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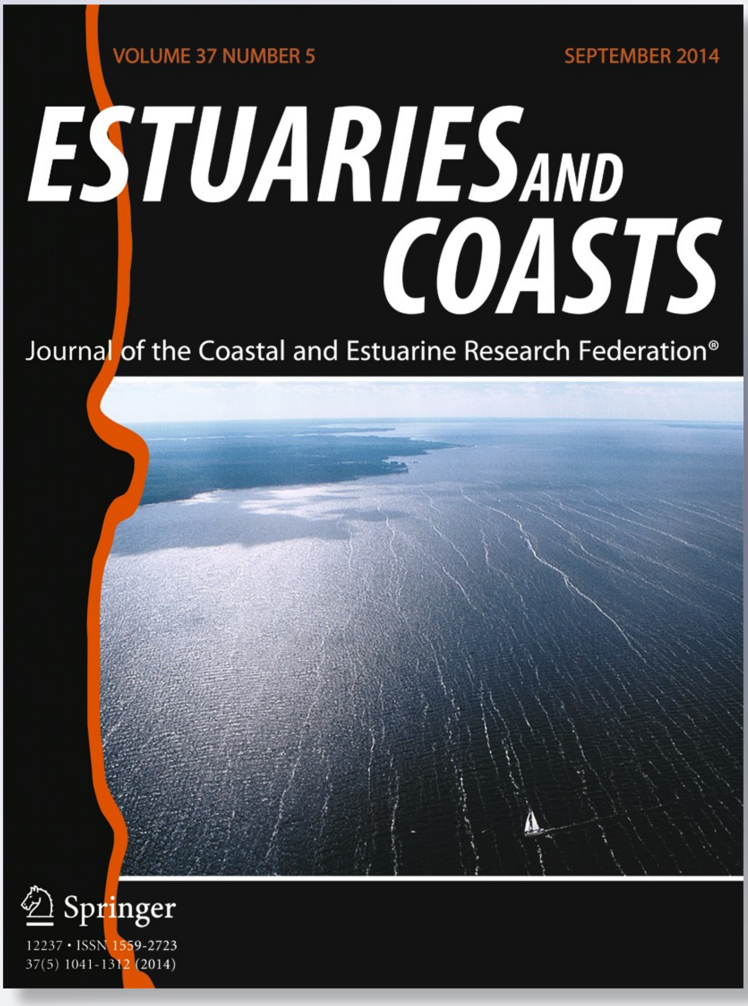

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Abstract The effectiveness of larval behavior in regulating transport between well-mixed, low-inflow estuaries and coastal waters in seasonally arid climates is poorly known. We determined the flux of an assemblage of benthic crustacean larvae relative to physical conditions between a shallow estuary and coastal waters on the upwelling coast of northern California (38°18′N, 123°03′W) from 29 to 31 March 2006. We detected larval behaviors that regulate transport in adjacent coastal waters and other estuaries for only two taxa in the low-inflow estuary, but they were apparent for taxa outside the estuary. Vertical mixing in the shallow estuary may have overwhelmed larvae of some species, or salinity fluctuations may have been too slight to cue tidal vertical migrations. Nevertheless, all larval stages of species that complete development in nearshore coastal waters were present in the estuary, because they remained low in the water column reducing seaward advection or they were readily exchanged between the estuary and open coast by tidal flows. Weak tidal flows and gravitational circulation at the head of the estuary reduced seaward transport during development for species that completed development nearshore, whereas larval release during nocturnal ebb tides enhanced seaward transport for species that develop offshore. Thus, nonselective tidal processes dominated larval transport for most species back and forth between the low-inflow estuary and open coastal waters, whereas in adjacent open coastal waters, larval behavior in the presence of wind-induced shear was more important in regulating migrations between adult and larval habitats along this upwelling coast.

Keywords Larval transport · Vertical migration · Turbulent mixing · Advection · Estuary · Upwelling

Introduction

There has been a long history of investigating larval transport by invertebrates and fishes in stratified estuaries that experience substantial freshwater input year-round. Larvae exploit two-layer flow to complete development within the estuary or migrate to the open coast (reviewed by Morgan 1995a, 2006; Young 1995; Gibson 2003; Queiroga and Blanton 2005). Rates and directions of larval transport in stratified flow are mediated by depth preferences of larvae and the timing, duration, and amplitude of their vertical migrations. Larval retention is facilitated by occupying bottom waters, where net current flow is landward, and larval export is enhanced by occupying surface waters, where net current flow is seaward.

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Larval retention also is facilitated by ontogenetic (young larvae at surface and old larvae at depth) and tidal (rise on flood and descend on ebb tide) vertical migrations, and larval export is expedited by reverse ontogenetic and reverse tidal vertical migrations (opposite of classic vertical migrations). The timing of vertical swimming may be controlled by endogenous clocks with free-running periods that approximate tidal and diel cycles, thereby enabling larvae and postlarvae to anticipate and reliably time vertical migrations (Forward and Tankersley 2001; Kingsford et al. 2002; Gibson 2003; Morgan and Anastasia 2008; López-Duarte et al. 2011). Thus, larvae of some species are retained in estuaries despite net seaward flow by migrating vertically between residual currents that generally flow seaward near the surface and landward near the bottom or by remaining at mid-depth near the level of no net motion; whereas larvae of other species leave estuaries by rising into outflowing surface currents and return later in development in inflowing bottom currents (reviewed by Forward and Tankersley 2001; Queiroga and Blanton 2005; Morgan 2006; Kunze et al. 2013; Miller and Morgan 2013a). Once on the open coast, larvae of some species complete larval development close to shore while larvae of other species are transported across the continental shelf (reviewed by Morgan 1995a, 2006; Epifanio and Garvine 2001; Queiroga and Blanton 2005). During this time, larvae encounter different physical conditions than in estuaries, and behavior may change resulting in interspecific differences in cross-shelf transport.

On upwelling coasts along the western margins of continents, wind stress from prevailing equatorward winds and Coriolis force drive near-surface waters offshore (Ekman transport) across the entire shelf while lowering sea level at the coast forcing upwelling of cold bottom waters near the shore (Kirincich et al. 2005). Coastline topography and shallow depths reduce offshore Ekman transport and diminish alongshore currents over the inner shelf (Lentz and Chapman 1989; Largier et al. 1993; Kaplan et al. 2005) and specifically in a coastal boundary layer (Nickols et al. 2012). Larvae of most species of benthic invertebrates complete development close to shore by remaining below the shallow Ekman layer or by undertaking a diel vertical migration, only rising into productive surface waters to forage at night when offshore flow is weakest (Marta-Almeida et al. 2006; Morgan et al. 2009b, 2012; Shanks and Shearman 2009; Morgan and Fisher 2010). Some of them may avoid being carried to the surface in upwelled waters and are trapped in an onshore flow convergence near the coast (Genin et al. 2005; Shanks and Brink 2005). Larvae of other species migrate farther onto the shelf by undertaking an ontogenetic vertical migration in which they spend more time in the Ekman layer early in development and return onshore by residing deeper in the water column late in development. Late-stage larvae also can return to shore by undertaking a reverse ontogenetic vertical migration by rising high in the water column, where internal waves or infrequent wind relaxations transport them shoreward (Shanks 1995; Poulin et al. 2002; Morgan et al. 2009a; Morgan and Fisher 2010).

There has been some progress understanding larval transport in low-inflow estuaries along upwelling coasts in Mediterranean and arid climates, where rainfall is insufficient to stratify estuaries during much of the year (Largier et al. 1997; Largier 2002). In these estuaries, which may be hypersaline or hyposaline (Largier 2010; Nidzieko and Monismith 2013), the density of water in the estuary is similar to that in the ocean, and tidal diffusion rather than two-layer "estuarine circulation" controls exchange between the estuary and open coast. Consequently, larvae may be less able to regulate depth and, hence, the rates and directions of transport. While reverse tidal vertical migration facilitates seaward transport of benthic crustacean larvae in several low-inflow estuaries, this behavior requires migration to the bottom boundary layer (very close to the seabed) and appears to be better defined in some estuaries and species than others (Queiroga et al. 1997; Pereira et al. 2000; DiBacco et al. 2001; Hsueh 2002; Breckenridge and Bollens 2011). Classic tidal vertical migrations facilitating larval retention have not been detected in low-inflow estuaries, and occupying bottom waters has been found only once (Pereira et al. 2000). Therefore, larval retention in low-inflow estuaries may occur primarily at the head of estuaries, where tidal exchange is weak and longer retention times are observed (Largier et al. 1997; Chadwick and Largier 1999; DiBacco and Chadwick 2001; DiBacco et al. 2001).

Here, we investigate behavioral–physical processes regulating larval transport between low-inflow estuaries and coastal waters. Specifically, we determined the effectiveness of larval behavior by benthic crustaceans in regulating larval transport between a low-inflow estuary and coastal waters. We hypothesize that previously documented larval behaviors in adjacent coastal waters may not be evident in the estuary due to tidal vertical mixing and turbulence in shallow water (Breckenridge and Bollens 2011; Kunze et al. 2013) or the lack of low salinity or pronounced salinity fluctuations to cue tidal vertical migrations (Miller and Morgan 2013a). Thus, we concurrently looked for vertical migrations in adjacent nearshore waters where salinity fluctuations are similar, but tidal flows and the strength of vertical mixing are weaker. Even so, all larval stages of species that are retained nearshore may still occur in low-inflow estuaries, because they are readily transported back and forth between the estuary and the adjacent nearshore waters over the tidal cycle. Hence, late larval stages of retained species should occur in the estuary, whether by passive transport alone or due to larval behavior. In contrast, only newly released larvae and recruiting postlarvae of species that develop offshore will occur in these estuaries.

Intensive physical and biological sampling over tidal and diel cycles is required to determine whether the horizontal and vertical distributions of larvae result from turbulent vertical mixing, passive advection, or behaviorally mediated migrations from the estuary to adjacent coastal waters. We repeatedly surveyed the larval assemblage of benthic crustaceans and physical conditions for 48 h on 29 to 31 March 2006 to determine (1) larval distributions along the axis of the estuary, (2) the flux of larvae between the estuary and coastal waters, and (3) the vertical distributions of larvae in the estuary and in adjacent coastal waters (Fig. 1a). The study was conducted when larvae of nearshore benthic crustaceans are developing in the plankton (Mace and Morgan 2006) and tidal amplitudes were equal during the daytime and nighttime to ensure similar tidal transport over the diel cycle (Hill 1991). The presence of all larval stages will indicate that larvae complete development nearshore, whereas the presence of first-stage larvae and postlarvae will indicate that larvae are released nearshore, developed offshore, and returned onshore to settle. The absence of depth preferences or vertical migrations will indicate that larvae are not effectively regulating depth in the estuary. A predominance of larvae during ebb tides at the mouth of the estuary will indicate net export from estuary to coastal waters, and conversely, a predominance of larvae during flood tides will indicate net import from the ocean.

Methods

Study System

The study was conducted in Bodega Harbor, CA, USA (38°19′22, 123°02′56), which is a small low-inflow estuary that connects to the nearshore waters of northern Bodega Bay through a dredged channel between a pair of jetties (Fig. 1). A non-armored, narrow channel occurs along the length of the estuary, between extensive intertidal mud flats and limited fringing saltmarsh. The water column is well mixed, and most of the water is exchanged over one tidal cycle, except near the head of the estuary where the tidal flow is about half that near the mouth (Largier et al. 1997; Rasmussen et al. 2004). Tides are mixed semidiurnal with a tidal range of 1.2–2.9 m.

The estuary discharges into Bodega Bay, which is an open bay facing southwest on the leeward side of a small headland. The bay mouth is approximately 11 km wide from the northern tip at Bodega Head to the southern tip at Tomales Point, and it is 20–25 m deep (Fig. 1a). Upwelling is active in the wind-exposed bay, where newly upwelled surface waters move equatorward and offshore (Roughan et al. 2005). Cyclonic recirculation occurs at depth in the lee of Bodega Head during upwelling conditions, yielding vertical shear along the shoreline (Roughan et al. 2005).

On the open coast outside of the bay, near-surface waters also flow equatorward and offshore over the shelf (Winant et al. 1987; Largier et al. 1993; Dever et al. 2006). The coastline topography and shallow depths reduce offshore Ekman transport (Kirincich et al. 2005) and slow alongshore currents (Largier et al. 1993; Kaplan et al. 2005) as well as cross-shore mixing in a coastal boundary layer (Nickols et al. 2012). Larvae are concentrated <10 km from shore (Morgan et al. 2009b). Equatorward winds blow roughly parallel to the coast, with maximum strength in the afternoon and minimum at night. Prevailing northwesterly winds weaken or reverse about every 4–10 days, and flows over the inner shelf reverse and stratify. After a few days of weak winds, one observes the arrival of low-salinity waters from the Gulf of Farallones that is influenced by San Francisco Bay outflow (Send et al. 1987; Largier et al. 1993; Wing et al. 2003; Roughan et al. 2006; Morgan et al. 2012).

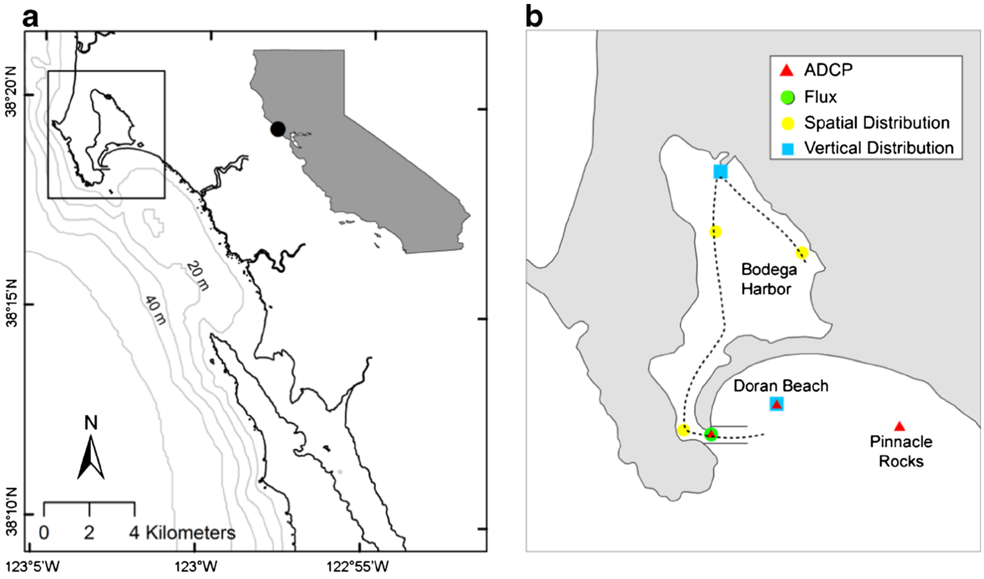


Fig. 1 Location of the study area. Locations of **a** Bodega Harbor and Bodega Bay, CA, USA and **b** acoustic Doppler current profilers and the three types of larval surveys from 29 to 31 March 2006. *Dashed line* represents the main axis of the channel

Moored Instruments

Vertical profiles of current velocity were measured continuously using three bottom-mounted acoustic Doppler current profilers (ADCP, RDI 1,200 kHz). ADCPs were deployed 0.25 m off the seabed in approximately 10 m of water at two sites in northern Bodega Bay (Doran Beach and Pinnacles Rocks) and the mouth of the estuary between the jetties in 5 m of water (Fig. 1b). We decided to locate two of the ADCPs in the bay, where flow is more complex and less well described than in the estuary, where our previous study had demonstrated that the water column is well mixed over tidal cycles throughout the estuary (Rasmussen et al. 2004).

Velocity data were obtained for 1- and 0.5-m depth bins at the two sites in Bodega Bay and at the entrance to the estuary, respectively. Velocity data were recorded as 3-min ensembles, and velocity ensembles were averaged hourly. In the bay, the "alongshore" component of flow was calculated at 31° and 325° north for Doran Beach and Pinnacle Rocks, respectively, as defined by the direction of the depth-averaged principal axis. Positive alongshore flow is poleward (negative equatorward) and positive cross-shore flow is onshore (negative offshore). In the estuary, an along-channel direction of 260° north was defined so that positive alongshore current velocities are landward, and negative alongshore current velocities are seaward. Data from 0.5 m above the instrument and from the top 10 % of the water column were omitted, as is routine for ADCP data to avoid noisy data near the instrument head and the reflection of side-lobe beams from the surface (Roughan et al. 2005). Tidal height was measured from the pressure sensor on the ADCP deployed at the entrance to the estuary.

Spatial Distribution in the Estuary

To determine whether larval retention or export occurred in the upper and lower reaches of the estuary, oblique plankton tows were taken during slack tides at three stations (head, middle, mouth) along the axis of the channel (Fig. 1b; spatial distribution). Two replicate samples were collected toward the end of each tidal cycle for the two daytime high tides and low tides and two nighttime high tides and low tides at each of the three sites for a total of 48 samples. Larvae were collected throughout the water column (0–6 m water depth) with a sled-mounted 0.5 m diameter ring that was fitted with a 335-μm mesh net. A flowmeter (General Oceanics model 2030) was mounted in the net opening to determine the volume of water sampled (30.2±6.2 m^3 SD). A three-way analysis of variance (ANOVA) was used to examine interspecific and ontogenetic differences in horizontal concentrations by tide, station, and diel cycle for each taxon and larval stage. Larval concentrations were transformed ($\mathrm{Log}_{10}\, x+1$) to meet assumptions of homogeneity of variances and normality, and Tukey's HSD multiple comparisons test revealed differences in concentrations among station, tide, and diel cycle.

Larval Abundance and Flux at the Mouth of the Estuary

Plankton was sampled continuously throughout the water column at the entrance to Bodega Harbor to determine larval abundance over tidal and diel cycles and the flux between the estuary and ocean (Fig. 1b; flux). Plankton was sampled by gradually raising a net from the bottom to the surface over 1-h intervals whereupon samples were collected. The plankton net consisted of a 0.5-m diameter ring fitted with a 335-μm mesh net and flowmeter (General Oceanics model 2030) to determine the volume of water sampled (150.5±120.0 m^3 SD). Based on the vertically uniform velocity (Fig. 2b) and negligible lateral gradients in velocity at the narrow entrance to the estuary (230 m), the instantaneous flux (number of larvae per second) of each larval stage and taxon was calculated by multiplying the hourly depth-averaged velocity (from the ADCP moored at the estuary entrance; meters per second) by the hourly depth-integrated larval concentration (number of larvae per cubic meter) and the tide-corrected cross-sectional area of the estuary entrance (square meter). Larval exchange for each taxon and larval stage was estimated for each tidal cycle ($n=3$ ebb and 3 flood) by integrating the hourly flux measurements from slack water through to the subsequent slack water for each tide. Net larval exchange is the sum of the average of the three larval exchange estimates for each species and larval stage (positive numbers indicate flux into the estuary and negative numbers indicate flux seaward). The first daytime flood and adjacent ebb tide were omitted from the exchange estimates because they did not represent a full 12-h semidiurnal cycle.

Depth Regulation in the Estuary and Bay

To determine the ability of larvae to regulate depth, the vertical distribution of larvae relative to water column structure was profiled hourly for 24 h with samples collected 1 m below the surface, at mid-depth, and bottom at stations in the middle of the estuary and bay on consecutive days (Fig. 1b; vertical distribution). Although it was beyond our means to sample the two sites simultaneously, they were sampled during consecutive days to minimize the effect of synoptic daily variability in physical conditions and larval abundances. The research vessel was double anchored to enable continuous physical and biological sampling of the passing water column over two tidal and one diel cycle at each site. Salinity and temperature were profiled using a CTD (Seabird Electronics SBE-19 Plus). A high-capacity centrifugal plankton pump and suction hose (7.6-cm diameter) were used to continuously sample larvae from the three depths. Each depth was sampled sequentially for 10 min (proceeding from the bottom to the top of the water column) yielding 6,000 L of water for each sample, which was

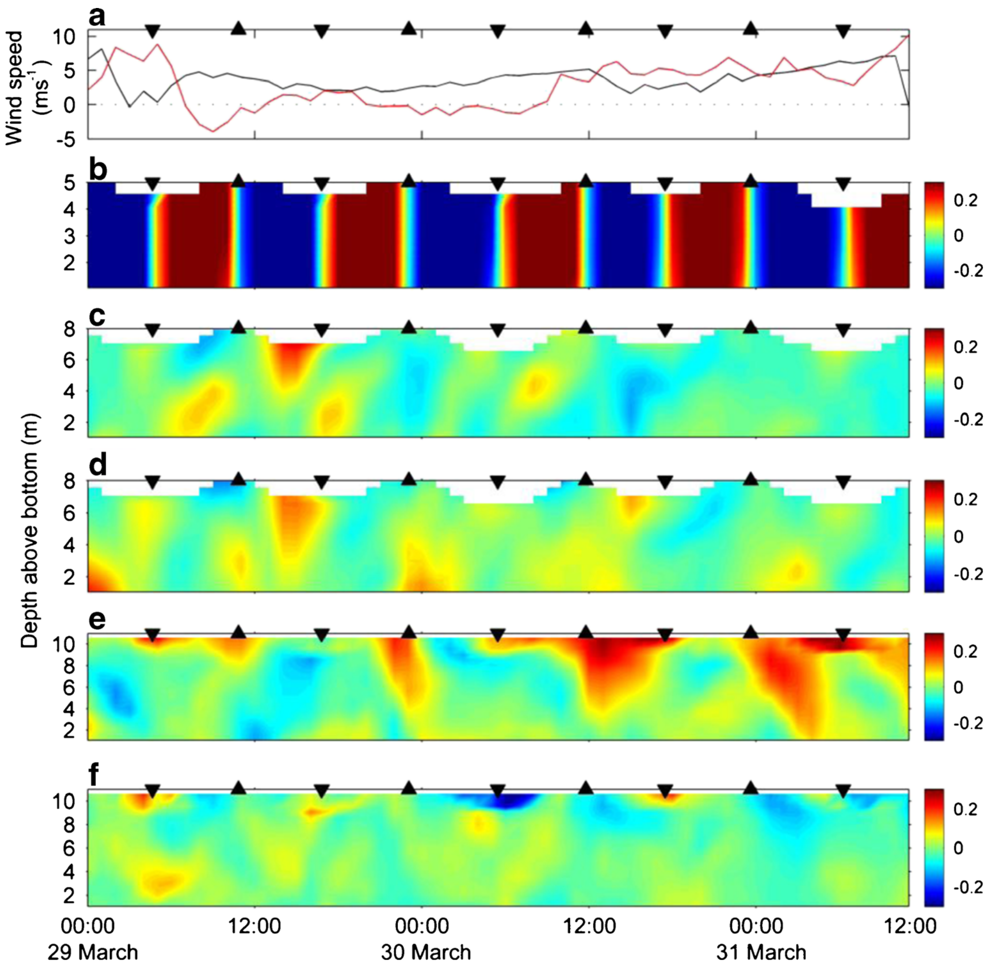


Fig. 2 Local winds and current velocity (meters per second) in the mouth of Bodega Harbor and two locations in Bodega Bay from 29 to 31 March 2006. **a** Wind velocity (meters per second)—alongshore wind (*black*) and cross-shore wind (*red*); **b** alongshore current velocity in 6 m of water in the mouth of Bodega Harbor; **c** alongshore; **d** cross-shore current velocity in 10 m of water off Doran Beach in Bodega Bay; and **e** alongshore and **f** cross-shore current velocity in 12 m of water off Pinnacle Rocks in Bodega Bay. Positive values of alongshore flow are poleward, and positive values of cross-shore flow are onshore. Data rotated to the depth averaged principal axis, and the uppermost 10 % of the water column was omitted. *Upward triangles* indicate high slack tide, and *downward triangles* indicate low slack tide

filtered through a series of two nets. A 1-cm mesh net excluded large organisms and debris, and a 335-μm net collected most larvae. A metal grate was attached beneath the opening of the intake hose so that larvae sampled at the bottom depth were sampled at the water–sediment interface without collecting sediment. Hoses were cleared by pumping for several minutes between samples.

A four-way ANOVA initially revealed whether larval concentrations differed by depth, larval stage, tidal phase, or diel phase and whether larvae undertook ontogenetic vertical migrations (stage × depth interaction), tidal vertical migrations (depth × tide interaction), or diel vertical migrations (depth × diel interaction). There were no significant interactions with larval stage so all stages were combined for further analysis in a three-way ANOVA. Larval concentrations were transformed ($\mathrm{Log}_{10}\,x+1$) to meet assumptions of homogeneity of variances and normality, and Tukey's HSD multiple comparisons test revealed differences in concentrations among depths.

Species Surveyed

Plankton samples were preserved with 70 % ethanol, and a Folsom plankton splitter was used to subdivide dense samples of larvae. Crustacean larvae were identified to species and stage when possible and counts were standardized to the volume of water sampled (numbers per cubic meter). The total number of larvae collected for each of the three types of larval surveys and the overall percent concentration for each species or taxon were determined. The concentrations of larval stages from all three types of larval surveys were used to indicate whether larvae of each species or taxon completed development nearshore or migrated farther offshore before recruiting onshore as postlarvae. We expected only first-stage larvae and postlarvae would be collected for species that develop offshore, whereas all larval stages would be collected for species that complete development nearshore.

Adults of the study species live within protected bays and estuaries as well as along the exposed coast, ranging from the intertidal zone (ghost shrimp *Neotrypaea californiensis*, barnacles, grapsids, pagurids, porcellanids) across the inner shelf (majids, pinnotherids) to the outer shelf (*Cancer* spp.; Morris et al. 1980). Larvae were identified to species when feasible. Two pairs of congeners were grouped after verifying that larval transport patterns were similar to simplify presentation: the barnacles *Balanus crenatus* and *Balanus glandula* and cancer crabs *Cancer magister* and *Cancer antennarius*.

Larval stages were combined to further simplify presentation after first verifying that transport patterns were similar, except for porcellanids and majids that have only early (I), late (II), and postlarval (megalopal) stages. Taxa that have six developmental stages (pinnotherids, grapsids, *Cancer* spp., *N. californiensis*) were grouped as early (I), mid (II–III), late (IV–V), and postlarva. Barnacles have seven stages and were grouped as early (I–III), mid (IV–V), late (VI), and postlarva (cyprid) stages. Early larval stages of barnacles were small enough to largely pass through the nets.

Results

Physical Conditions

The study was conducted when alongshore winds were poleward from 0 to 8 ms^{-1} (Fig. 2a). Poleward winds reached 8 ms^{-1} the first day, subsided until the evening of the second day, reaching 5 $\mathrm{m\,s}^{-1}$ during the night. Tidal current speed was similar throughout the well-mixed water column (Fig. 2b). Cross-channel flow was negligible at the narrow mouth of the estuary (data not shown). Off Doran Beach in Bodega Bay, subsurface flow was poleward and onshore during flood tide and equatorward and offshore during ebb tide (Fig. 3c, d). Surface flow generally was weak; however, it was strongly equatorward and offshore during one ebb tide and strongly poleward and onshore during a flood tide (Fig. 3c, d). Similar subsurface tidal currents occurred off Pinnacle Rock, but near-surface flow was primarily poleward and onshore due to southwesterly winds (Fig. 2a, c, d).

Tidal amplitude at the mouth of the estuary is shown in Fig. 3a. Rain (0.3 cm) occurred from 1,200 to 1,600 h on 29 March (Fig. 3b). Hourly profiles of temperature and salinity mid-estuary indicate that the whole water column was mixed by flood and ebb tides, and there was no evidence of density-driven vertical shear (estuarine circulation; Fig. 3c, e). Cold, relatively saline water from the estuary mixed from the bottom to the surface during ebb tide and warm, low-salinity water from outside the estuary mixed from the surface to near-bottom during the incoming tide, remaining inside the estuary partly through the following ebb tide (Fig. 3c, e). Surface salinity in the estuary was relatively low during most of the sampling period due to rainfall and runoff near the end of the wet season (Fig. 3b, e). Off Doran Beach in Bodega Bay, warm, low-salinity water occurred throughout the water column after the first low slack tide due either to local runoff from Bodega Harbor or from a small adjacent estuary (Estero Americano) or perhaps due to the arrival of water from the Gulf of the Farallones (Fig. 3d, f).

Ontogenetic Larval Distributions

We collected 23 taxa of crustacean larvae during the study (Table 1 and Supplementary Table S1). Two of them (pinnotherids and *N. californiensis*) accounted for 71.8 % of all larvae collected and combined with several more of them (*Balanus* spp., *Pagurus* spp., porcellanids, majids, *Hemigrapsus* spp., *Cancer* spp.) accounted for 96.9 % of all larvae collected and were used in statistical analyses. The relative abundance of larval stages indicated that pinnotherid and barnacle larvae released nearshore remained there

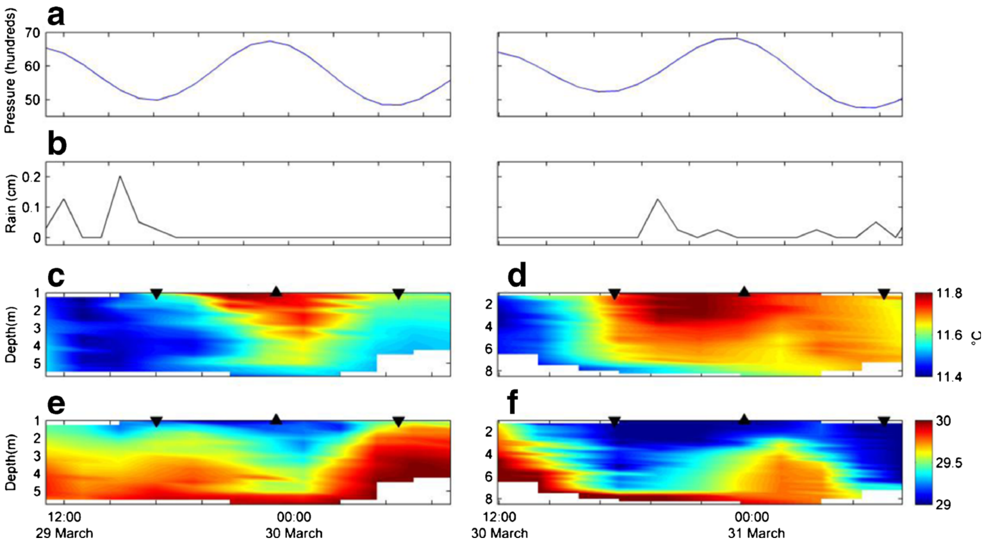


Fig. 3 Physical data for the head of Bodega Harbor and Doran Beach in Bodega Bay from 29 to 31 March 2006. **a** Tidal amplitude (ADCP); **b** rainfall (centimeter); temperature (degrees Celsius) contour in **c** Bodega Harbor and **d** off Doran Beach; and salinity contour in **e** Bodega Harbor and **f** off Doran Beach. Tidal amplitude recorded from the pressure from a moored ADCP at the entrance to Bodega Harbor, rainfall data recorded at Bodega Marine Laboratory, and temperature and salinity obtained from hourly CTD casts at the two sites. *Upward triangles* indicate high slack tide, and *downward triangles* indicate low slack tide

Table 1 Taxa of the most abundant crustacean larvae, number of larval stages, and total number of larvae (no. 100 m^{-3}) in oblique tows throughout Bodega Harbor (spatial distribution) and continuous oblique tows from the mouth of Bodega Harbor for 48 h from 29 to 31 March 2006 (flux), pumping at the surface, middle, and bottom of the water column (vertical distribution) at the head of Bodega Harbor (estuary) for 24 h from 29 to 30 March 2006 and off Doran Beach (bay) for 24 h from 30 to 31 March 2006 in Bodega Bay, CA and the overall percentage of larvae of all species for the entire study. See Supplementary Table S1 for additional taxa collected that were too few for statistical analysis

Taxa	Larval stage	Spatial distribution	Flux	Vertical distribution		% of total
		Estuary	Estuary	Estuary	Bay	
Balanus crenatus[a]	II–III	1,012	–	87	9	0.03
	IV–V	56,647	40,375	496	1,078	2.43
	VI	15,742	6,342	107	221	0.55
	PL	48,55	10,098	86	172	0.37
Balanus glandula[a]	IV–V	64,713	166,089	882	581	5.72
	VI	15,221	8,370	217	632	0.60
	PL	1,960	1,687	40	41	0.09
Neotrypaea californiensis	I	127,686	853,612	794	480	24.20
Pagurus spp.	I	3,889	7,961	31	41	0.29
	II	253	–	–	–	0.01
	PL	–	25	–	–	0.00
Porcellanidae	Prezoea	–	868	–	–	0.02
	I	13,114	96,898	30	29	2.71
Pinnotheridae	I	569,043	1,144,730	14,170	14,000	42.90
	II	32,018	136,693	717	1,278	4.20
	III	5,694	6,352	130	449	0.31
	IV	1,236	3,603	11	83	0.12
	VI	449	–	4	22	0.01
	PL	232	–	–	8	0.01
Majidae	I	7,171	80,812	99	23	2.17
Hemigrapsus spp.	I	27,159	30,334	605	75	1.43
	II	272	–	–	–	0.01
	PL	–	–	–	4	0.00
Cancer antennarius[a]	I	94,052	107,129	1,077	360	4.99
Cancer magister[a]	I	55,241	94,831	514	37	3.71

[a] Taxa combined for statistical analysis

throughout development (Table 1). All larval stages of pinnotherids were common in the estuary and bay, indicating nearshore retention, but the drop in concentration of second stage larvae followed by a gradual decline in subsequent stages in both the estuary and bay indicates substantial seaward transport or mortality of first-stage larvae. Although most early larval stages of barnacles passed through our nets, later stages occurred in high concentrations indicating nearshore larval development (except only cyprids of *Semibalanus cariosus* were present). Larvae of the remaining taxa of *N. californiensis*, *Emerita analoga*, *Pagurus* spp., porcellanids, *Hemigrapsus* spp., *Pachygrapsus crassipes*, majids, *Cancer* spp., *Carcinus maenas*, and *Lophopanopeus bellus* were abundant at the study site as first-stage larvae and later stages were absent or uncommon, indicating that larvae were transported offshore.

Larval Distributions over Tidal and Diel Cycles

Spatial Distributions in the Estuary Of the taxa that completed development nearshore, early and mid-stage barnacle nauplii were most abundant during ebb tides, and cyprids tended to be most abundant on flood tides, indicating initial seaward transport of nauplii and landward transport of recruiting cyprids (Fig. 4, Table 2a, and Supplementary Table S2). The last naupliar stage of barnacles (VI) was more abundant on ebb tides during the day. Early stages (I–III) of pinnotherids were most abundant in the upper estuary and first-stage larvae tended ($p=0.05$) to be more abundant on ebb tides, indicating abundant larval release in the inner estuary and seaward transport. The remaining larval stages were present during both tidal phases throughout the day, indicating a well-mixed larval population in the estuary and bay, no longer

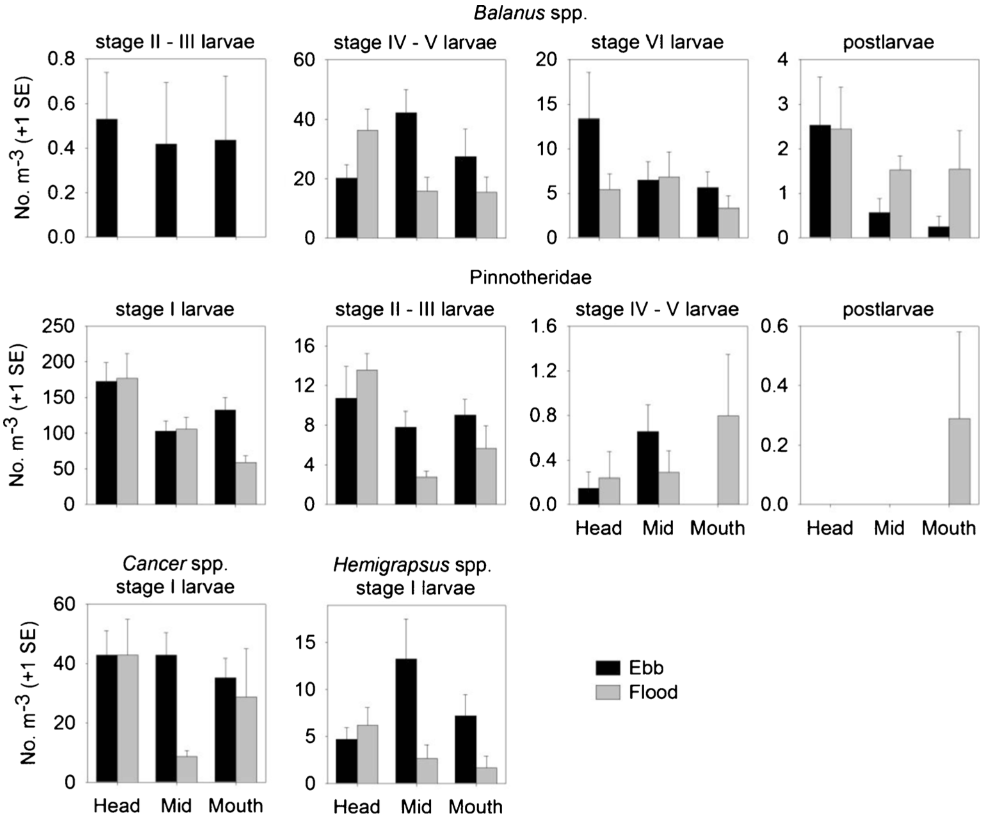


Fig. 4 Abundance (no. cubic meter +1 SE) of four taxa of crustacean larvae collected during ebb and flood tides at the head, middle, and mouth of Bodega Harbor for 48 h from 29 to 31 March 2006

influenced by the spatial pattern of larval release. Postlarvae were collected only during nocturnal flood tides at the mouth of the estuary, indicating recruitment back into the estuary. Of the taxa that were prevalent only as first-stage larvae, *Cancer* spp. and grapsids were most abundant on ebb tides and the rest (*Pagurus* spp., majids, porcellanids, and *N. californiensis*) were most abundant at night (82.1 % of *N. californiensis*, 97.2 % of porcellanids, 80.0 % of majids, and 71.7 % of *Pagurus* spp.), indicating seaward transport and nocturnal larval release.

Abundance and Flux at the Mouth of the Estuary At the mouth of the estuary, most taxa were more abundant on ebb than flood tides (Fig. 5), indicating an estuarine source of larvae. First-stage larvae typically were most abundant during nocturnal ebb tides (Fig. 5), indicating peak larval release occurred at night with seaward transport. Larvae of *N. californiensis*, *Cancer* spp., *Hemigrapsus* spp., and porcellanids were almost solely collected during ebb tides resulting in rapid export from the estuary (Fig. 6 and Table 3). However, all stages of barnacles and pinnotherids and first-stage *Pagurus* spp. were common on both ebb and flood tides (Fig. 5), indicating that larvae were released in both the estuary and bay, or were released in the estuary and exchanged between the estuary and bay, with a net exchange into the estuary over a semidiurnal tidal cycle (Fig. 6 and Table 3).

Vertical Distribution in the Estuary and Bay Only two taxa appeared to regulate depth in the estuary (Fig. 7, Table 2b, and Supplementary Table S3). Barnacle larvae were most abundant in the upper water column. In contrast, pinnotherids were most abundant near the bottom on nocturnal ebb tides and at the surface during the daytime and flood tides, perhaps suggesting little net displacement. Strong depth preferences and tidal, diel, and ontogenetic vertical migrations were not evident (nonsignificant depth interactions) for other taxa, but the abundance of some taxa differed over tidal and diel cycles. All stages of pinnotherid and early stage *Hemigrapsus* spp. larvae were most abundant on flood tides, all stages of barnacle and pinnotherid larvae were most abundant during the daytime, and early stage porcellanid larvae were only present during daytime flood and nighttime ebb tides.

There was stronger evidence of depth regulation in the bay than the estuary (Fig. 8, Table 2b and Supplementary Table S3). All stages of both barnacles and pinnotherids were most abundant at the bottom, but there was no clear evidence of tidal, diel, or ontogenetic vertical migrations (nonsignificant depth interactions). First-stage *Cancer* spp. larvae were most abundant during nocturnal ebb tides at the bottom ($T\times Z\times D$). First-stage *N. californiensis* larvae were most abundant at the bottom during flood tides ($T\times Z$), perhaps indicating reverse tidal vertical migration. First-stage majid larvae did not appear to regulate depth and were more abundant on flood than ebb tides.

Table 2 Summary results from a three-way analysis of variance for abundant taxa of crustacean larvae in (A) oblique tows throughout Bodega Harbor for 48 h from 29 to 31 March 2006 and (B) pumping at the surface, middle, and bottom of the water column at the head of Bodega Harbor and off Doran Beach in Bodega Bay, CA for 24 h each from 29 to 30 and 30–31 March 2006. Capital letters indicate significant differences with A being greater than B. See Supplementary Table S2 for statistical details

A

Taxa	Larval stage(s)	Tide (T) p value	Ebb	Flood	Station p value	Head	Mid	Mouth	Diel (D) p value	Day	Night	$T\times D$ p value
Spatial distribution												
Balanus spp.	II–III	0.001	A	B	ns	ns			ns	ns		ns
	IV–V	0.02	A	B	ns	ns			ns	ns		ns
	VI	ns	ns		ns	ns			ns	ns		0.02
	PL	ns	ns		ns	ns			ns	ns		ns
Pinnotheridae	I	0.05	A	B	0.003	A	B	B	ns	ns		ns
	II–III	ns	ns		ns	ns			ns	ns		ns
	IV–V	ns	ns		ns	ns			ns	ns		ns
	PL	ns	ns		ns	ns			ns	ns		ns
Cancer spp.	I	0.02	A	B	ns	ns			ns	ns		ns
Hemigrapsus spp.	I	0.005	A	B	ns	ns			ns	ns		ns

B

Taxa	Larval stage(s)	Tide (T) p value	Ebb	Flood	Depth (Z) p value	Surface	Mid	Bottom	Diel (D) p value	Day	Night	$T\times Z$ p value	$Z\times D$ p value	$T\times Z\times D$ p value
Vertical distribution														
Bodega Harbor														
Balanus spp.	II–PL	ns	ns		0.05	A	AB	B	0.003	A	B	ns	ns	ns
Pinnotheridae	I–V	0.003	B	A	0.006	AB	B	A	0.03	A	B	<0.001	0.03	ns
Porcellanidae	I	ns	ns		ns	ns			ns	ns		ns	ns	ns
Hemigrapsus spp.	I	0.01	B	A	ns	ns			ns	ns		ns	ns	ns
Bodega Bay														
Balanus spp.	II–PL	0.06	ns		0.04	B	B	A	0.09	ns		ns	ns	ns
Pinnotheridae	I–V	ns	ns		<0.001	B	B	A	ns	ns		ns	ns	ns
Cancer spp.	I	ns	ns		ns	ns			ns	ns		<0.001	0.006	0.05
Majidae	I	0.04	B	A	0.07	ns			0.07	ns		ns	ns	ns
Neotrypaea californiensis	I	ns	ns		ns	ns			ns	ns		0.001	ns	ns

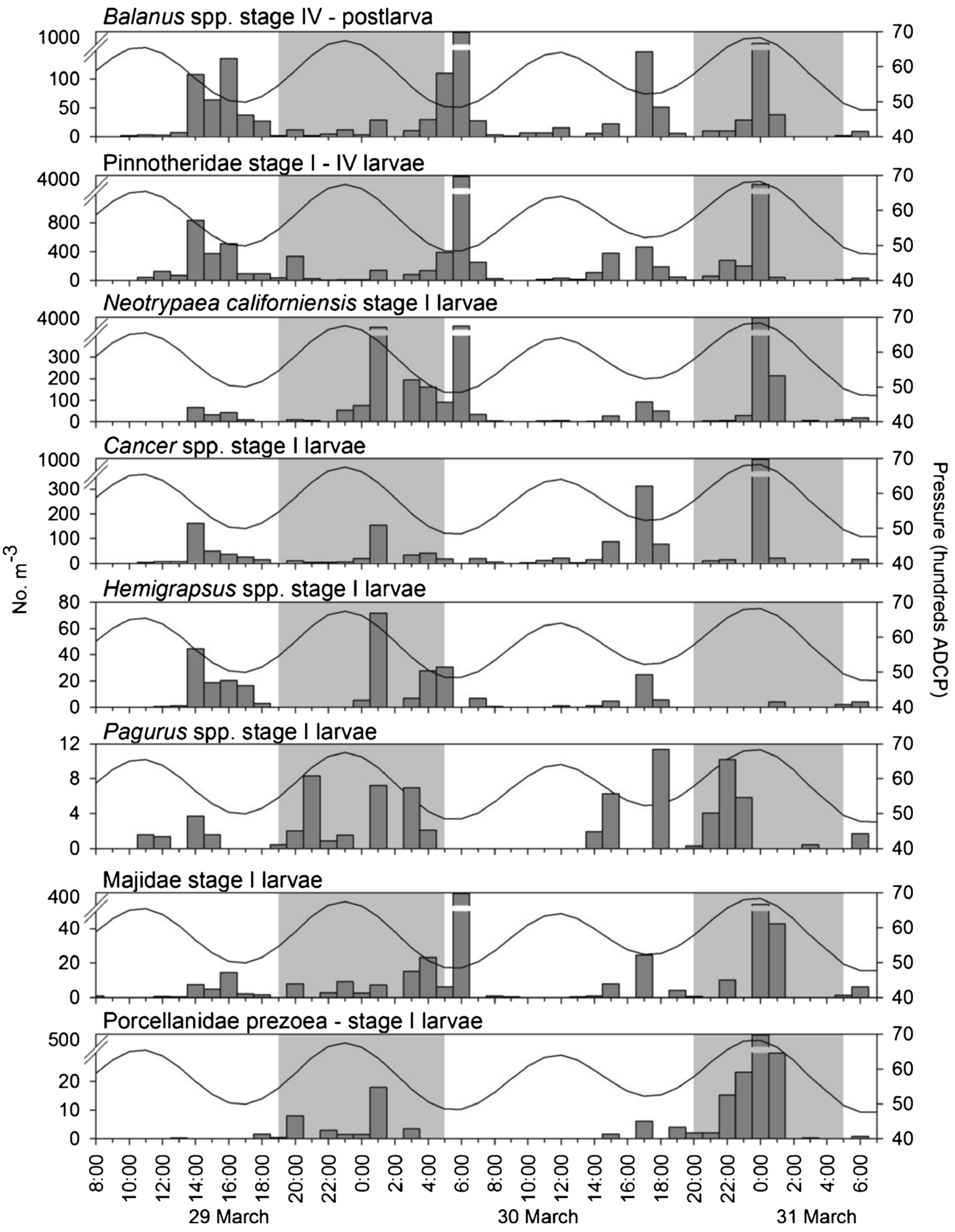
Discussion

The prevalence of all larval stages of barnacles and pinnotherids in the estuary and bay indicated that planktonic development of these species was completed nearshore in March 2006. In contrast, the remaining taxa were prevalent only as first-stage larvae and postlarvae indicating that planktonic development was completed farther from shore. These interspecific differences in cross-shelf migrations have been documented during our concurrent and previous cross-shelf surveys in the study area (Morgan et al. 2009a, b, 2011a, 2012; Morgan and Fisher 2010) and elsewhere along the west coast of the USA (Lough 1974; Shanks and Shearman 2009).

We found evidence of behavior that regulates interspecific differences in larval transport in the estuary with larvae of two taxa regulating depth. Barnacle and pinnotherid larvae both exhibited depth preferences, but previously described diel vertical migrations in coastal waters were not evident in the estuary (Morgan and Fisher 2010). Depth preferences as well as diel and ontogenetic vertical migrations that have been previously documented seaward of the estuary for other species (Morgan et al. 2009b, 2012; Morgan and Fisher 2010) were not detected in the estuary. Selective tidal stream transport was not evident either, even though reverse tidal vertical migrations have been reported for several species in other low-inflow estuaries (Queiroga et al. 1997; Pereira et al. 2000; Hsueh 2002; Breckenridge and Bollens 2011), including one of our study species (*P. crassipes*) in San Diego Bay (DiBacco et al. 2001).

In addition to barnacle and pinnotherid larvae, two other taxa regulated depth in the bay even though they did not do so in the estuary. *Cancer* spp. appeared to undertake diel vertical migrations, whereas *N. californiensis* appeared to undertake reverse tidal vertical migrations. Previously, larvae of both

Fig. 5 Abundance (no. cubic meter +1 SE) of eight taxa of crustacean larvae collected hourly for 48 h at the mouth of Bodega Harbor relative to tidal height and diel cycle from 29 to 31 March 2006. Tides displayed as changes in pressure from the moored ADCP and darkness shaded



taxa were found to undertake diel vertical migrations in this region (Morgan and Fisher 2010; Morgan et al. 2012).

It is unlikely that our sampling design failed to detect vertical migrations that were occurring in the estuary, because sampling spanned the water column, including the sediment–water interface. We suggest that vertical mixing in the shallow tidal estuary could have disrupted depth regulation by larvae of these species. As discussed by others (Durham et al. 2009; Hoecker-Martínez and Smyth 2012), the vorticity in strong turbulence may prevent plankton from orienting, thereby overwhelming their ability to navigate even if the turbulent velocities do not overwhelm swimming speeds. In contrast, larvae appeared to undertake tidal vertical migrations in the bay where velocity gradients were apparent. An alternative explanation for the absence of vertical migrations in this low-inflow estuary is that the weak salinity signal was inadequate to cue behavior (Rasmussen et al. 2004; Miller and Morgan 2013a).

Other species (*P. crassipes*, *Hemigrapsus oregonensis*, *Petrolisthes cinctipes*) either do not undertake tidal vertical migrations or may only do so when a low-salinity signal is present, because a complementary laboratory study did not detect endogenous tidal vertical migrations for these species in uniformly mixed seawater (Miller and Morgan 2013b). However, an endogenous reverse tidal vertical migration by larvae was apparent for one of these species (*H. oregonensis*)

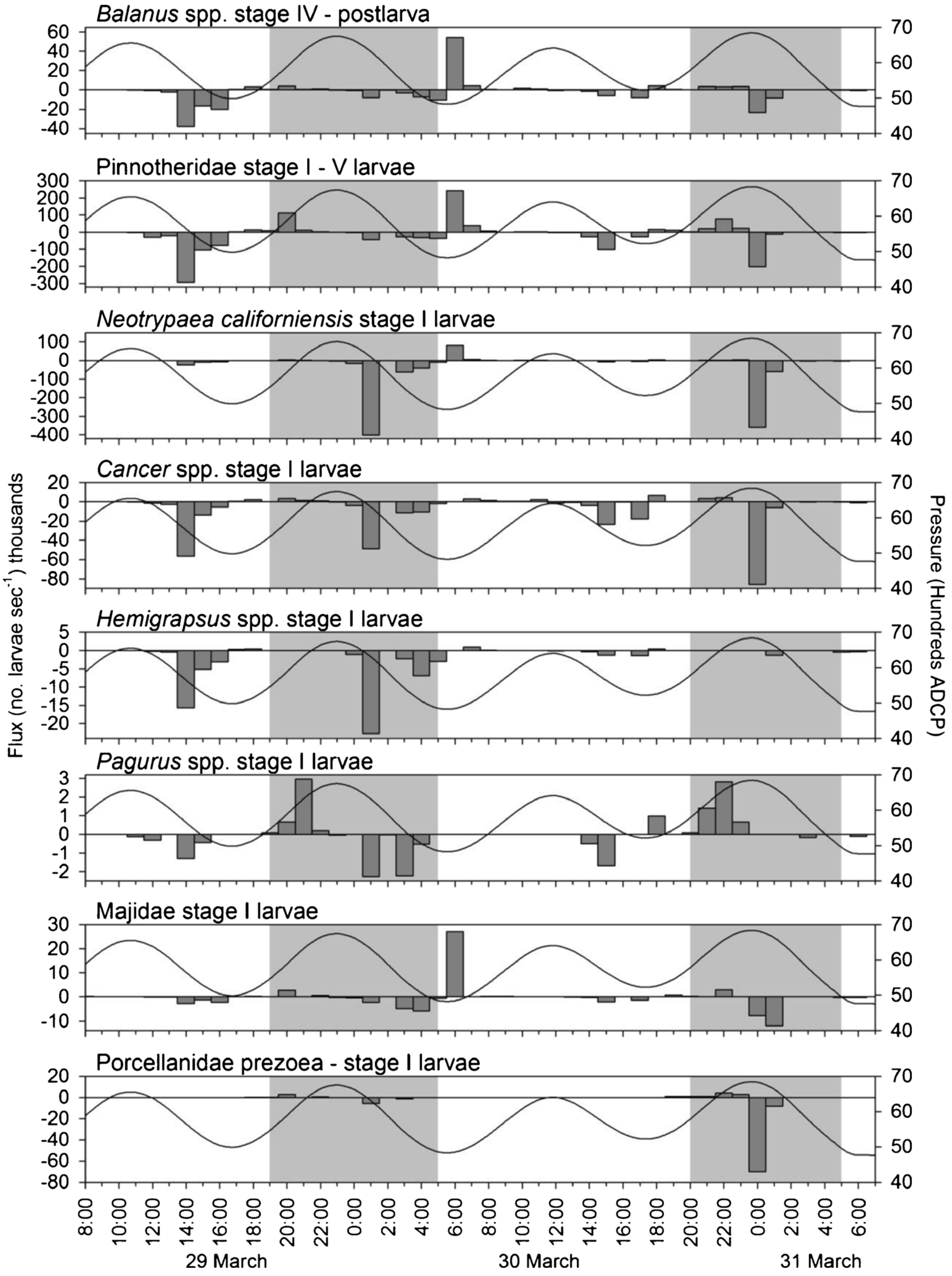


Fig. 6 Larval flux (no. per second) of eight taxa of crustacean larvae collected hourly for 48 h at the mouth of Bodega Harbor relative to tidal height and diel cycle from 29 to 31 March 2006. *Negative and positive values* represent larvae leaving and entering the estuary, respectively. Tides displayed as changes in pressure from the moored ADCP and darkness shaded

in neighboring San Francisco Bay (Miller and Morgan 2013a), where low-salinity water may cue the endogenous tidal rhythm.

Barnacle and pinnotherid larvae complete development in nearshore coastal waters by either remaining below the shallow Ekman layer throughout development (barnacles) or rising to the surface at night after winds have subsided (pinnotherids; Morgan et al. 2009a, b; Morgan et al. 2011a; Morgan et al. 2012; Morgan and Fisher 2010). By remaining nearshore, larvae can persist in low-inflow estuaries even in the absence of effective depth regulation in the estuary itself (Morgan et al. 2009a, b, 2011a, 2012; Shanks and Shearman 2009; Morgan and Fisher 2010). Larvae were exchanged between the estuary and bay over tidal cycles; they were transported from the estuary during ebb tides and transported back into the estuary during flood tides with an overall net exchange into the estuary. Longitudinal tidal exchange is slow in the upper estuary, as is typical for low-inflow estuaries (Largier et al. 1997; Chadwick and Largier 1999; DiBacco and Chadwick 2001; Rasmussen et al. 2004), enhancing retention of at least early stage pinnotherid larvae during our study. Successive later larval stages became increasingly less abundant as more larvae were advected to coastal waters or more larvae died during development.

Table 3 Mean larval exchange (no. larvae ±1 SE) of abundant taxa at the mouth of Bodega Harbor across tidal cycles. Larval exchange calculated by integrating larval flux from hourly plankton tows across each tidal cycle. Mean and SE calculated from observations of three tidal cycles. Net larval exchange over a complete semidiurnal tidal cycle (no. larvae) and the percent net exchange into or out of the estuary for each taxon. Positive numbers indicate larval flux into the estuary, and negative numbers indicate larval flux seaward

Taxa	Larval stage(s)	Larval exchange (± 1 SE)		Net larval exchange	
		Ebb	Flood	No. larvae semidiurnal cycle^{-1}	% of larval exchange
Balanus spp.	IV–PL	-2.6×10^4 (4.9×10^3)	2.9×10^4 (1.7×10^4)	3.1×10^3	10.6
Pinnotheridae	I–V	-1.8×10^5 (2.3×10^4)	2.0×10^5 (4.9×10^4)	2.3×10^4	11.6
Neotrypaea californiensis	I	-3.2×10^5 (1.6×10^5)	3.5×10^4 (2.7×10^4)	-2.9×10^5	89.0
Cancer spp.	I	-7.2×10^4 (1.3×10^4)	1.0×10^4 (2.2×10^3)	-6.2×10^4	85.6
Hemigrapsus spp.	I	-1.4×10^4 (1.1×10^4)	8.9×10^2 (1.9×10^2)	-1.3×10^4	93.4
Pagurus spp.	I	-2.5×10^3 (1.4×10^3)	3.3×10^3 (1.7×10^3)	7.9×10^2	24.1
Majidae	I	-1.3×10^4 (4.8×10^3)	1.2×10^4 (7.9×10^3)	-1.1×10^3	8.7
Porcellanidae	Prezoea–I	-2.9×10^4 (2.5×10^4)	4.2×10^3 (2.6×10^3)	-2.5×10^4	85.3

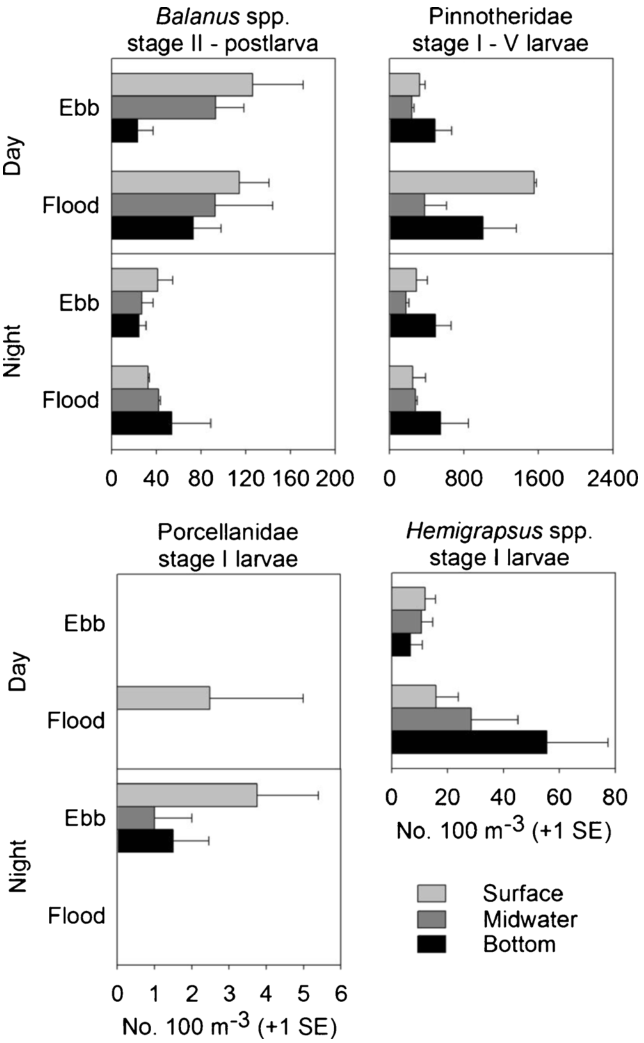


Fig. 7 Abundance of four taxa of crustacean larvae collected hourly at the surface, middle, and bottom of the water column in Bodega Harbor for 24 h from 29 to 30 March 2006. Taxa without vertical or diel patterns are not shown

Later larval stages of the remaining species were absent or rare during our study, indicating that these larvae were transported away from the estuary entrance and adjacent coastal waters. It is unlikely that late-stage larvae were missed during this 48-h study, because these same patterns have been documented in previous studies (Lough 1974; Morgan et al. 2009a, b, 2011a, 2012; Morgan and Fisher 2010). It is more likely that these species were passively transported from the estuary into the bay, and seaward transport was expedited by the release of larvae on ebb tides, especially at night (Morgan 1995b; Hovel and Morgan 1997; Pereira et al. 2000; Thurman

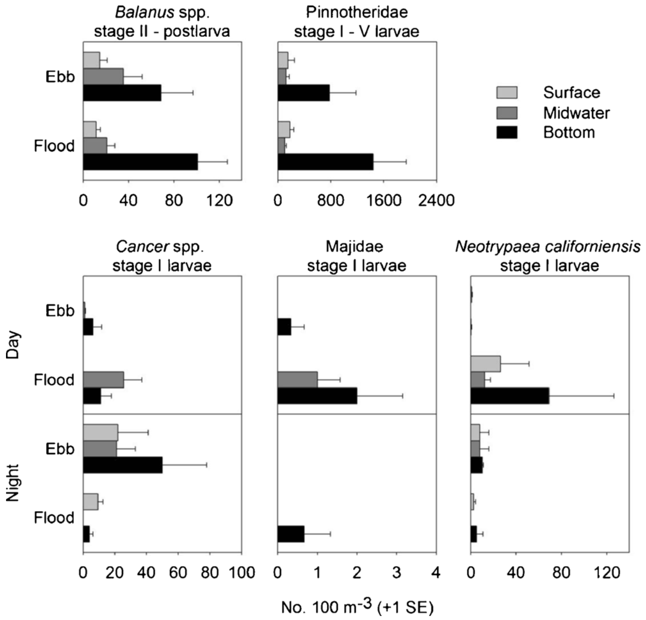


Fig. 8 Abundance of five taxa of crustacean larvae collected hourly at the surface, middle, and bottom of the water column off Doran Beach in Bodega Bay for 24 h from 30 to 31 March 2006. Daytime and nighttime tides combined for *Balanus* spp. and Pinnotheridae. Taxa without vertical or diel patterns are not shown

2004; López-Duarte et al. 2011; Morgan et al. 2011b). Once in the bay, larvae may escape the deep recirculation feature and retention in the bay by rising into surface waters (Roughan et al. 2005; Mace and Morgan 2006; Morgan et al. 2011a, 2012), transporting them onto the open coast (Morgan et al. 2009a, b; Morgan and Fisher 2010). A companion study revealed that later larval stages of some species occurred farther offshore rather than nearshore (Morgan et al. 2009a, b), precluding transport back into the estuary by flood tides. Furthermore, the limited withdrawal zone for tidal flows from the bay into the estuary reduces the likelihood of flood tide reentry of larvae that are not retained in the northernmost part of the bay. Postlarvae of these species may have been uncommon, because recruitment is low in March (Mace and Morgan 2006).

In the bay, a lens of lower salinity water may have suppressed diel vertical migrations by crab larvae, except *Cancer* spp. larvae, as previously observed in our study area (Morgan et al. 2012). In both studies, the vertical distributions of larvae were affected by a small vertical gradient in salinity (<1). Larvae were uncommon near the surface at night, even though most species of crab larvae undertake diel vertical migrations (Morgan and Fisher 2010; Morgan et al. 2012). The warm, low-salinity water may have originated from local runoff (e.g., Estero Americano) or from San Francisco Bay, being transported to the study area during downwelling winds (Send et al. 1987; Wing et al. 2003; Morgan et al. 2009b, 2012). Barnacle and pinnotherid larvae do not undertake diel vertical migration and remain deep throughout the day even in the absence of low-salinity water (Morgan et al. 2009b, 2011a, 2012; Morgan and Fisher 2010).

Our results may be broadly applicable to coastal upwelling systems along the western margins of continents and in Mediterranean climates where small, shallow, low-inflow estuaries are common (Largier 2002). Furthermore, our results should be equally applicable to estuaries that discharge along an open coast in upwelling regions (rather than bays), because the same interspecific differences in larval transport occur on the open coast as we found in the bay (Lough 1974; Morgan et al. 2009b, 2011a; Morgan and Fisher 2010). Similar low-inflow estuary–bay–ocean configurations are common elsewhere. For example, Elkhorn Slough connects to the open ocean through Monterey Bay and Estero Punta Banda in Baja California connects through Todos Santos Bay; other examples are Morro Bay and San Quentin Bay. Our results likely do not apply to large, deeper estuaries where the water column may be stratified or partially stratified, rather than well mixed, and where there is more freshwater inflow. For example, depth regulation by larvae appears to be well expressed in thermally stratified San Diego Bay (e.g., DiBacco et al. 2001) and thermohaline-stratified San Francisco Bay (e.g., Bennett et al. 2002).

In conclusion, larvae cross hydrodynamic regimes during their migrations between nearshore adult habitats and larval nursery areas spanning different distances across the nearshore seascape and continental shelf, raising the question of how attuned larval behavior is to each regime. In our study estuary, only two taxa displayed depth preferences by primarily occurring in the lower water column, and none of them migrated vertically in response to tidal or diel cues. These depth preferences may have contributed to the presence of all larval stages in the estuary and a net influx of larvae into the estuary. However, passive tidal exchange of larvae between the estuary and coastal waters alone may also account for the presence of late larval stages of these species, because larvae are retained nearshore by remaining below the Ekman layer in open bays and coastal waters (Morgan et al. 2009a, 2011a; Shanks and Shearman 2009; Morgan and Fisher 2010). Only first-stage larvae of the other species occurred in the estuary, because they were common in the upper half of the water column once in the bay and coastal waters, where they were exposed to offshore advection. Larval release during nocturnal ebb tides enhances seaward transport of these species at the start of their offshore migration.

In contrast, four taxa maintained depth or undertook diel or reverse tidal vertical migrations in the bay, as had been previously documented for many taxa of benthic crustaceans on the open coast in this region (Morgan et al. 2009a, 2012; Morgan and Fisher 2010). The contrast between behavior in adjacent bay and estuary waters suggests that vertical mixing and turbulence by tidal flows in the estuary may have overwhelmed larval behaviors of many species (except those that remain in the lower water column). Alternatively, low freshwater inflow into the estuary may not have cued reverse tidal vertical migrations, while the lower salinity water of the bay did so for taxa that develop offshore. The absence of low-salinity water is typical in low-inflow estuaries from late spring to fall along the West Coast, and the effects of turbulence and the lack of a low-salinity cue on larval depth regulation should be examined. If turbulent mixing is important in disrupting vertical migrations, then (1) weakly swimming ciliated larvae, such as mollusks and echinoderms, should be even less able to regulate depth effectively while stronger swimming fish larvae should be better able to do so (Kunze et al. 2013) and (2) larvae should be better able to regulate depth in deeper well-mixed estuaries. If freshwater inflow and lower salinity is important, then tidal vertical migrations should occur in estuaries with substantial freshwater inflow, but not in low-flow estuaries when larvae are abundant, regardless of estuary depth. Comparing taxa among estuaries with different depths and freshwater inputs may reveal why larval behavior is more apparent in some taxa and in some estuaries along upwelling coasts.

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