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Larval retention, entrainment, and accumulation in the lee of a small headland: Recruitment hot spots along windy coasts

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Abstract

We surveyed crustacean larvae in the plankton in the lee of Bodega Head, California, for 2 months during late spring and summer and cross-correlated the larval abundance and stage of development of 16 taxa with 8 indicators of upwelling–relaxation conditions. Larvae in all stages of development for 11 of these taxa were entrained and accumulated in a recirculation feature in Bodega Bay, found in the lee of this small headland as soon as upwelling-favorable winds began, and persisted until winds weakened. The remaining taxa were more prevalent during relaxation events when the recirculation feature dissipated and a poleward coastal current transported larvae into and through the bay. During upwelling conditions, a vertically sheared flow occurs in the lee of the headland that accounts for the accumulation of plankton. However, larval behavior did not have a substantial effect on density and persistence in the lee of the headland, regardless of whether taxa were more prevalent during upwelling or relaxation conditions or whether they developed entirely nearshore or migrated offshore later in development. Thus, larvae and postlarvae of many, diverse taxa are concentrated in the plankton in the lee of small headlands in upwelling areas, which is consistent with previously reported recruitment hot spots in small upwelling bays. These headland-related hot spots increase spatial structure in population density and community structure in recruitment-limited upwelling regions and other wind-driven coasts.

Larval transport is a key determinant of the dynamics and structure of marine populations and communities. Temporal and spatial variation in upwelling has been proposed to regulate the intensity of settlement and postsettlement interactions among invertebrates along the western margins of continents (Yoshioka 1982; Broitman et al. 2001; Menge et al. 2004). Strong winds coupled with the Coriolis effect drive an offshore flow of waters in the surface boundary layer, known as Ekman transport (Dever et al. 2006). This offshore transport of larvae may limit the number of recruits to coastal communities and subsequent interactions among them in regions of persistent upwelling. Peak recruitment onshore was proposed to occur infrequently and episodically when winds weaken (relax) or reverse, delivering postlarvae (final larval stage before settlement) onshore and poleward alongshore (Farrell et al. 1991; Wing et al. 1995; Connolly et al. 2001). Subsequent studies have shown that most species remain close to shore throughout development (Poulin et al. 2002; Morgan et al. 2009a; Shanks and Shearman 2009) and recruit onshore during upwelling conditions (Mace and Morgan 2006a; Jacinto and Cruz 2008; Morgan et al. 2009b) or when internal tides are active (Pineda 1994; Shanks 2002, 2006). Further, spatial and temporal variation in surf zone hydrodynamics now has been proposed to limit larval recruitment along upwelling coasts (Bustamante and Branch 1996; Rilov et al. 2008; Shanks et al. 2010).

Recruitment hot spots occur in otherwise recruitment-limited regions along upwelling coasts. Recirculation features form in the lee of capes during prevailing equatorward currents that are driven by upwelling-favorable winds (Graham and Largier 1997; Wing et al. 1998;

Largier 2004). Larvae that originate in the lee of capes could be retained there and those originating in other areas could be entrained into recirculation features for as long as equatorward winds persist. When prevailing winds weaken, larvae are transported poleward around capes, supplying larvae to recruitment-limited populations along the open coast (Wing et al. 1995, 2003; Lundquist et al. 2000).

Recruitment hot spots also occur in the lee of small headlands (Roughan et al. 2005; Mace and Morgan 2006b). A recirculation feature forms in the lee of the small promontory of Bodega Head, California (Roughan et al. 2005), and more invertebrate larvae are recruited there than on the adjacent open coast (Mace and Morgan 2006b). The low-lying headland does not entirely block prevailing winds, so that surface waters still move equatorward, but recirculation occurs at depth (Roughan et al. 2005). The equatorward flow over the shelf separates from the shoreline at the southern end of Bodega Head, forming a shear zone that entrains water from the bay (Fig. 1a). Onshore winds and flow at the southern boundary of the bay form a poleward pressure gradient in the bay (Roughan et al. 2005). The shear zone and poleward pressure gradient together generate cyclonic (anticlockwise) circulation in subsurface waters in the bay (Roughan et al. 2005). Thus, upwelled water enters the bay through the deeper channel in the south and flows northward along the eastern side of the bay, potentially transporting larvae from the outer coast into this recirculation feature (Roughan et al. 2005). In addition, larvae that hatch in the lee of the headland could be retained there as long as upwelling-favorable winds persist. Retention in the recirculation feature may depend on larvae staying in the lower water column or undertaking diel vertical migrations between surface and bottom currents (Roughan et al. 2005). Larvae

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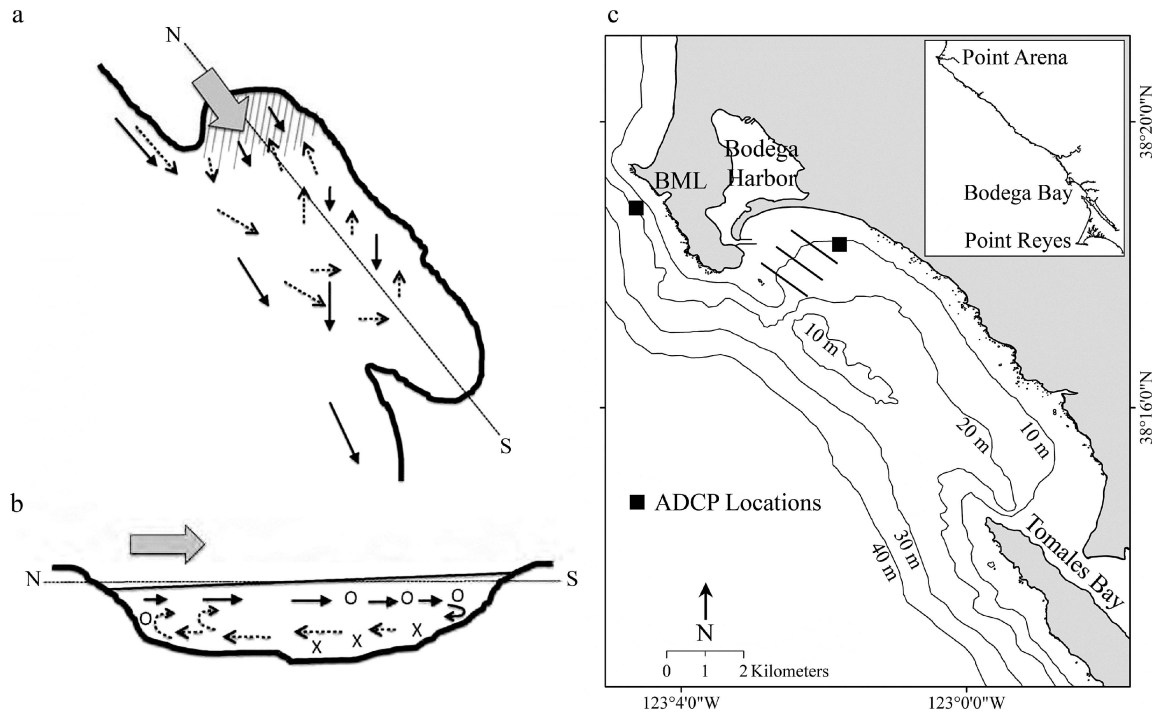


Fig. 1. Schematic representation of circulation in Bodega Bay deduced from observations of currents and water properties in this study and Roughan et al. (2005). (a) Plan view of circulation, with surface flows represented by solid arrows and circulation at depth represented by dashed arrows; the large block arrow represents wind stress during upwelling; hatching in the northern bay represents wind-driven setdown of the water level, whereas wind-driven setup of water level occurs in the southern bay, which accounts for the northwestward pressure gradient through the bay that drives deeper currents. The dashed line N-S indicates location of section view. (b) Vertical section view of circulation for line N-S down the center of the bay with currents represented by arrows with circles for flow out of the page and crosses for flow into the page; water-level setup and setdown are exaggerated and shown relative to a dotted line representing the still water level. The length of the arrows indicates relative current strength. (c) Location of replicate plankton transects ($n = 3$) sampled every other day in the lee of Bodega Head, California from 07 June to 10 August 2005. BML denotes the location of the Bodega Marine Laboratory where salinity was measured, and the squares denote the location of the moored ADCPs.

of other species that rise into surface waters may be transported equatorward and out of the bay, although they may return onshore later in development (Morgan et al. 2009a,c; Morgan and Fisher 2010).

Despite these clear patterns of enhanced recruitment in the lee of a small headland in an upwelling region, understanding of the underlying mechanism requires plankton studies that can show that larvae are accumulated in the headland eddy during active upwelling. Although a previous study did not find that most species were more concentrated in Bodega Bay than on the adjacent open coast (Morgan and Fisher 2010), the study was conducted in a year of below-average upwelling with frequent and prolonged relaxation events (Largier et al. 2006; Morgan et al. 2009b). The upwelling index in 2005 was 115.0 ± 10.4 SE $\text{m}^3 \text{s}^{-1}$ per 100 m of coastline in an area where it typically ranges between 100 to 200 $\text{m}^3 \text{s}^{-1}$ per 100 m of coastline (Morgan et al. 2009b,c). We now report a temporal analysis identifying upwelling events and showing greatest larval accumulation in the bay in response to a headland eddy during the strongest upwelling events. Hence during years of strong, persistent upwelling, higher densities are expected in the bay than on the open coast, which is consistent with observations that postlarvae settled more abundantly in the lee of the headland during two

moderate upwelling years (2001, 2002), when the upwelling index was 155.5 ± 9.4 and 150.9 ± 10.4 $\text{m}^3 \text{s}^{-1}$ per 100 m of coastline (Mace and Morgan 2006a). Thus, strong persistent upwelling produces the mechanism to accumulate larvae in the lee of small headlands in recruitment-limited and other wind-driven regions, and recruitment will be greater in bays than on the open coast in years of strong upwelling.

The purpose of the present study was to determine whether planktonic larvae accumulate in the lee of Bodega Head during upwelling events, regardless of whether species develop entirely nearshore or migrate farther offshore. Here, we complement our previous spatial comparative approach (Morgan and Fisher 2010) with concurrent, high-frequency monitoring that resolves upwelling-relaxation variability, enabling us to determine whether larvae accumulate in the lee of the headland during upwelling conditions. Larvae of intertidal and shallow subtidal crustaceans were sampled every other day in the lee of Bodega Head for 2 months and were identified to species and developmental stage. Larval abundance should increase in the lee of this small headland as long as upwelling conditions and the associated headland eddy persist, but high densities of larvae may extend into relaxation periods depending on how long it takes for the recirculation feature

to dissipate. Larval accumulation in the bay is not expected for species that primarily are delivered to the study area during relaxation events when recirculation in the bay may not occur (Wing et al 1998; Roughan et al. 2005; Kaplan and Largier 2006). Alternatively, the recirculation feature may only retain larvae that are released in the bay or it may just detain larvae that are transported into the bay by slowing their passage back to the open coast. However, neither of these two alternatives would increase larval density in the bay.

Methods

Study system—Bodega Head is located in one of the windiest regions on the West Coast of North America and is characterized by persistent equatorward winds during the spring and summer (Dorman et al. 2006; Fig. 1b). Near-surface waters flow equatorward and offshore over the shelf (Winant et al. 1987; Largier et al. 1993; Dever et al. 2006). Shallow depths reduce offshore Ekman transport and slow alongshore currents over the inner shelf, extending several kilometers from shore (Lentz and Chapman 1989; Largier et al. 1993; Dever et al. 2006). Equatorward winds blow roughly parallel to the coast, with maximum strength in the afternoon and minima at night. Waves generated by these winds are refracted onshore as they shoal and may be important in transporting larvae onshore, especially when upwelling winds are strong and persistent (Morgan et al. 2009b). The prevailing northwesterly winds weaken or reverse about every 4 to 10 d, and flow over the inner shelf reverses within a day or two of winds weakening (Send et al. 1987; Largier et al. 1993; Roughan et al. 2006).

Small-scale upwelling in the lee of the headland is active where winds blow offshore across the northern shore of the bay and surface waters move offshore even more rapidly than on the open coast (Roughan et al. 2005). Tides are mixed semidiurnal with a tidal range of 1.2 to 2.9 m. The headland consists of rocky habitat but the bay consists of a mix of sandy beaches (north and south shorelines), rocky shore (east shoreline and Bodega Rock), and muddy sand benthic habitats.

Sampling—A time series of larval densities was generated by collecting plankton every other day in oblique plankton tows for 2 months in northern Bodega Bay. Plankton were collected throughout the water column (10–15 m) with a sled-mounted 0.5-m-diameter ring net fitted with 335- μ m mesh and a flow meter (General Oceanics model 2030) to determine the volume of water sampled (mean 45.2 m³ \pm 1 SD 18.6m³). Three replicate tows were collected parallel to the shoreline and approximately 0.75 km apart (Fig. 1) on alternate days from 07 June to 10 August 2005 ($n = 33$ cruises). Sampling conditions were classified as upwelling 17 times, relaxation 15 times, and downwelling once, on the basis of covarying current velocity, wind velocity, temperature, salinity, significant wave height, and upwelling indices.

Wind speed, direction, and significant wave height were obtained from the buoy National Data Buoy

Center (NDBC) 46013 (www.ndbc.noaa.gov/station_page.php?station=46013) located 28 km offshore of Bodega Bay. Wind data also were obtained from the Bodega Marine Laboratory (BML) for comparison (bml.ucdavis.edu/boon/wind.html). Along- and cross-shore wind stress (dynes cm⁻²) were calculated from hourly data and adjusted to a height of 10 m above sea level using a neutral stability wind profile, and they were rotated in the alongshore direction to principal axes of 320° and 305° for NDBC 46013 and BML, respectively (Roughan et al. 2005). Negative values of alongshore wind stress indicate equatorward (upwelling-favorable) wind forcing. Relaxation refers to periods of low wind stress and significant positive values indicate downwelling. Positive cross-shore wind stress indicates onshore wind forcing.

Daily upwelling indices (m³ s⁻¹ per 100 m of coastline) for our region (39°N, 125°W) were obtained from the Pacific Fisheries Environmental Laboratory, Pacific Grove, California (http://las.pfeg.noaa.gov/las6_5/servlets/dataset?catitem=1708). These estimates of offshore Ekman transport are regional-scale aggregates that are calculated from atmospheric pressure data, given that a cross-shore gradient in atmospheric pressure drives geostrophic winds, which in turn drive Ekman transport. High positive values indicate upwelling and offshore transport of surface waters, whereas low positive values indicate relaxation of upwelling and negative values indicate downwelling and onshore Ekman transport due to poleward wind stress.

Vertical profiles of currents, temperature, and salinity were measured near plankton transects and along the open coast. Current velocity was measured continuously using bottom-mounted RDI acoustic Doppler current profilers (ADCP) deployed at 10 m in northeastern Bodega Bay (1200 kHz) and at 30 m along the open coast off Bodega Head (300 kHz; Fig. 1b). Velocity data were obtained for 1- and 2-m-depth bins and 3- and 10-min ensembles for 10-m and 30-m sites, 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, defined by the depth-averaged principal axis. Positive alongshore flow is poleward (negative equatorward) and positive cross-shore flow is onshore (negative offshore). Temperature at 9-m depth was recorded every 6 min using an Onset Optic StowAway® TidbiT thermistor ($\pm 0.2^\circ\text{C}$) that was attached 1 m above the bottom to a mooring placed alongside the ADCP located inside the bay. Lower temperatures indicate the presence of upwelled water in the bay. Open-coast salinity and temperature data from 5-m depth were also available from a Sea-Bird Electronics thermosalinograph (SBE 45 MicroTSG) deployed in the BML seawater intake line at Bodega Head (Fig. 1b). Higher salinities indicate the presence of upwelled waters, whereas lower salinities indicate the presence of offshore or Gulf of Farallones waters (Wing et al. 1998; Roughan et al. 2006).

Species surveyed—All crustacean larvae were identified to species and stage when possible and counts were standardized to number per volume of water sampled (m⁻³). The mean larval density across sampling dates and

Table 1. Life history information for species of crustacean larvae that were collected every other day in oblique plankton tows from 07 June to 10 August 2005 ($n = 33$ d) in the lee of Bodega Head, including number of larval stages, larval duration, primary location of larval release, and cross-shelf larval distributions. Larval durations were obtained from field and laboratory studies that were conducted at water temperatures that most resembled those of our study region. Sheltered habitats refer to bays, estuaries, and harbors vs. the open coast.

Family	Taxa	No. stages	Duration (d)	Primary release site	Cross-shelf distribution*
Cirripedia	<i>Balanus crenatus</i>	7	14–21†(E)‡	Sheltered–exposed	Nearshore
	<i>Balanus glandula</i>	7	11–14§(L)	Sheltered–exposed	Nearshore
	<i>Balanus nubilus</i>	7	na	Sheltered–exposed	Outer shelf
	<i>Chthamalus</i> spp.	7	18–30 (L)	Sheltered–exposed	Nearshore
Thalassinidea	<i>Neotrypaea californiensis</i>	5	42¶(F)	Sheltered	Nearshore
Hippidae	<i>Emerita analoga</i>	6	120# ^F	Sheltered–exposed	Unknown
Paguroidea	<i>Pagurus</i> spp.	5	26–81**(F)	Exposed	Nearshore
	Unidentified Pagurid	5	49–90**(F)	Exposed	Mid-shelf
Porcellanidae	<i>Pachycheles</i> spp.	3	34–40††(L)	Exposed	Nearshore
	<i>Petrolisthes</i> spp.	3	32–51‡‡(L)	Sheltered–exposed	Nearshore
Pinnotheridae	Pinnotheridae	6	30–200**(F)	Sheltered–exposed	Nearshore
Majidae	<i>Mimulus foliatus</i> and <i>Pugettia richii</i>	3	45–53**(F)	Sheltered–exposed	Outer shelf
	<i>Scyra acutifrons</i> and <i>Pugettia producta</i>	3	45–53**(F)	Sheltered–exposed	Outer shelf
	<i>Grapsus</i> spp.	6	40–70**(F)	Sheltered	Mid-shelf
Grapsidae	<i>Pachygrapsus crassipes</i>	6	74–142**(F)	Sheltered–exposed	Mid-shelf
	Canceridae	<i>Cancer antennarius</i>	6	36–46§§(L)	Sheltered–exposed
<i>Cancer magister</i>		6	105–125 (F)	Sheltered–exposed	Outer shelf
<i>Cancer oregonensis</i>		6	105–140**(F)	Sheltered–exposed	Outer shelf
<i>Cancer productus</i>		6	97¶¶(L)	Sheltered–exposed	Outer shelf
<i>Lophopanopeus bellus</i>		5	30–100**(F)	Sheltered–exposed	Outer shelf

* Morgan et al. 2009a.

† Morris et al. 1980.

§ Brown and Roughgarden 1985.

|| Miller et al. 1989.

¶ McCrow 1972.

Johnson and Lewis 1942.

** Lough 1974.

†† MacMillan 1971.

‡‡ Gonor 1970.

§§ Roesijadi 1976.

|| Reilly 1983.

¶¶ Trask 1969.

‡ E, estimate; L, lab; F, field; na, not applicable.

the mean larval density per sampling trip were calculated for each species to report their overall abundance during the 2-month sampling period. The percentage of the total number of larvae collected and the percentage of sampling days that each taxon was present also were calculated to reveal their relative abundance and temporal patchiness.

The barnacles collected in this study (*Balanus crenatus*, *Balanus glandula*, *Balanus nubilus*, *Chthamalus* spp.) molt through six larval stages and a postlarval stage (cyprid), spending about 2 to 4 weeks in the plankton (Table 1). *Balanus crenatus* releases larvae year-round, *Chthamalus* spp. releases larvae from spring through fall, and *B. glandula* releases larvae from winter through spring in our region (Morris et al. 1980; Strathmann 1987). The timing and duration of the reproductive season of *B. nubilus* is not well known. Adult barnacles of all species in this study primarily occur in sheltered bays and estuaries on pier pilings and on rocks along the exposed coast (Morris et al. 1980). With the exception of *B. nubilus*, the larvae of all species of barnacles remain nearshore throughout develop-

ment (Morgan et al. 2009a). *Balanus nubilus* mid-late-stage larvae occur over the outer shelf before the postlarvae return to the nearshore to settle. *Chthamalus dalli* and *Chthamalus fissus* both occur in the study area but could not be distinguished reliably.

The anomuran and brachyuran crabs in this study, and the mud shrimp, *Neotrypaea californiensis*, spend weeks to months in the plankton, developing through two to five larval stages and a postlarval stage (megalopa) before returning to the benthos as juveniles (Table 1). Cancerids reside on the inner shelf with some species ranging to the outer shelf or slope, and they recruit to Bodega Bay year-round, peaking in May and June (Morris et al. 1980). Grapsids, majids, pagurids, porcellanids, and pinnotherids peak from May to August (Morris et al. 1980; Mace and Morgan 2006a). Adults of most of these species live within protected bays and estuaries as well as along the exposed coast, ranging from the intertidal zone (grapsids, pagurids, porcellanids) to the inner shelf (majids, pinnotherids; Morris et al. 1980). The mud shrimp, *N. californiensis*, is

Table 2. Species of crustacean larvae that were collected every other day in oblique plankton tows from 07 June to 10 August 2005 ($n = 33$ d) in the lee of Bodega Head, California. The total mean abundance (± 1 SE) across sampling dates ($n =$ three tows) and the mean (± 1 SE) per 2-d sampling period are reported as well as the percentage of the total number of larvae collected and the percentage of sampling days that each taxa was present.

Family	Taxa	Total mean ($m^{-3} \pm 1$ SE)	Mean trip ⁻¹ ($m^{-3} \pm 1$ SE)	% Total	% Time
Cirripedia	<i>Balanus crenatus</i>	934.6 \pm 190.3	29.1 \pm 7.8	14.2	90.9
	<i>Balanus glandula</i>	135.8 \pm 59.5	4.2 \pm 2.7	2.1	81.8
	<i>Balanus nubilus</i>	47.8 \pm 45.6	1.5 \pm 0.9	0.7	48.5
	<i>Chthamalus</i> spp.	84.0 \pm 34.4	2.6 \pm 1.4	1.3	45.5
Thalassinidea	<i>Neotrypaea californiensis</i>	31.1 \pm 10.4	1.0 \pm 0.3	0.5	60.6
Hippidae	<i>Emerita analoga</i>	65.5 \pm 6.6	2.0 \pm 0.7	1.0	78.8
Paguroidea	<i>Pagurus</i> spp.	66.3 \pm 24.0	2.0 \pm 1.1	1.0	63.6
	Unidentified Pagurid*	0.6 \pm 0.2	0.1 \pm 0.01	<0.1	12.1
Porcellanidae	<i>Pachycheles</i> spp.†	317.9 \pm 232.4	9.4 \pm 8.2	5.0	54.5
	<i>Petrolisthes</i> spp.†	20.6 \pm 12.7	0.6 \pm 0.4	0.3	39.4
Pinnotheridae	Pinnotheridae	4726.2 \pm 2434.5	145.0 \pm 90.5	72.0	93.9
Majidae	<i>Mimulus foliatus</i> and <i>Pugettia richii</i> †	7.0 \pm 2.0	0.2 \pm 0.1	0.1	48.5
	<i>Scyra acutifrons</i> and <i>Pugettia producta</i> †	3.0 \pm 0.6	0.1 \pm 0.03	<0.1	42.4
Grapsidae	<i>Hemigrapsus</i> spp.	63.4 \pm 19.9	1.9 \pm 0.7	1.0	90.9
	<i>Pachygrapsus crassipes</i>	14.8 \pm 4.1	0.4 \pm 0.2	0.2	51.5
Cancridae	<i>Cancer antennarius</i>	16.6 \pm 8.7	0.5 \pm 0.2	0.3	45.5
	<i>Cancer magister</i>	5.1 \pm 1.9	0.2 \pm 0.1	0.1	21.2
	<i>Cancer oregonensis</i> †	0.3 \pm 0.2	0.01 \pm 0.01	0.0	15.2
	<i>Cancer productus</i> †	0.7 \pm 0.5	0.02 \pm 0.01	0.0	15.2
Xanthidae	<i>Lophopanopeus bellus</i>	15.4 \pm 3.0	0.5 \pm 0.1	0.2	57.6

* Too few larvae were collected for analysis.

† Taxa that were combined for analysis.

found in burrows in muddy bays and estuaries, whereas *Emerita analoga* resides in sandy beaches in wave-swept bays and on the exposed coast (Morris et al. 1980). The cross-shelf larval distributions vary among taxa (Morgan et al. 2009a,c). All larval stages of the mud shrimp, porcellanids, pinnotherids, and *Pagurus* spp. occur nearshore throughout development. The mid-late stages of an unidentified pagurid, the grapsids, and *Cancer antennarius* occur over the midshelf, whereas the mid-late stage larvae of the majids, *Lophopanopeus bellus*, and three other species of cancrids (*Cancer magister*, *Cancer oregonensis*, *Cancer productus*) occur over the outer shelf.

Not all anomuran and brachyuran crab larvae could be readily identified to species. Consequently, larvae of the two groups of majids were combined into *Mimulus foliatus* and *Pugettia richii* and *Scyra acutifrons* and *Pugettia producta*. Five species of porcellanid crabs (*Petrolisthes cinctipes*, *Petrolisthes eriomerus*, *Petrolisthes manimaculis*, *Pachycheles rudis*, *Pachycheles pubescens*) and three species of hermit crabs (*Pagurus samuelis*, *Pagurus hirsutisculus*, *Pagurus granosimanus*) occur in our study region and were classified by genus. At least six species of pinnotherid crabs occur primarily on the inner shelf in our area (*Fabia subquadrata*, *Scleroplax granulata*, *Pinnixa tubicola*, *Pinnixa longipes*, *Pinnixa franciscana*, *Pinnixa schmitti*) and were classified by family, because their larvae cannot be reliably identified using morphological traits.

Twenty of the 21 taxa collected were sufficiently abundant for statistical analysis (Table 2). Four of these 20 taxa were combined (*Petrolisthes* spp. and *Pachycheles* spp., *M. foliatus* and *Pugettia richii* and *Scyra acutifrons*

and *P. producta*, *C. oregonensis*, and *C. productus*) for presentation after determining that the relative abundance over upwelling–relaxation cycles was similar. The final 16 taxa were categorized into groups of larval stages to simplify presentation, except for porcellanids and majids that have only three developmental stages. Taxa that have four developmental stages (*L. bellus* and pagurids, and *N. californiensis*) were grouped as follows: I, II–III, IV, and postlarva and I, II–III, IV–V, respectively. Taxa that have six developmental stages (*E. analoga*, pinnotherids, grapsids, cancrids) were categorized as follows: I, II–III, IV–V, and postlarva. Barnacles have seven stages and were grouped as follows: I–III, IV–V, VI, and postlarva, because the first three larval stages passed through nets and were not collected.

Data analysis—Mean densities of larval stages were used to indicate whether larvae of each of these 16 taxa completed development nearshore or migrated onto the shelf before recruiting onshore as postlarvae. The presence of all larval stages indicates that larvae complete development nearshore, whereas the presence of primarily first-stage larvae and postlarvae indicates that species develop offshore and return onshore to settle.

Fluctuations in larval densities relative to upwelling–relaxation cycles indicated whether larval densities increased in the lee of Bodega Head primarily during prevailing upwelling-favorable winds or during relaxation events. Larval densities were transformed ($\log_{10}x + 1$) to meet assumptions of normality and were cross-correlated with environmental variables: alongshore wind stress,

Table 3. Continued.

Species or taxa	Alongshore wind stress NDBC (dynes cm ⁻²)		Cross-shore wind stress NDBC (dynes cm ⁻²)		Open-coast surface currents (m s ⁻¹)		Current shear inside the bay (m s ⁻¹)		Wave height (m)		Bottom temperature (°C)		Salinity		Upwelling index (m ² s ⁻¹ per 100 m of coastline)	
	Day	Value	Day	Value	Day	Value	Day	Value	Day	Value	Day	Value	Day	Value	Day	Value
<i>Hemigrapsus</i> spp. II-PL	2	0.213	2	-0.271	0	0.352	2	0.368	0	-0.216	0	0.443	0	-0.272	ns	ns
	ns	-0.251	4	-0.251	2	0.335	2	0.368	2	0.380	2	0.380	2	0.380	2	0.380
<i>Pachygrapsus crassipes</i> I and PL	ns	ns	ns	ns	0	-0.332	0	-0.278	2	-0.259	ns	ns	ns	ns	2	-0.199
	ns	ns	ns	ns	0	-0.235	ns	ns	0	-0.216	2	0.255	4	-0.388	4	-0.220
<i>Lophopanopeus bellus</i> I	ns	ns	ns	ns	2	0.356	2	0.343	ns	ns	ns	0.421	ns	ns	ns	ns
	ns	ns	ns	ns	ns	ns	4	0.251	2	-0.208	ns	ns	ns	ns	ns	ns
Porcellanidae I-PL	ns	ns	ns	ns	ns	ns	ns	ns	2	-0.208	ns	ns	ns	ns	ns	ns
	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
<i>Balanus nubilus</i> IV-VI	ns	ns	ns	ns	ns	ns	ns	ns	2	-0.208	ns	ns	ns	ns	ns	ns

cross-shore wind stress, open-coast surface currents, bay current shear, significant wave height, bay subsurface temperature, open-coast salinity, and the Bakun upwelling index. Previous studies in our region have demonstrated that these environmental variables are cross-correlated and perform well as indicators of upwelling, relaxation, and downwelling conditions. Equatorward wind stress, cold, saline water, large waves, and a positive upwelling index are associated with upwelling conditions (Lundquist et al. 2000; Wing et al. 2003; Morgan et al. 2009b). Because sampling occurred every second day, lags resulting from cross-correlation analyses are resolved in 2-d increments (Table 3). Cross-correlations for all developmental stages of a species were similar and were combined and reanalyzed to simplify presentation, except for *B. nubilus* and *Hemigrapsus* spp. All data were analyzed using the SAS JMP statistical software package.

Results

Physical characteristics of the recirculation feature—Alongshore winds were predominantly equatorward during the study, with upwelling-favorable winds over 5 m s⁻¹ persisting from 08 to 14 June, 01 to 08 July, and 06 to 10 August (events 1, 3, and 7 in Fig. 2a). Briefer upwelling-favorable wind events occurred from 21 to 22 June, 11 to 12 July, 22 to 24 July, and 31 July to 01 August (events 2, 4, 5, and 6 in Fig. 2a). At other times, winds were light and variable. Changes in wind conditions over upwelling and relaxation cycles were reflected in alongshore currents, which typically flowed equatorward during upwelling conditions and poleward during relaxation events (Fig. 2b). Cold, saline waters characterized upwelling conditions, and temperature rose and salinity fell during prolonged relaxation events that occurred in late June and again in late July (Fig. 2c,d).

Currents in the lee of the headland exhibited strong tidal and synoptic variability (Fig. 2e,f). During and immediately after upwelling-favorable winds, strong vertical shear was observed, with equatorward flow occurring at the surface and poleward flow occurring at depth (Fig. 2e). Between upwelling events, poleward flow usually occurred at all depths along the northeastern shore of the bay. However, brief events of equatorward flow occurred at all depths and appeared to be unrelated to local winds (28 June, 19 July, 29 July). The development of the surface-current response in the bay depended on wind strength; rapid development occurred over a couple of days in events 1 and 5, whereas slow development occurred after several days of weak winds in events 2 and 3. At this 10-m-deep location, the depth of flow reversal was about 5 to 7 m below the surface once it was fully developed, with near-surface equatorward flows approaching 0.2 m s⁻¹ and near-bottom poleward flows approaching closer to 0.1 m s⁻¹. For some events (e.g., event 1), this sheared bay circulation continued for 2 to 3 d after the weakening of upwelling winds. Weak onshore flow occurred during upwelling events, and weak offshore flow occurred during relaxation events (Fig. 2f).

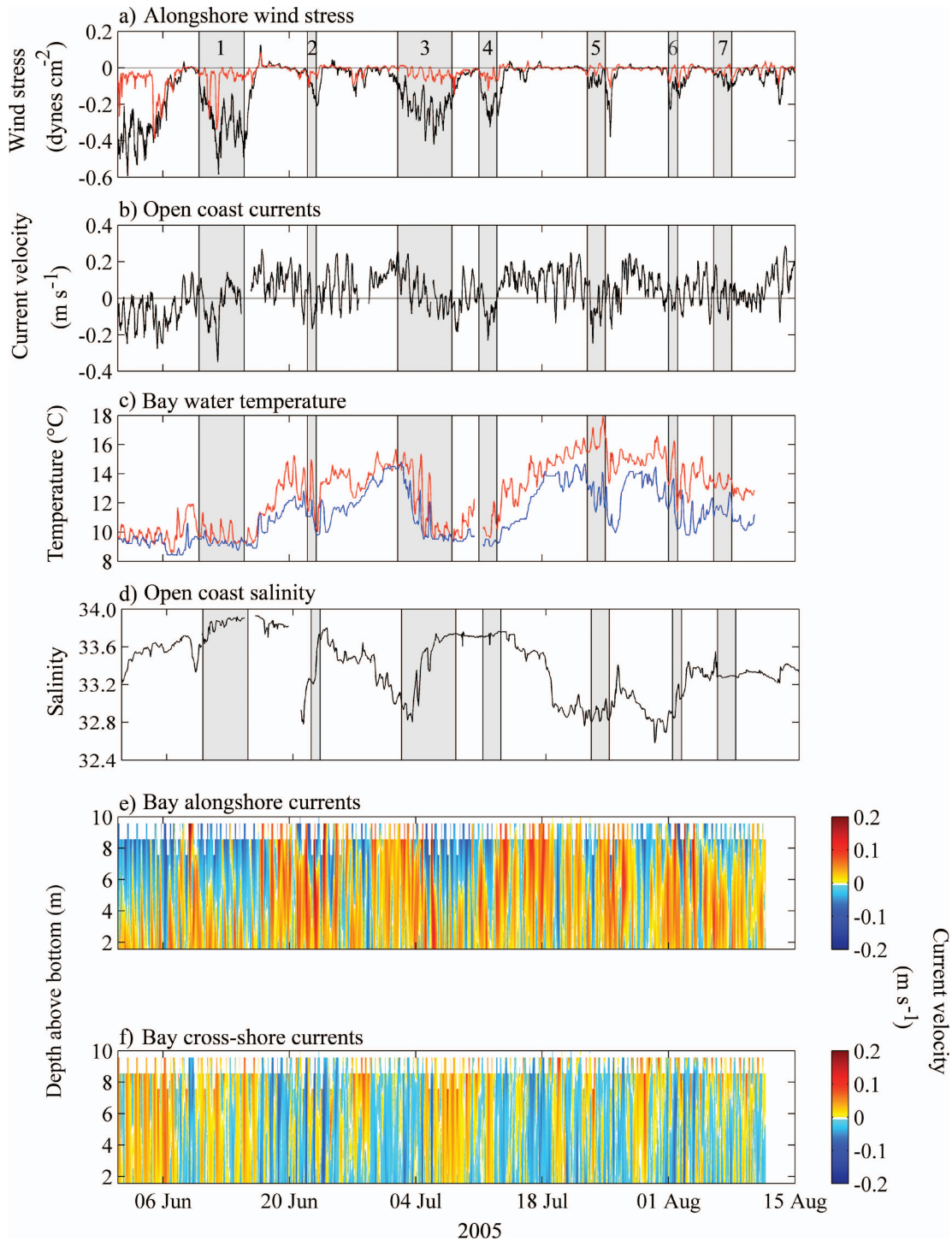


Fig. 2. Time series of (a) wind stress (dynes cm⁻¹) at NDBC 46013 (black) and an onshore station on Bodega Head (red), (b) average alongshore current velocity (m s⁻¹) for the upper 12 m of the water column measured off Bodega Head, (c) water temperature (°C) at the surface (red) and bottom (blue) in northern Bodega Bay, (d) salinity measured at Bodega Head, (e) alongshore and (f) cross-shore current velocity (m s⁻¹) measured in northern Bodega Bay from 01 June to 15 August 2005. Positive alongshore wind and current velocities are poleward and positive cross-shore current velocities are shoreward. Gray shading indicates upwelling conditions (events 1–7), defined as times when alongshore wind speed exceeded 5 m s⁻¹.

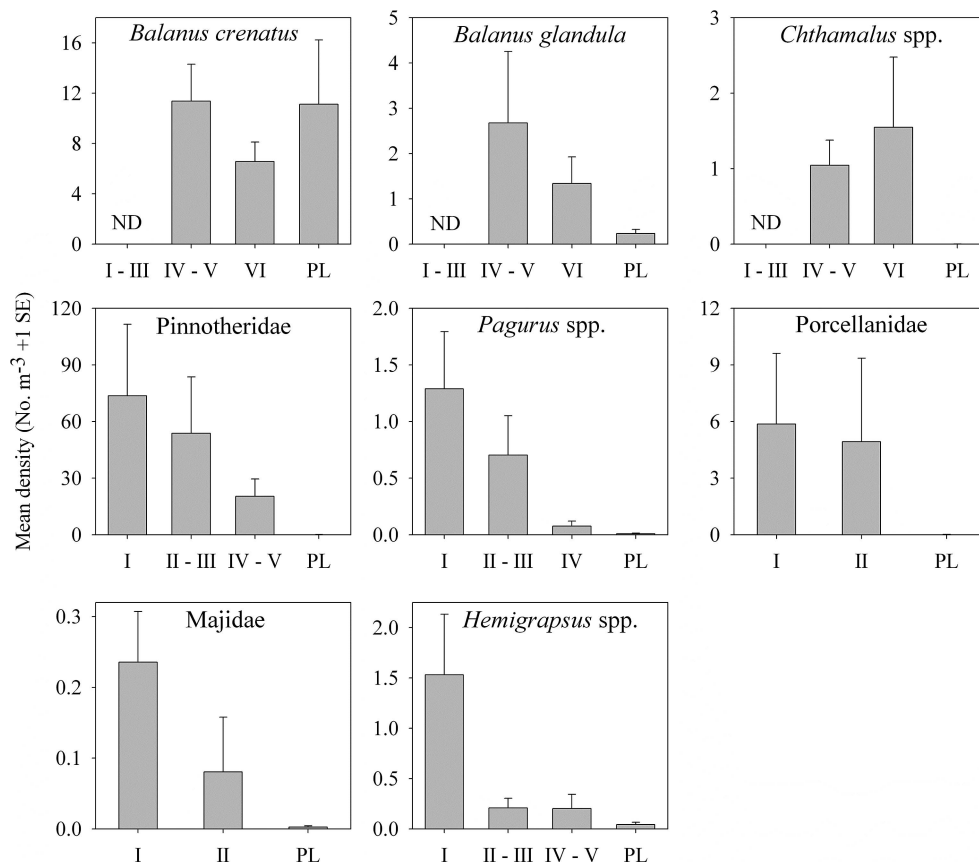


Fig. 3. Mean larval density of three taxa of barnacles and five taxa of decapod crustaceans that were prevalent throughout development in the lee of Bodega Head, California. Roman numerals represent the stage of larval development, and PL represents the postlarval stage. ND denotes no data since the barnacle larval stages I–III passed through our nets.

Larval accumulation and retention in the lee of the headland—Three of the 20 taxa of crustacean larvae collected during the 2-month study composed the vast majority (91.4%) of all larvae collected (Table 2). The six species of pinnotherids composed 72.0% of larvae with a mean of 145 m^{-3} (± 90 SE) per trip followed by *B. crenatus* (14.2%) and *Pachycheles* spp. (5.0%). Five taxa were frequently present ($> 75\%$ of sampling days) and half the taxa were present more than 50% of the time. An unidentified pagurid was the rarest taxon (occurring 12.1% of the time) and was not analyzed statistically.

We collected the same number of taxa in the lee of the headland that develop nearshore as offshore, indicating that vertical distributions regulating cross-shelf transport do not affect entrainment into the lee of the headland. Differences in the relative abundance of larval stages in the lee of Bodega Head indicated that 8 of 16 taxa were released nearshore and remained throughout development in the lee of Bodega Head (Fig. 3). Although the first three larval stages of barnacles passed through our nets, later stages of three of the four barnacle taxa (*B. crenatus*, *B. glandula*, *Chthamalus* spp.) occurred in high densities. All larval stages of pinnotherids, *Pagurus* spp., porcellanids, and majids were abundant as early-stage larvae and steadily declined during development. The steeper decrease

of *Hemigrapsus* spp. between early and later stages suggests that more of these larvae may have been transported away from the study area. Later larval stages did not occur more abundantly for any of these eight taxa, indicating that there was not an influx of these stages from outlying areas. All larval stages of these taxa also were common close to shore in cross-shelf surveys, although late larval stages of *Hemigrapsus* spp. and majids also occurred on the mid- to outer shelf, respectively (Table 1).

Larvae of seven taxa were abundant in the lee of Bodega Head as early-stage larvae and later stages were absent or uncommon (Fig. 4). Larvae of *E. analoga*, *N. californiensis*, *Pachygrapsus crassipes*, *L. bellus*, and three taxa of cancrids likely migrated offshore or were advected alongshore away from the study area after hatching. Larval stages of *B. nubilus* were uncommon and postlarvae were very abundant, suggesting that most larvae migrated farther from shore than the other species of barnacles before recruiting onshore as postlarvae (Fig. 4). Crab postlarvae were uncommon presumably because their faster swimming speeds enabled them to better avoid nets than larvae in the daytime (Chia et al. 1984). A concurrent study revealed that postlarvae of all five species of the crabs recruited to passive collectors that were moored in the lee of the headland (Morgan et al. 2009b). Later

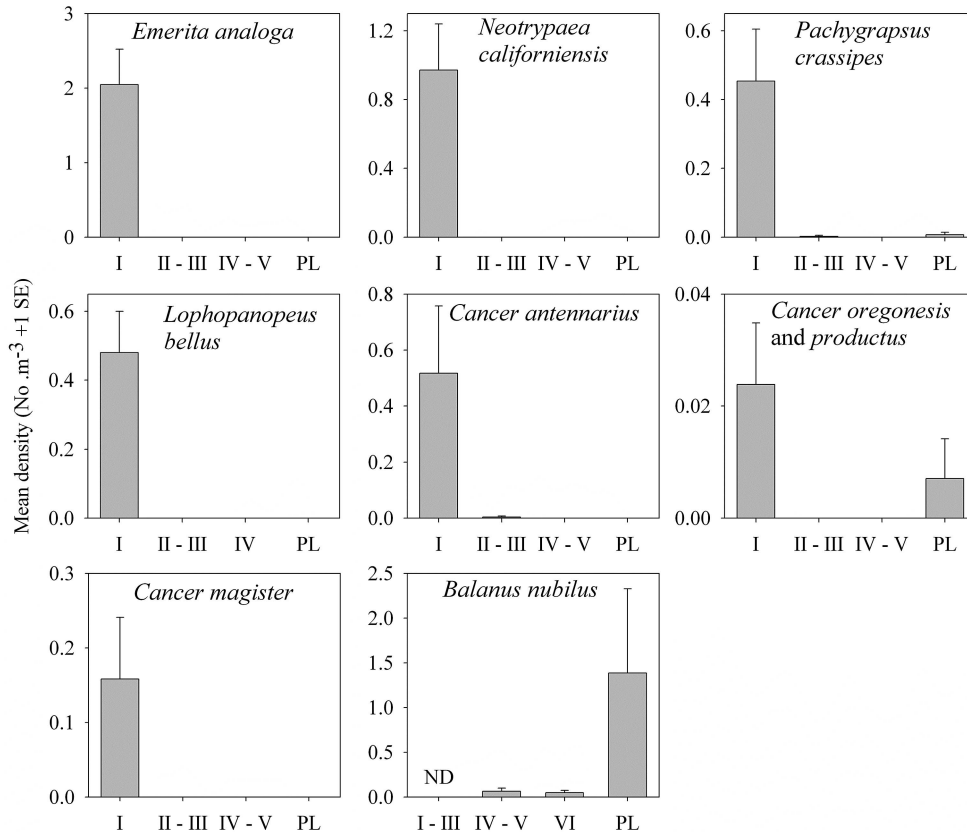


Fig. 4. Mean larval density of eight taxa that were prevalent only as early-stage larvae or postlarvae in the lee of Bodega Head, California. Roman numerals represent the stage of larval development, and PL represents the postlarval stage. ND denotes no data since the barnacle larval stages I–III passed through our nets.

developmental stages of all of these taxa also occurred from the mid- to outer shelf in the cross-shelf surveys, except for *N. californiensis*, which was prevalent throughout development nearshore (Table 1). Overall, the cross-shelf transport patterns inferred from the relative abundance of larval stages for the 16 taxa were consistent with those found during cross-shelf larval surveys (Table 1), and interspecific differences in depth preferences of larvae did not appear to affect entrainment into the lee of the headland.

Timing and duration of larval entrainment and retention—Larvae were entrained during prevailing upwelling conditions, suggesting they were entrained by recirculation in the lee of the headland (Table 3; Figs. 5, 6). Larvae of 11 of 16 taxa were most prevalent at the onset of upwelling conditions or shortly thereafter, regardless of whether larvae completed development nearshore or migrated offshore. Larvae of all 11 taxa were prevalent in the lee of the headland only as long as upwelling-favorable winds persisted and were largely absent during prolonged relaxation periods in mid-June and mid-July. Larval abundance of 9 of the 11 taxa peaked during the strongest upwelling event of the sampling season in early June (all except *Chthamalus* spp., *Cancer oregonensis*, and *C. productus*). Six of the 11 taxa also increased in abundance

during the upwelling event in the beginning of July when water temperatures remained cold for a week (*Chthamalus* spp., *B. crenatus*, *B. glandula*, *B. nubilus*, *Hemigrapsus* spp., *Cancer antennarius*, *C. oregonensis*, and *C. productus*). Larvae of the 11 taxa are released in exposed and sheltered habitats (Table 1) and likely originated from the adjacent open coast or Bodega Bay and Bodega Harbor. Larvae from the open coast would have been entrained into the bay by the recirculation feature as currents flowed equatorward past the Bodega headland. Larvae from Bodega Harbor (and perhaps Tomales Bay) would have been flushed by ebb tides into the adjacent bay where they can be retained by recirculation, whereas larvae released in the bay would also be retained by this feature.

Nine of the 11 taxa, consisting of 79% of all larvae collected, were well correlated with upwelling conditions, including *B. crenatus*, *B. glandula*, *B. nubilus* postlarvae, *N. californiensis*, *Pagurus* spp., pinnotherids, first-stage *Hemigrapsus* spp., *C. antennarius*, and *C. productus*, and *C. oregonensis* (Table 3; Figs. 5, 6). They were correlated with at least seven of the eight physical variables with high densities beginning at the onset of equatorward and onshore wind stress, equatorward surface currents along the open coast, increased current shear inside the bay, increased wave height, cold, saline water, and upwelling, and persisting for as long as 4 d. Two taxa were cross-

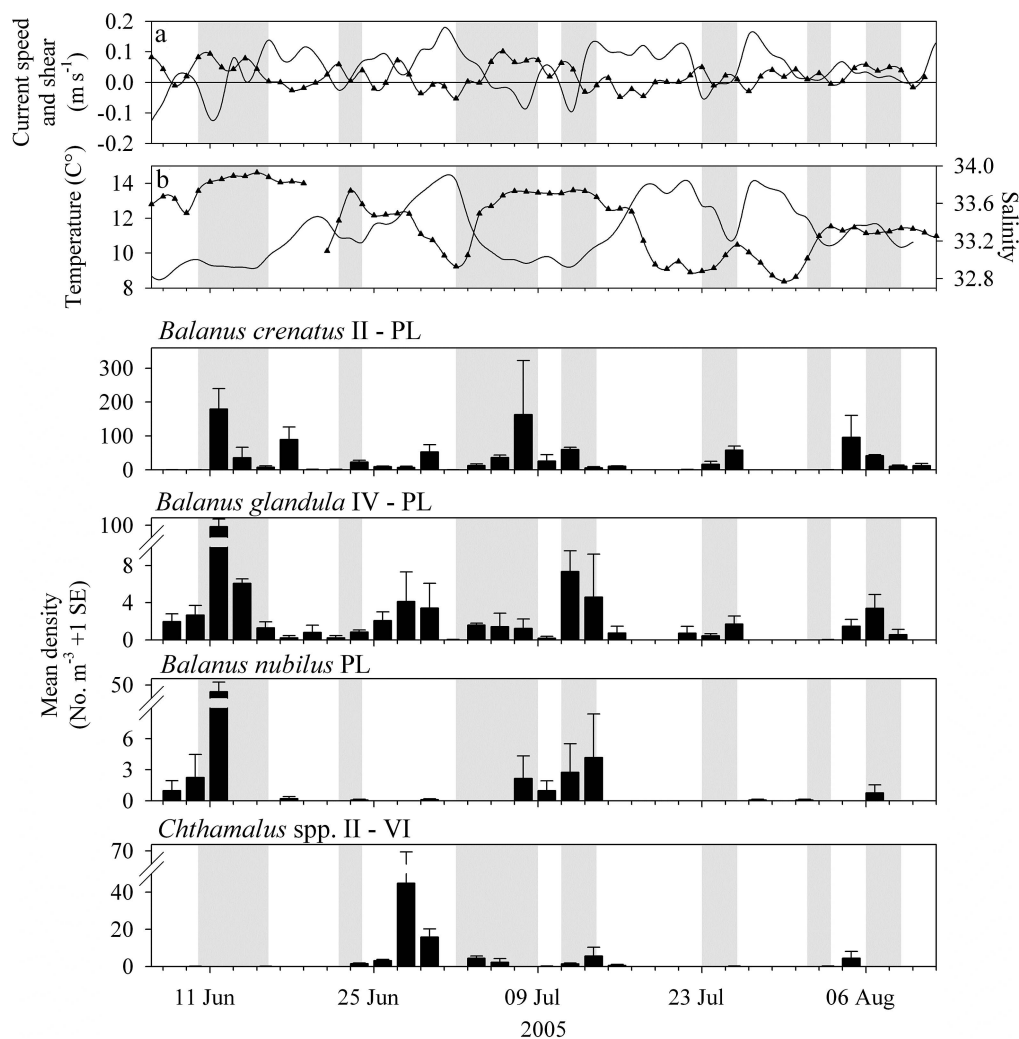


Fig. 5. Four taxa of barnacle larvae (four lower panels) that were cross-correlated with upwelling conditions. Mean larval density (black bars) is shown relative to alongshore (a) current speed along the open coast for the upper 12 m of the water column (solid line), and current shear in northern Bodega Bay (triangles); (b) bottom temperature (solid line), and salinity (triangles). Oblique plankton tows were taken every other day in the lee of Bodega Head, California from 07 June to 10 August 2005. Gray shading indicates upwelling conditions, defined as times when alongshore wind speed exceeded 5 m s^{-1} .

correlated with only two and four of the eight physical variables: *Chthamalus* spp. and *Cancer magister*. High salinity was the best indicator, with all 11 taxa being cross-correlated with this variable, followed by nine taxa being cross-correlated with along- and cross-shore wind stress, open-coast surface currents, bay current shear, temperature, and the upwelling index, and eight taxa being cross-correlated with wave height. Cross-correlations were based on all larval stages for five of the taxa (*B. crenatus*, *B. glandula*, *Chthamalus* spp., *Pagurus* spp., pinnotherids), whereas they primarily depended on first-stage larvae or postlarvae for six taxa (*B. nubilus*, *N. californiensis*, *Hemigrapsus* spp., *Cancer antennarius*, *C. productus*, and *C. oregonensis*, *C. magister*).

Peak abundance of the five remaining taxa occurred during relaxation events (Table 3; Fig. 7), indicating that larvae were delivered to the study area by the poleward

coastal boundary current. Larvae of 5 of the 16 taxa (*E. analoga*, early stage majids, later stages of *Hemigrapsus* spp., *Pachygrapsus crassipes*, *L. bellus*) were most prevalent at the onset of relaxation conditions or shortly thereafter. Larval abundance of four of these five taxa peaked or increased over a 2-d period during the prolonged relaxation event in mid-June and was uncommon before this event (all except *P. crassipes*), suggesting that larvae did not originate in the immediate vicinity of Bodega Head. Two of these taxa peaked again during the relaxation event in mid-July (*E. analoga*, *Hemigrapsus* spp.). *Pachygrapsus crassipes* larvae increased in abundance before the onset of upwelling in the beginning of the study and peaked during the relaxation event mid-July. Larvae of all five taxa remained in low numbers throughout the study period after their initial influx into the lee of the headland regardless of oceanographic conditions, except later stages of *Hemi-*

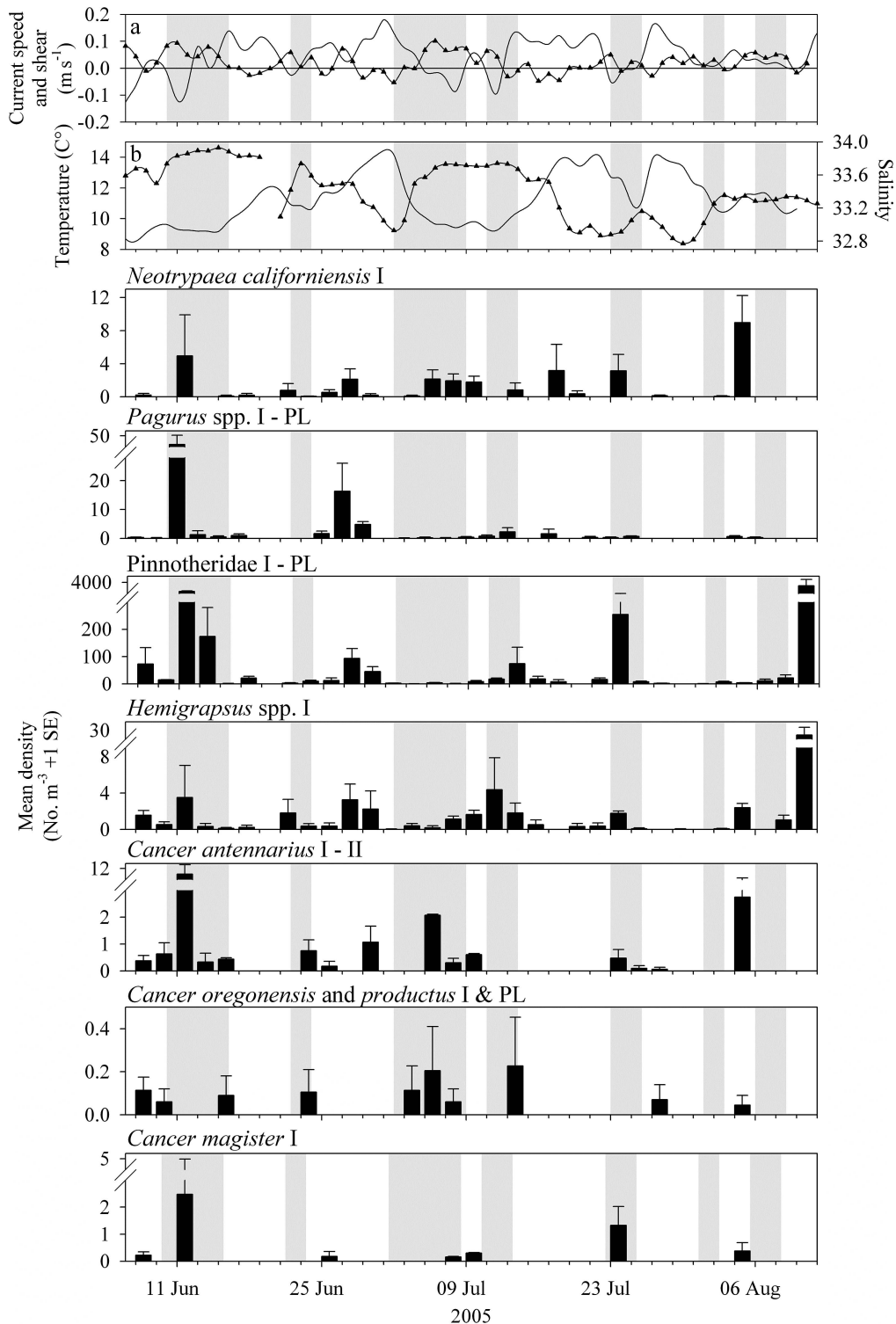


Fig. 6. Seven taxa of decapod crustaceans (seven lower panels) that were cross-correlated with upwelling conditions. Mean larval density (black bars) is shown relative to alongshore (a) current speed along the open coast for the upper 12 m of the water column (solid line), and current shear in northern Bodega Bay (triangles), (b) bottom temperature (solid line), and salinity (triangles). Oblique plankton tows were taken every other day in the lee of Bodega Head, California from 07 June to 10 August 2005. Gray shading indicates upwelling conditions, defined as times when alongshore wind speed exceeded 5 m s⁻¹.

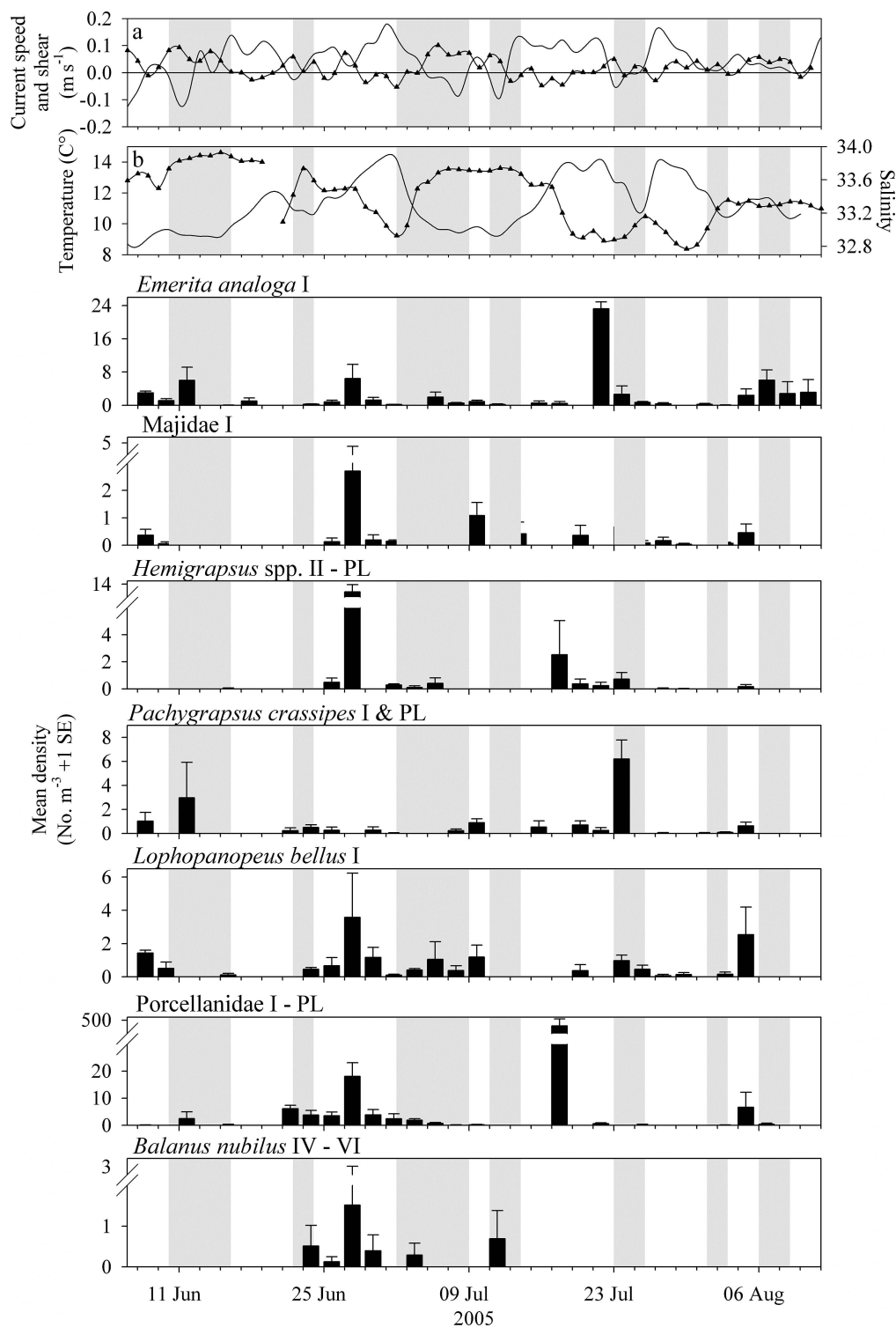


Fig. 7. Five taxa of crustaceans that were cross-correlated with relaxation conditions and two taxa that were not related to upwelling–relaxation cycles (seven lower panels). Mean larval density (black bars) is shown relative to alongshore (a) current speed along the open coast for the upper 12 m of the water column (solid line), and current shear in northern Bodega Bay (triangles), (b) bottom temperature (solid line), and salinity (triangles). Oblique plankton tows were taken every other day in the lee of Bodega Head, California from 07 June to 10 August 2005. Gray shading indicates upwelling conditions, defined as times when alongshore wind speed exceeded 5 m s^{-1} .

grapsus spp. only occurred during the prolonged relaxation events in mid-June and mid-July.

Larvae of these five taxa generally were not as well correlated with physical variables as the 11 taxa that were prevalent during upwelling conditions (Table 3, Fig. 7). Furthermore, fewer of these taxa were prevalent at the onset of relaxation conditions than were the taxa that were prevalent at the onset of upwelling conditions. Later stages of *Hemigrapsus* spp. and majid larvae were cross-correlated with seven or four of the eight physical variables indicating relaxation conditions, respectively, beginning at the onset of relaxation conditions. However, three other taxa were prevalent beginning 2 to 4 d after the onset of relaxation conditions and were cross-correlated with four (*E. analoga*), three (*L. bellus*), or two (*P. crassipes*) physical variables indicating relaxation conditions. Small waves were the best indicator, with all five taxa being cross-correlated with wave height, followed by four taxa being cross-correlated with warm temperature, three taxa being cross-correlated with poleward wind stress and low salinity, two taxa being cross-correlated with offshore wind stress, and one taxon being cross-correlated with weak upwelling. Cross-correlations were based primarily on first-stage larvae for four taxa (*E. analoga*, majids, *P. crassipes*, *L. bellus*) and later stages for *Hemigrapsus* spp. The two taxa (majids, later stages of *Hemigrapsus* spp.) peaking at the onset of relaxation conditions likely originated nearby from the south bay, Tomales Bay, or the open coast off Tomales Point. In contrast, the three taxa (*E. analoga*, *P. crassipes*, *L. bellus*) peaking 2 to 4 d after the onset of relaxation likely came from a more distant source. All of these taxa develop along the open coast and likely were transported from the pool of larvae developing in the coastal boundary layer off Point Reyes or even to the south of it, given that it takes several days after the onset of relaxation for crab postlarvae from the lee of Point Reyes to be transported to Bodega Head by poleward currents (Wing et al. 1995).

Two more taxa appeared to occur in the lee of the headland primarily during relaxation conditions but were not well correlated with physical variables (Table 3, Fig. 7). Porcellanids occurred during two relaxation events; a very large pulse occurred during one day in mid-July with most of the rest of them occurring in late June and they were cross-correlated with poleward surface currents along the open coast and reduced current shear inside the bay. Porcellanid larvae complete development in high densities nearshore both north and south of Bodega Head (Morgan et al. 2009c), where they could be entrained into the recirculation feature during upwelling or transported to the lee of the headland by a poleward current during relaxation (Send et al. 1987; Wing et al. 1995). Porcellanid postlarvae previously have been found to recruit to the lee of Bodega Head during both upwelling and relaxation events over a 5-yr period (Morgan et al. 2009b). The few late-stage larvae of *B. nubilus* collected occurred during the relaxation event in late June, with an even smaller number occurring during upwelling in early July. Late-stage *B. nubilus* larvae were cross-correlated only with small waves. These larvae were uncommon because they primarily develop farther from shore (Table 1).

Discussion

Data on time-varying densities of planktonic larvae in Bodega Bay showed clear associations with upwelling and relaxation cycles, and peaks in larval abundance occurred as specific events. To better understand these events, one can identify a variety of transport mechanisms that may be responsible for larval import to or retention in the bay. These processes are associated with either the recirculation feature, which was present in the lower water column during upwelling conditions this year as it was during the previous year (Roughan et al. 2005), or the poleward current, which is observed over the inner shelf and in the bay during relaxation periods (Send et al. 1987; Largier et al. 1993; Roughan et al. 2005). A simple model demonstrated that larvae could be retained in the circulation feature either by remaining in the lower water column or by undertaking diel vertical migrations (Roughan et al. 2005), and field studies showed that high larval densities are associated with the waters that flow poleward along this coast during relaxation (Wing et al. 1998; Papastephanou et al. 2006).

As described by Roughan et al. (2005), near-surface waters in the bay moved south and out of the bay, whereas subsurface waters moved onshore in the southern bay and then northward through the bay. Subsurface waters either upwelled at the north shore and leaked offshore across the northern mouth of the bay or recirculated southward along the western margin of the bay. Thus, larvae may accumulate in the bay during upwelling conditions under the following circumstances: (1) Larvae that remain in the lower water column will accumulate where waters upwell, leading to a convergent larval flux in the northern bay; (2) larvae that move vertically between the surface and lower water column, either through active migrations or passive mixing, will experience weak net transport and may remain in the bay for several days (Roughan et al. 2005); and (3) larvae that undertake tidal or diel migrations in association with periodically fluctuating currents will accumulate more strongly than in the second scenario if they typically occur near-surface during times of weaker southward flow, as occurs at night. Larvae that remain very near the surface will neither be entrained nor retained in the bay. However, under strong wind conditions, it is only the strongest swimmers or most buoyant larvae that would be capable of resisting the energetic vertical mixing at these times.

During relaxation, the nearshore poleward current forming close to the coast (Send et al. 1987; Largier et al. 1993; Kaplan et al. 2005) is driven by a combination of barotropic and baroclinic pressure gradients (Pringle and Dever 2009). During the first couple of days of relaxation, nearshore waters from north of Point Reyes are transported into the bay, followed by the arrival of a front and the subsequent arrival of warmer, low-salinity waters from south of Point Reyes (Largier et al. 2006). During relaxation conditions, larvae may be delivered to the bay in high or low densities under the following circumstances: (1) Larvae that occur nearshore along the northern shore of Point Reyes during upwelling conditions (Morgan et al. 2009c) will be delivered to the bay during the first couple of days of relaxation; (2) larvae that accumulate at a front by

swimming upward (Shanks and Eckert 2005) will be delivered to the bay in high densities as the front of the low-salinity waters propagates through the bay; (3) larvae that occupy low-salinity, warm near-surface waters south of Point Reyes during upwelling conditions (Wing et al. 1998) will be delivered to the bay 2 to 3 d after the start of relaxation; and (4) larvae that reside nearshore in the lower water column under calm stratified conditions during relaxation will be delivered rapidly to the bay in high densities at the end of the relaxation event as upwelling resumes.

High larval densities of 11 of 16 taxa occurred during strong, persistent upwelling events (1, 3, 7; Figs. 6, 7) that are consistent with upwelling-related bay circulation, as described above. Larvae accumulated despite differences with upwelling-related circulation that entrain larvae and other zooplankton in the lee of larger capes (Graham et al. 1992; Graham and Largier 1997; Lagos et al. 2005). Five other taxa exhibited maxima during relaxation events that were associated with the arrival of low-salinity warm waters in mid-July. However, we found little evidence that behavior enhanced retention in the recirculation feature in the lee of Bodega Head more than it does on the open coast. Species that complete development nearshore avoid the shallow Ekman layer or ascend to the surface only at night when winds subside, whereas those that migrate offshore commonly reside in the Ekman layer where they are advected offshore (Peterson et al. 1979; Batchelder et al. 2002; Morgan et al. 2009a). These interspecific differences in vertical distributions did not appear to affect whether larvae at some stage in development were entrained into the lee of the headland or how long they persisted there. Larvae released nearshore were entrained into the lee of the small headland and remained there briefly, regardless of whether they were prevalent close to shore throughout development, only prevalent as early-stage larvae, or were returning to settle as postlarvae. Whether larvae are entrained into the recirculation feature appears to depend only on their presence nearshore in the vicinity of the headland during upwelling, and larval residence time in the bay depends only on the duration of the upwelling event. However, given that the strength and persistence of the larval flux convergence associated with the headland eddy depends on upwelling strength and persistence, more larvae will be entrained and denser concentrations will accumulate during stronger and longer upwelling events, which are more common in typical strong upwelling years. Larvae of the remaining five taxa were delivered to the study area during relaxation events when the recirculation feature dissipated (Roughan et al. 2005; Kaplan and Largier 2006), but there was no evidence of accumulation in the lee of the headland at these times.

Taking an event-based approach to analyzing larval densities, 24 peaks occurred for the 18 taxa during the study period (Figs. 5–7). Eight of these peaks occurred on 11 June, which was the strongest upwelling event observed. Five more peaks were observed while flow was sheared in the bay: three persisted between upwelling events 3 and 4, and two occurred on 10 August. Thus, more than half the peaks in larval density among the 18 taxa occurred during the strongest upwelling events, and all of these peaks coincided with times of well-developed vertically sheared

flow in the bay. Nine sampling dates have larval densities that were an order of magnitude higher than at other times. Such anomalously high densities indicate that larvae accumulated by a specific convergence mechanism, such as a front or the vertically sheared flow observed in the bay. Seven of these nine peaks occurred during peak upwelling conditions on 11 June and 10 August (*B. glandula*, *B. nubilus*, *Pagurus* spp., *Pinnotheridae*, first-stage *Hemigrapsus* spp., and *C. antennarius*). The two other anomalous peaks appeared to be associated with the arrival of the salinity front in the bay on 27 June and 17 July (*E. analoga*, later stages of *Hemigrapsus* spp.). Although frontal aggregations are common in the bay and open coast in this region, the aggregation of larvae in a small bay during upwelling has not been shown previously.

Mortality likely was responsible for the steady declines during development for species that were retained over the inner shelf. Larval mortality was estimated to be low during the study (White et al. unpubl.), which is consistent with the observed steady declines in larvae throughout development. In contrast, larvae of one taxon (*Hemigrapsus* spp.) showed a much steeper decline during development that was greater than expected by mortality alone, indicating that more of these larvae were transported away from the study area. The remaining species were present almost entirely as larvae and postlarvae, clearly indicating that larvae developed offshore and returned to settle in adult habitats.

The accumulation of planktonic larvae in a bay resulting in a small-scale recruitment hot spot is due to recirculation in the lee of the bay headland (headland eddy) and is likely to be a common feature in upwelling systems and other wind-driven regions. Although previous studies have shown correlations between recruitment and winds in upwelling areas (Farrell et al. 1991; Wing et al. 1995) and elsewhere (Archambault and Bourget 1999; Jenkins and Hawkins 2003), this study identified a specific mechanism due to the interaction of wind-driven alongshore flow with a topographic feature and the subsequent interaction of a headland eddy and surface wind stress in the bay. Further, most prior work reported the wind-correlated temporal variability in recruitment, whereas we showed that a distinct spatial pattern is expected on the basis of the effect of coastline topography on plankton distributions, further supporting the argument that the time dependence of recruitment is largely driven by temporal variability in transport. Previous studies of topographic eddies include island wake effects (Wolanski and Hamner 1988) and larger headland recirculation features (Penven et al. 2000). In general, small-scale headlands in upwelling regions have been neglected on the basis of the expectation that surface wind stress rapidly flushes small bays and precludes the stratification that is typically associated with vertically sheared flow and the potential for retention and accumulation (as in upwelling shadows, Graham and Largier 1997; Marin et al. 2001; Pinones et al. 2007). We showed that larvae do accumulate in smaller bays in upwelling regions, despite strong surface wind stress and the absence of stratification. Indeed, it is the wind stress combined with the flow reversal due to the headland eddy that produces the vertical circulation and thus the accumulation mecha-

nism observed in Bodega Bay. This vertical circulation is driven by competing surface wind stress and barotropic pressure gradients in the bay, with surface stress dominating the balance of forces near the surface and the pressure gradient dominating near the bottom. Just as in estuaries, the vertical circulation provides an opportunity for a convergent flux of larvae in the bay. This phenomenon is likely to be important in many small bays in upwelling regions, such as Estero Bay, Drakes Bay, and Avila Bay off California; Cartagena Bay, Concepcion Bay, and Coquimbo Bay off Chile; and Walker Bay, Saldanha Bay, and Table Bay off South Africa. Indeed, larval accumulation and enhanced recruitment, especially during strongest winds, are expected wherever coastal winds lead to alongshore flows and headland eddies while imposing surface stress on the bay.

Most taxa of crustaceans were entrained at various stages of development into the lee of this small headland as soon as upwelling-favorable winds began and remained there for as long as these winds persisted. These winds dominate during the upwelling season in our region so that recruitment would be greater in the lee of the headland than on the open coast (Roughan et al. 2006; Mace and Morgan 2006a). The remaining taxa were more prevalent during relaxation events, transported to the lee of the headland by a recurrent poleward current as the recirculation feature dissipated (Send et al. 1987; Wing et al. 1995, 2003). Hence, larval delivery increases during upwelling and relaxation conditions, creating a recruitment hot spot in the lee of this small headland even during years of weak upwelling (Roughan et al. 2006; Mace and Morgan 2006a). Frequent sampling over upwelling-relaxation cycles was needed to determine whether larvae accumulated in the lee of the headland during upwelling events, because on average larvae were at least as abundant over the retentive inner shelf along the open coast (Morgan and Fisher 2010). Consequently, comparing average larval densities inside and outside the recirculation feature is not an effective way to detect the headland effect.

Contrary to earlier expectations, small headlands can serve as recruitment hot spots in recruitment-limited upwelling regions along the western margins of continents, where larval supply more strongly influences the distribution and abundance of adults than in density-dependent regions (Todd 1998; Morgan 2001; Underwood and Keough 2001). The underlying mechanism involves vertically sheared circulation, which is due to the combination of a headland eddy with surface wind stress in the bay. This is expected to occur in many other small bays in upwelling regions and other wind-driven coastal regions. These recruitment hot spots are likely to be an important factor in explaining spatial variation in population density and community structure along the West Coast of the U.S.A. and other windy coasts.

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