prolonged relaxation when the water column was strongly stratified (29 Jun, 02 Aug, 04 Aug).

Strong structure in the larval assemblage largely reflected the observed structure in physical conditions (Fig. 6B; NMDS 2D stress = 0.05), which was mainly separated by wind forcing (ANOSIM $R = 0.76$, $p = 0.018$). The larval assemblages during the three upwelling dates were closely related and well-separated from the five relaxation dates. Strong groupings occurred within the relaxation dates, unlike the little structure observed in the physical NMDS for those dates. The larval assemblage was similar during 29 June and 05 August, and it also was alike during 02 August and 04 August. The assemblages on these two pairs of dates differed from that on 27 June. The larval assemblage patterns were well-correlated with the temperature and salinity patterns (RELATE $\rho = 0.51$ $p = 0.014$).

The effect of upwelling-relaxation cycles on water-column structure and larval distributions are displayed for three phases of the cycle (Figs. 7–9): upwelling (07 Jul), early relaxation (29 Jun) and prolonged relaxation following a few days of weakly upwelling-favorable winds (02 Aug). During upwelling, the water column was character-ized by cold, high-salinity water with low chlorophyll fluorescence and turbidity. Little stratification was evident, except in the bay where surface waters were marginally warmer due to warm water flowing into the bay from Bodega Harbor and Tomales Bay. Larvae of the eight representative taxa showed a variety of vertical and horizontal distributions. Larvae of four taxa (barnacles, anomurans, *L. bellus*, grapsids) occurred deep in the bay, and most of them also occurred at a similar depth on the open coast (10–12 m). Most pinnotherid and porcellanid larvae occurred outside the bay and were higher in the water column than the other four taxa (5–10 m deep), although some porcellanid larvae also occurred deep in the water column. *Cancer antennarius* occurred deepest in the water column across the study area, whereas its congener, *C. magister*, occurred highest in the water column.

During the onset of relaxation, the water column was stratified, with relatively warm, low-salinity water occur-ring near the surface (Fig. 8). Chlorophyll fluorescence was highest in the pycnocline (5–15 m) and the water column was less turbid at depth in open coastal waters. Larvae of all taxa occurred deep in the water column. Six of the eight taxa occurred primarily on the open coast, whereas pinnotherid and grapsid larvae primarily occurred in the bay.

Following prolonged relaxation, the water column was stratified, with relatively warm, low-salinity water, which extended deeper in the water column and farther offshore than during incipient relaxation conditions (Fig. 9). Chlo-rophyll fluorescence was greatest and turbidity was highest in the upper water column inside the bay. Larvae of all eight taxa were largely absent from the bay and most of them occurred 4–5 km from shore. Larvae of four taxa primarily occurred in the lower water column (barnacles, pinnotherids, *C. antennarius*, grapsids), and larvae of three taxa occurred higher in the water column (anomurans, *L. bellus*, porcellanids). Only *C. antennarius* was common in
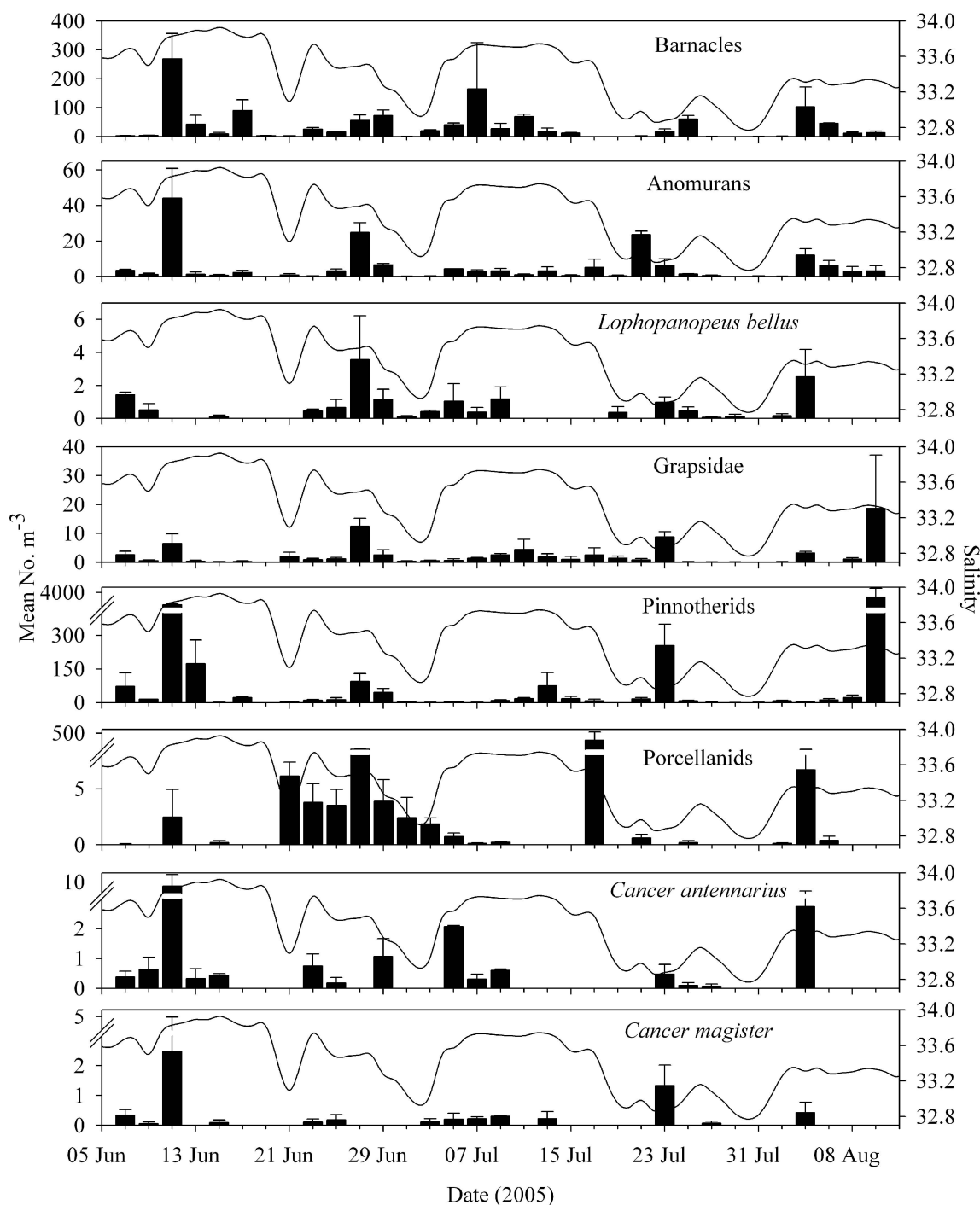
Fig. 5. Mean larval concentration (± 1 SE) of eight representative taxa relative to salinity in Bodega Bay from 07 June to 05 August 2005.

surface waters that were warmer than 13°C and a salinity < 33.4.

Two days later at night, warm low-salinity water no longer extended to the bottom of the water column due to the onset of weak upwelling conditions (Fig. 10A). The water column was stratified, with warm low-salinity water occurring near the surface. Larvae of all eight taxa primarily occurred on the inner shelf rather than in the bay. Five taxa were concentrated deep in the water column,

with few larvae occurring in surface waters (anomuran, *L. bellus*, grapsid, porcellanid, *C. antennarius*), whereas *C. magister* only occurred near the surface. Results were not shown for barnacle and pinnotherid larvae because they do not undertake diel vertical migrations (Morgan and Fisher 2010). Upwelling strengthened by the next night; the water column was not as strongly stratified and relatively warm, low-salinity water again extended throughout the water column (Fig. 10B). Larvae of all six taxa peaked 3 km from
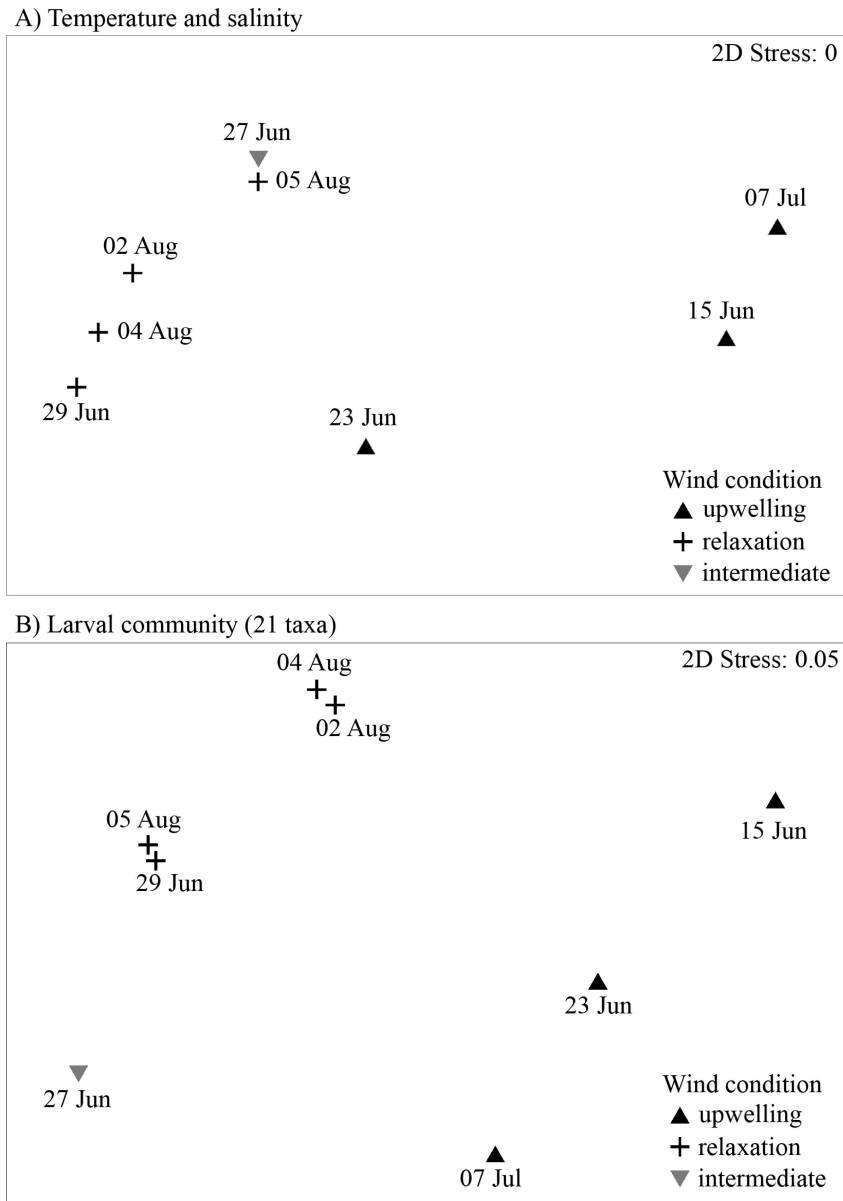
A) Temperature and salinity

2D Stress: 0

27 Jun
▽
+ 05 Aug

07 Jul
▲

02 Aug
+

15 Jun
▲

+ 04 Aug

+
29 Jun

23 Jun
▲

Wind condition
▲ upwelling
+ relaxation
▽ intermediate

B) Larval community (21 taxa)

2D Stress: 0.05

04 Aug
+
+
02 Aug

▲
15 Jun

05 Aug
+
+
29 Jun

▲
23 Jun

▽
27 Jun

Wind condition
▲ upwelling
+ relaxation
▽ intermediate

▲
07 Jul

Fig. 6. Nonmetric multidimensional scaling plots of (A) temperature and salinity averaged over the three depths and six transects for each of the eight cruises that were conducted during the daytime inside and outside Bodega Bay, and (B) the concurrent larval assemblages. Dates were classified as occurring during upwelling or relaxation conditions using wind and temperature data.

shore in the neuston, indicating that they were undertaking diel vertical migrations.

Discussion

Few larvae occupied the poleward surface current of warm, low-salinity water during the three relaxation events, indicating that larvae of most species were not transported from the retention zone in the lee of Point Reyes to our study area. The low concentration of larvae during relaxation conditions is consistent with observed patterns of greater recruitment by most species occurring during prevailing upwelling conditions (Wing et al. 2003; Mace and Morgan 2006a; Morgan et al. 2009a). Larvae remained in cold, saline waters and typically did not enter the warm, low-salinity waters of the boundary current, being limited to bottom waters during early relaxation and offshore waters during late relaxation events when the boundary current spanned the depth of the water column close to shore. Larval avoidance of the surface lens of warm, low-salinity water was especially apparent when diel vertical migrations were suppressed. Only larvae of *C. magister* undertook diel vertical migrations when the boundary current was present, and it is the only crustacean that recruits more during relaxation conditions in some years (Wing et al. 2003; Mace and Morgan 2006a). Thus, we have
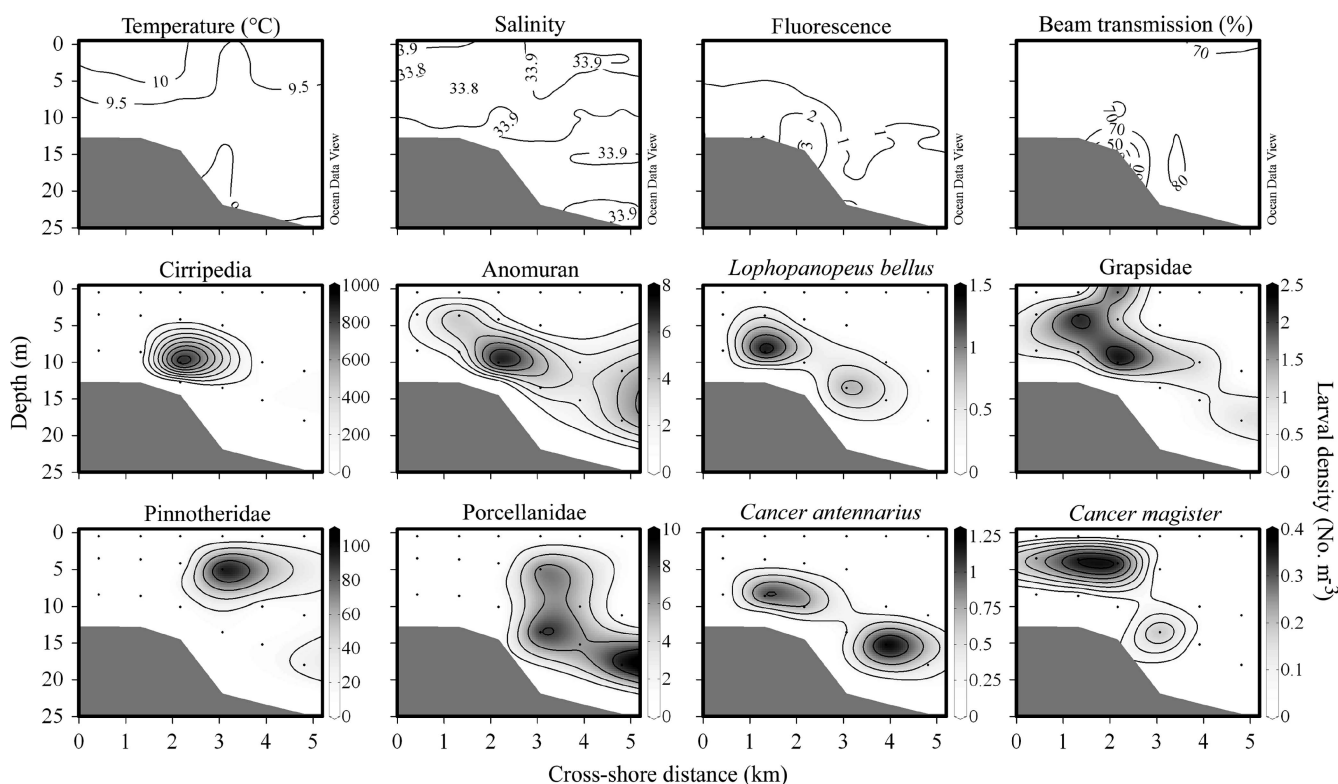
Fig. 7. Water-column profiles of temperature (°C), salinity, chlorophyll fluorescence, and transmissivity (four upper panels) and larval distributions of eight representative taxa (eight lower panels) across the six transects following prolonged upwelling on 07 July 2005. The water column was profiled at the beginning and end of each transect. Larvae were collected during the daytime at three depths (neuston, surface, bottom) along each transect, as indicated by dots. Neuston samples were omitted because few larvae were collected. Split vertical distributions within taxa largely arose from differences in vertical distributions among species and developmental stages within species. Density structure of the water column was closely aligned with temperature and is not shown.

shown how shifting currents over upwelling-relaxation cycles alter larval behavior and displace nearshore larval assemblages, thereby limiting larval recruitment during relaxation events in a region of strong, persistent upwelling.

Intensively profiling larvae in space and time revealed changes in vertical and horizontal distributions over upwelling-relaxation cycles and complements our previous research that was focused on prevailing upwelling conditions. Previously described interspecific differences in the vertical distributions of larvae during prevailing upwelling conditions also were evident throughout the study area during upwelling in the present study (Morgan et al. 2009*c*; Morgan and Fisher 2010). Surface water originated from the northwest during prevailing winds and the vertical distributions of larvae differed among taxa. These interspecific differences in vertical distribution determine the extent to which larvae complete development nearshore or migrate across the continental shelf (Morgan et al. 2009*b*,*c*; Morgan and Fisher 2010). Larvae of many nearshore species complete development close to shore by remaining in waters where cross-shore and alongshore flow is reduced (Largier et al. 1993; Roughan et al. 2006). They do this by remaining below the shallow Ekman layer at all times or rising into productive surface waters to forage only at night when offshore flow is weakest (Batchelder et al. 2002; Morgan et al. 2009*c*). Larvae of other species ascend to

surface waters, where they are advected offshore by Ekman transport (Morgan et al. 2009*c*). Postlarvae of these species descend beneath the Ekman layer, where they are advected back onshore by upwelling (Morgan et al. 2009*c*) or rise into the neuston, where internal waves or infrequent wind relaxations and reversals may transport them shoreward (Poulin et al. 2002; Morgan et al. 2009*c*). In turn, the depth preferences of postlarvae partially determine the timing of recruitment relative to ocean conditions (Mace and Morgan 2006*a*,*b*; Morgan et al. 2009*a*).

Larvae of all taxa were much less abundant during relaxation events, as revealed by the time series of larval concentrations in the bay, as well as the plots of larval concentration on temperature–salinity diagrams (relative to upwelling and relaxation conditions for larvae collected both inside and outside the bay). In addition to greatly diminishing larval abundance, relaxation events had a dramatic effect on larval distributions. In contrast to the interspecific differences in vertical distribution during upwelling, widespread interspecific similarity in vertical and horizontal distributions of larvae was evident during relaxation events. Larvae of all species occurred in the lower water column following the onset of relaxation, with only two taxa occurring in the bay and the other six taxa occurring only offshore. Larvae occurred below the lens of warm low-salinity water originating from the southeast,
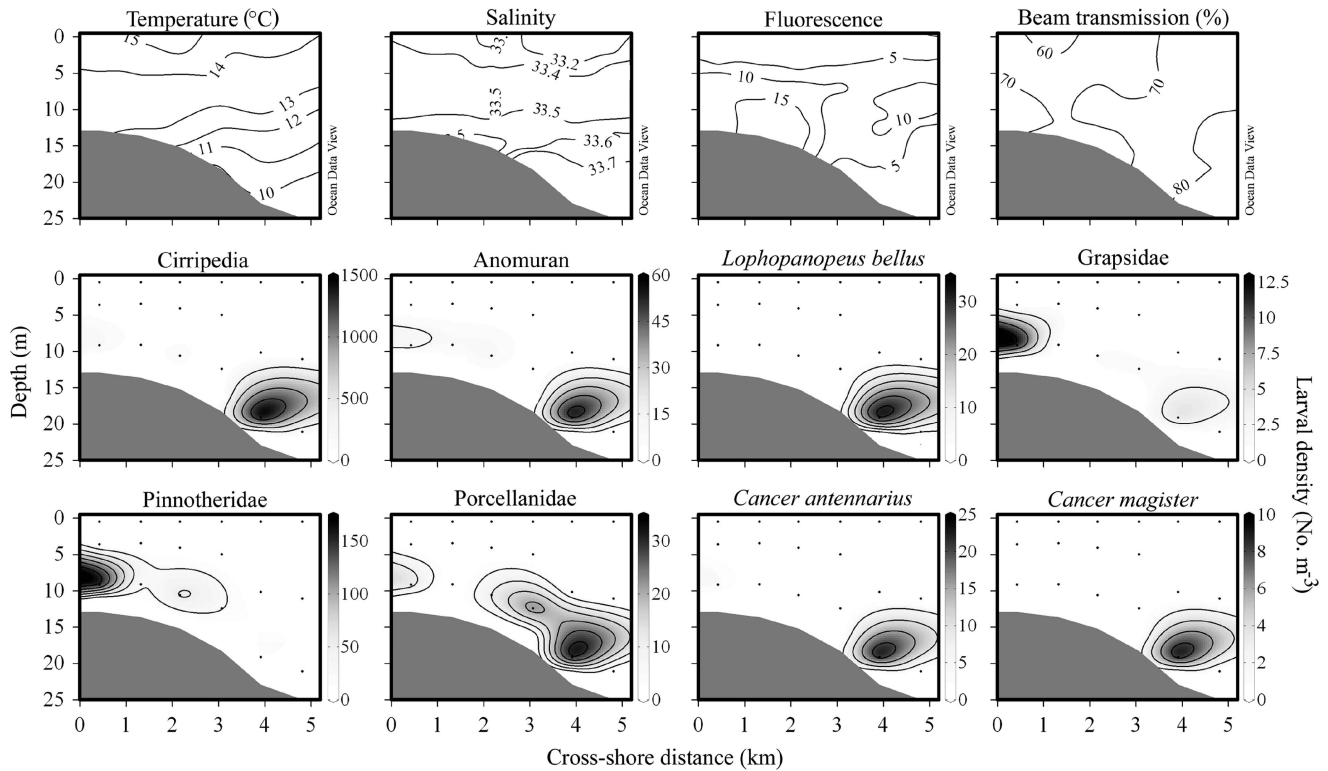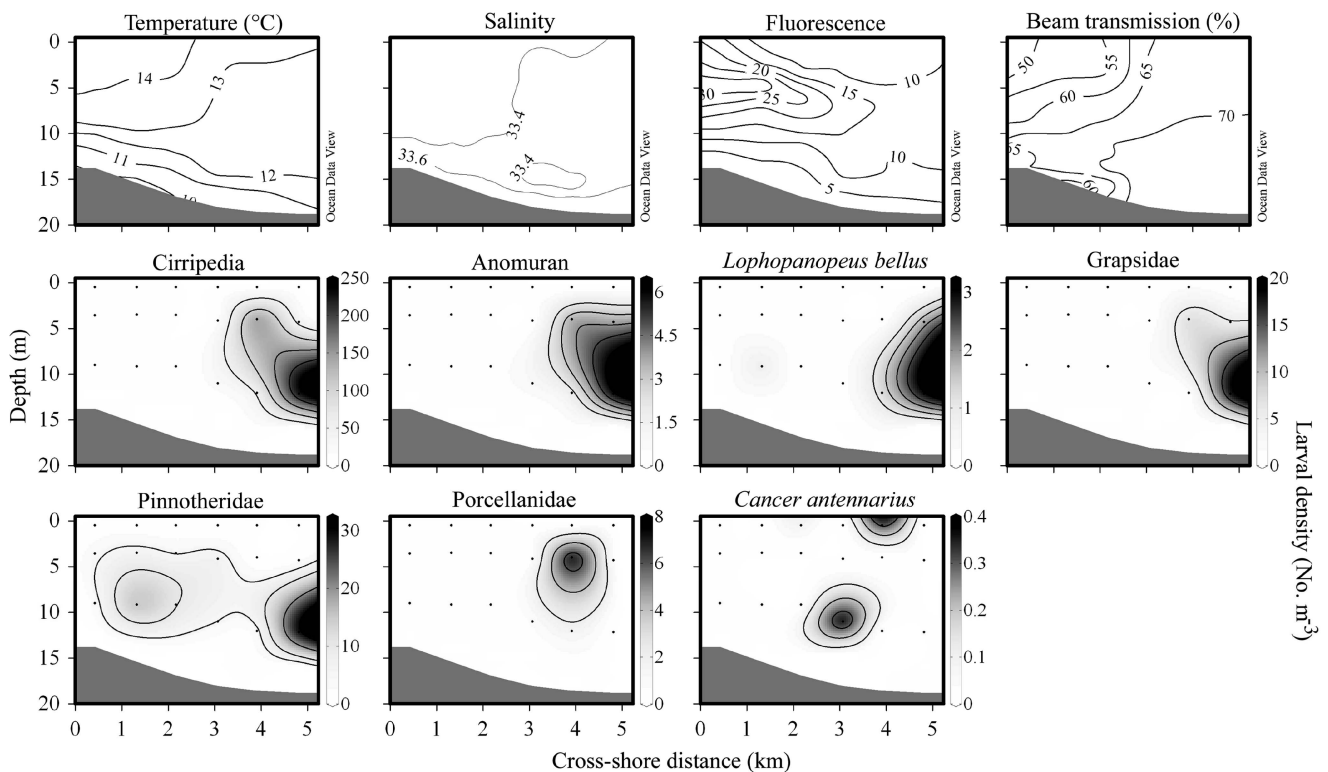
Fig. 8. Water-column profiles of temperature (°C), salinity, chlorophyll fluorescence, and transmissivity (four upper panels) and larval distributions of eight representative taxa (eight lower panels) across the six transects at the onset of relaxation on 29 June 2005. *See* Fig. 7 for details.

Fig. 9. Water-column profiles of temperature (°C), salinity, chlorophyll fluorescence, and transmissivity (four upper panels) and larval distributions of eight representative taxa (seven lower panels) across the six transects following prolonged relaxation on 02 August 2005. *Cancer magister* larvae were not collected. *See* Fig. 7 for details.
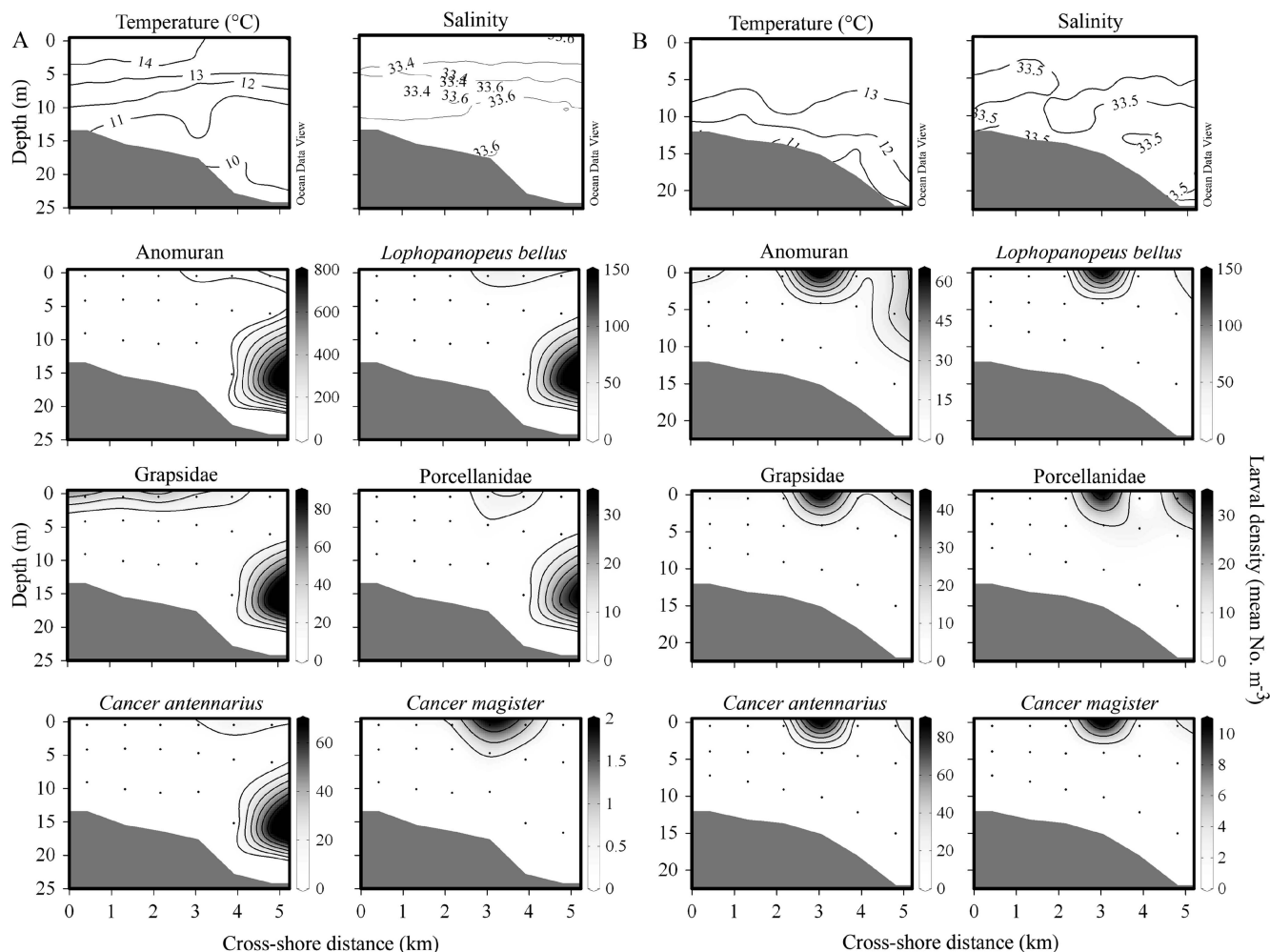
Fig. 10. Water-column profiles of temperature (°C) and salinity (four upper panels) and larval distributions of eight representative taxa at night (12 lower panels) across the six transects when the water column was (A) strongly stratified (04 Aug 2005) and (B) weakly stratified (05 Aug 2005). Two taxa (barnacles, pinnotherids) were not displayed because they do not undertake diel vertical migrations (Morgan and Fisher 2010). *See* Fig. 7 for details.

which is consistent with the previously described poleward coastal boundary current (Largier et al. 1993, 2006; Wing et al. 2003). Following a prolonged relaxation event in spring, warm low-salinity water filled the bay and up to 3 km from shore. At this time, larvae of all taxa were nearly absent from the bay, and few of them occurred within 3 km from shore. The low-salinity, poleward flow was confined to a few kilometers from shore, and larvae were more common and no longer restricted to depth seaward of this feature. Interspecific vertical distributions of these larvae were similar to those observed nearshore following prolonged upwelling events. Thus, the low-salinity near-surface coastal current filled the bay and inner shelf, displacing larvae offshore into deeper water.

The absence of larvae in warm, low-salinity surface waters during relaxation events suggests that larvae also were absent in the coastal current that originated in the Gulf of Farallones and not transported poleward from there to our study site. Larvae remained in cold, saline water rather than entering this lens of warm, low-salinity water. This was particularly apparent at night while the

water column was sharply stratified, because larvae did not undertake diel vertical migrations that previously were documented during upwelling conditions (Morgan and Fisher 2010). Previous field studies also have shown that larval assemblages stay with water masses of particular temperature and salinity (Banse 1986; Kunze 1995) and may concentrate near the pycnocline (Metaxas et al. 2009). By remaining within their preferred water mass of cold, saline water during relaxation events, larvae were displaced seaward in offshore flow even though they could have maintained their vertical distributions by entering the warm, low-salinity water of the boundary current. Entering the boundary current should not have been overly stressful, because the temperature and salinity change was slight. Remaining with their preferred water mass would keep larvae of these open-coast species from dispersing toward and settling near estuaries, where they would be subject to physiologically stressful conditions. Regardless of whether the observed changes in vertical distributions of larvae were behaviorally mediated, larvae of most taxa clearly changed in a similar way upon the arrival of the buoyant boundary

current. In the absence of the distinctive signature of low-salinity waters, larvae would be prevalent in the surface layer of the coastal boundary current, making it difficult to detect changes in the vertical and horizontal distributions of larvae in the local assemblage.

Only *C. magister* larvae occurred in the lens of warm, low-salinity water during both nights, presumably because they are more tolerant of these conditions than other species. Unlike most of the other study species, *C. magister* larvae recruit abundantly to the low-salinity waters of San Francisco Bay (Wild and Tasto 1983). The ability of *C. magister* to tolerate warm, low-salinity water may explain the reason that recruitment of this species is best correlated with the arrival of the coastal boundary current to our study area (Wing et al. 2003; Mace and Morgan 2006a), and it could partially account for the reason that *C. magister* is not well-correlated with the arrival of the low-salinity, coastal layer every year (Wing et al. 2003; Morgan et al. 2009a). Although larval recruitment is best correlated with warm, low-salinity water during years when prolonged relaxation events repeatedly occur (Wing et al. 2003), it is possible that additional variation could be accounted for by the amount of precipitation. In years of high precipitation, the salinity of the coastal current may be too low for even *C. magister* larvae to enter, thereby limiting poleward transport to our study site, as may have occurred during the very wet year of 1995 (Wing et al. 2003). The timing of the spring transition to peak upwelling conditions also may affect the inter-annual variability in the number of recruiting postlarvae (Shanks and Roegner 2007). The spring transition was late during our study, and *C. magister* postlarvae did not recruit during a companion study that was conducted in our study area (Morgan et al. 2009a). After the peak upwelling season began, upwelling conditions were typical (Morgan et al. 2009a), so that the effect of upwelling-relaxation cycles on larval distributions described during our study would be evident most years.

Although larvae remain within preferred water masses and migrate different distances from natal origins by regulating depth, larval behavior previously was found to exert little influence on whether larvae are entrained into retention zones in the lee of headlands (Morgan et al. 2011). Larvae of the diverse assemblage of benthic crustaceans accumulated in the lee of Bodega Head during upwelling conditions when vertically sheared flow arises, regardless of interspecific differences in larval behavior. Larval behaviors regulating cross-shelf and alongshore transport have evolved in response to typical ocean conditions across species' ranges and do not appear to facilitate entrainment in the lee of headlands.

The results of our present study are expected to be repeatable and broadly applicable elsewhere. The effect of the boundary current on a diverse larval assemblage was observed three times during typical relaxation conditions, revealing the process behind the 13-yr record of low recruitment by most species during relaxation events—both inside Bodega Bay and off an exposed headland (Wing et al. 2003; Mace and Morgan 2006a; Morgan et al. 2009a). Our results should apply to the many other small headlands

and bays (Morgan et al. 2011), as well as straight coastlines in upwelling regions. During relaxation events along upwelling coasts, offshore flow is associated with poleward coastal boundary currents, as has been observed from Point Arena to Reyes including sites that are well-removed from Bodega Bay (Largier et al. 1993; Wing et al. 2003; Dever et al. 2006). This offshore flow will transport larvae away from the shoreline, whether it is due to offshore deflection of the poleward flow throughout the water column at headlands or offshore transport in the bottom Ekman layer. The former process should affect the entire larval assemblage at headlands either in the presence or absence of a low-salinity surface intrusion, whereas the latter process should have the most pronounced effects on larvae of open-coast species in the presence of a low-salinity surface intrusion.

In conclusion, a clearly identifiable physical signal provided insight into the dynamic interaction between physics and larval behavior in determining the fate of larvae in a highly advective upwelling regime. Profiling the effects of targeted specific oceanographic events on a larval assemblage can complement shore-based recruitment studies anywhere by providing a mechanistic understanding of observed recruitment patterns (Parnell 2001). Recognizing the distinctive signature of different water masses relative to current velocities and abundances of species in a larval assemblage can reveal processes regulating larval recruitment to a study area. Sampling many species concurrently reveals how widespread the effect of the oceanographic event is on the vertical and horizontal distributions of the larval assemblage, and, hence, the ability of multiple species to regulate their vertical and horizontal positions in response to shifting ocean conditions. Frequent sampling of larval assemblages complements widespread monitoring of recruitment from shore and is essential for providing a deeper mechanistic understanding for how shifting ocean conditions affect the distribution and abundance of larvae, recruitment dynamics and the connectivity of populations along topographically complex coastlines.

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