

# Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange

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**ABSTRACT:** Rhythmic vertical migration has been well documented as a behavioral mechanism of brachyuran larvae that are actively exported from or retained within estuaries with net tidal residual flows, such as partially mixed estuaries. However, the effectiveness of vertical migratory behavior in mediating net larval transport in a low-inflow estuary (LIE), which is characterized by little or no freshwater inflow for extended periods of time, has not been addressed. Larval transport hypotheses, developed using a validated hydrodynamic model of San Diego Bay (SDB; an LIE), predicted that vertical migratory behavior was necessary to transport larvae out of the bay, while larvae lacking vertical migratory behavior would be retained within the bay. These predictions were tested in a field study that examined the temporal and spatial (vertical and horizontal) distribution of 2 brachyuran families, *Pachygrapsus crassipes* (Grapsidae) and *Lophopanopeus* spp. (Panopeidae), sampled at 2 sites within SDB. *P. crassipes* zoeae exhibited vertical migratory behavior, which enhanced their net export from the bay. Stage I *P. crassipes* zoeae were concentrated in surface layers (0 to 2 m) during nocturnal ebb tides, but exploited low-velocity conditions associated with the benthic-boundary layer, which retarded transport back into the bay during flood tide. The lack of Post-Stage I *P. crassipes* zoeae within SDB suggests that the observed vertical migratory behavior was an effective means for exiting the bay. Stage I and Post-Stage I *Lophopanopeus* spp. larvae were sampled within SDB, but exhibited no clear rhythmic migration patterns. The lack of vertical migratory behavior and the presence of all larval stages of development suggest that *Lophopanopeus* spp. larvae were retained within the bay throughout meroplanktonic development. Heterogeneous horizontal distributions of Stage I *P. crassipes* and *Lophopanopeus* spp. zoeae reflect hatching sites and physical circulation features which concentrate larvae at specific areas. Differences in larval behavior observed for grapsid and panopeid larvae in SDB had a significant effect on their dispersal and retention.

**KEY WORDS:** Larval behavior · Selective tidal stream transport · Low-inflow estuary · Vertical migration · Zoeae · Larvae · Numerical simulations · San Diego Bay · *Pachygrapsus crassipes* · *Lophopanopeus* spp.

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## INTRODUCTION

The majority of marine benthic invertebrates have 1 or more planktonic larval stages of development (mero-

plankton) that may act as an agent for increased dispersal and gene flow between sessile or sedentary adult populations (McConaugha 1992, Levin & Bridges 1995). Studies of meroplankton spawned within estuaries have revealed species that are retained throughout larval development until ready to settle and recruit to local adult populations (Cronin 1982). The larvae of other taxa are exported to open coastal waters, where

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they develop prior to reentering estuaries and recruiting to adult populations (Christy 1982). The coupling of vertical migration by larvae with differential horizontal advection associated with tidal phase, termed selective tidal stream transport, can mediate the horizontal distribution and dispersal of planktonic larvae (Epifanio 1988, McConaugha 1988). Bousfield (1955) recognized that vertical movements out of seaward-moving water layers could facilitate larval retention within an estuary. Vertical migratory behavior has been well documented in decapod larvae (recent studies include Paula 1989, Queiroga et al. 1994, 1997, Lochmann et al. 1995, Rodriguez et al. 1997, Garrison 1999). These studies have characterized the temporal and spatial (usually vertical) distribution of larvae to understand and predict transport within estuaries and between estuaries and the nearshore coastal environment.

The studies cited above were conducted in estuaries where freshwater input results in significant non-tidal residual flows and a net flux of water from the bay (partially mixed estuary) (Pritchard 1952, Dyer 1997). San Diego Bay (SDB) is representative of 'low-inflow estuaries' (LIE), where freshwater input is negligible or absent for extended periods of time (Largier et al. 1996, 1997). In these estuaries, buoyancy fluxes are dominated by air-water interactions, with a positive buoyancy flux due to heating and a negative buoyancy flux due to evaporation. The resultant buoyancy flux is often too weak to bring about vertical stratification, and instead of density-driven circulation the exchange of water with the nearshore coastal environment is tidally driven. This difference may influence the net transport of marine invertebrate larvae. For example, while uniformly distributed pelagic larvae will experience a net flux out of bays characterized by significant freshwater input due to non-tidal residual flows, the same larvae would experience significantly longer residence times within an LIE. We hypothesize that species that export their larvae into coastal waters during planktonic development will exploit tidally induced currents in LIE rather than rely on downstream residual flows that are weak or absent. Conversely, we hypothesize that species which retain their larvae within embayments may not require any vertical migratory behavior to achieve retention within LIE waters having long residence times (e.g., SDB). Differences in physical transport processes within partially mixed and low-inflow estuaries may influence the dispersal and exchange of planktonic larvae; however, such comparisons have never been made.

This study examines these larval transport hypotheses, developed using a hydrodynamic model of SDB, with field observations that characterize temporal and spatial (vertical and horizontal) distribution patterns of brachyuran larvae over tidal and diel cycles in SDB.

Field observations and model simulations are used to evaluate the influence of temporal changes in the vertical and horizontal distribution of larvae on their retention and dispersal within SDB and between the bay and coastal waters. This study represents one of a few that have sampled the sediment-water interface while considering the vertical distribution of meroplankton (see also Prytherch 1928, Carriker 1951). We have established the presence of zoeae on the bottom during critical phases of the tide, which has implications for larval behavior on net transport.

## MATERIALS AND METHODS

**Study area.** This study was conducted in San Diego Bay ( $32^{\circ} 40' N$ ,  $117^{\circ} 10' W$ ; Fig. 1), a crescent-shaped embayment approximately 25 km long. The outer half of the bay averages 1 to 2 km in width, while the inner bay is 2 to 4 km wide. Bay and ocean waters are exchanged through a single channel, which averages 1 to 2 km in width and is 10 to 15 m deep. The inner portion of the bay is about 12 m deep in the dredged shipping channel and 1 to 4 m deep elsewhere. Tides in SDB are mixed diurnal/semidiurnal, with a dominant semidiurnal component (Peeling 1974). Spring high tides consistently occur early in the evening following dusk during late-spring and summer months, when this study was conducted. The tidal range from MHHW to

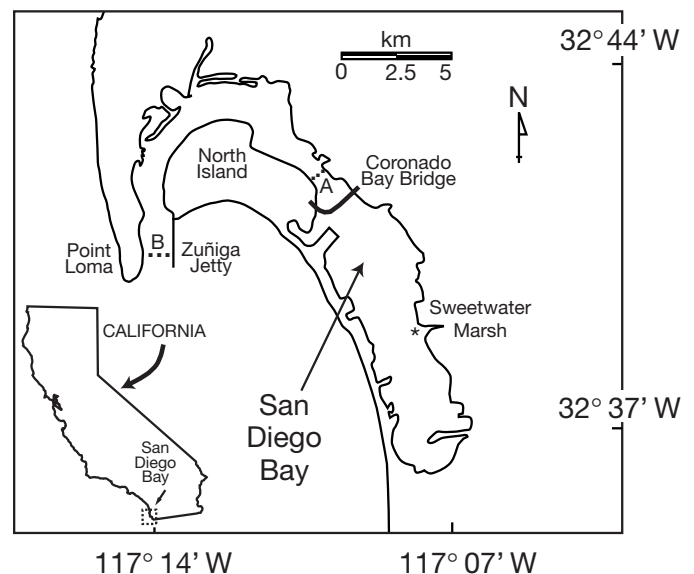


Fig. 1. Sampling locations within San Diego Bay. A: Coronado Bay Bridge transect; B: San Diego Bay Entrance transect; dots indicate positions of eastern, middle and western stations of each transect. Sweetwater Marsh served as the point-source release site (\*) of simulated larvae for hydrodynamic model simulations

MLLW is about 1.7 m. Currents are strongest near the mouth, with maximum velocities between about 50 to 100 cm s<sup>-1</sup> (Chadwick & Largier 1999). Currents decrease toward the head of the bay due to a reduction in the upstream tidal prism. In south SDB, currents are usually less than 10 cm s<sup>-1</sup>.

SDB, like other estuaries located in arid or Mediterranean climate regions of the world, experiences a dry season that typically extends from spring to autumn when freshwater inflow is negligible or absent. San Diego's climate is semi-arid, with an annual rainfall of about 25 mm. Rainfall is associated with episodic storm events primarily during winter. Freshwater flows into the bay via several creeks; the most significant of these is the Sweetwater River (drainage area 540 km<sup>2</sup>; Conway & Gilb 1989). Other sources of freshwater include non-point source runoff during winter storms and incidental runoff from agricultural and landscape watering. The negligible freshwater inflow results in sluggish circulation and a marked increase in average residence time estimates for the inner regions of SDB (Largier et al. 1996, 1997, Chadwick & Largier 1999).

**Larval transport simulations.** The extent to which physical processes and larval behavior mediate the transport and dispersal of brachyuran larvae spawned in SDB was examined using computer simulations. A 2-dimensional (depth-averaged) hydrodynamic model (TRIM2D: tidal, residual, intertidal mudflat model), originally developed to describe tidal and residual circulation within San Francisco Bay (Cheng et al. 1993), was adapted to SDB to conduct transport and fate simulations of contaminants introduced to the bay via spills or storm-drain outfalls. We adapted TRIM2D to include simulated larvae with and without vertical migratory behavior for use as a predictive tool of larval transport. The model uses a finite-difference numerical scheme to solve 2-dimensional shallow water equations governing circulation and resolves circulation features to a horizontal resolution of 100 m. Bottom depth values are derived from bathymetry data sets generated from a variety of depth sounding surveys. The water surface elevation along the open-ocean boundary in the model is driven by tidal forcing conditions corresponding to the dates of larval surveys (described below). The model calculates convective and diffusive transport components and has been calibrated and shown to be in good agreement with independently measured hydrodynamic variables using tide gauges, acoustic Doppler current profilers (ADCP), and mechanical current meter data (Wang et al. 1998). Since SDB receives little or no freshwater during most of the year, especially summer, buoyancy fluxes are dominated by air-water exchange. The resultant buoyancy flux from heating and evaporative processes in SDB is too weak to bring about vertical stratification

and buoyancy-driven exchange (Largier et al. 1996). Therefore, SDB can be effectively represented using a 2-dimensional model.

*A priori* TRIM2D simulations were used to model bay-wide transport of (1) passive larvae with a uniform distribution in the water column and (2) active larvae with a rhythmic vertical migratory behavior that optimizes their chances for exchange out of SDB: larvae migrate into the upper 20% of the water column (top 2 m) during ebb tide and onto the bottom during flood tide to minimize transport back into the bay. The vertical distribution of Stage I *Pachygrapsus crassipes* zoeae (see 'Results') suggested that zoeae may settle on the bottom during the flood tide to minimize transport into SDB. The efficiency of settling on the bottom versus aggregating in the bottom boundary layer (2 m above the bottom) to maximize net transport from SDB was examined using TRIM2D simulations.

Vertical current profiles in SDB have been shown to be logarithmic, with flow velocity approaching zero at the sediment-water interface and a depth-averaged value occurring in the upper half of the water column. Horizontal larval transport velocities experienced by simulated larvae were determined from site-specific logarithmic velocity profiles and modeled larval depth distributions. During ebb tide, when migratory larvae were predicted to aggregate at the sediment-water interface, water velocity was set to zero. During flood tide, when larvae were concentrated in the upper 2 m of the water column, water-velocity estimates approached 1.2 times the depth-averaged velocity. TRIM2D simulations of non-migratory larvae employed tidal phase-specific, depth-averaged velocity estimates. The model simulation time-step was 6 min. Since Stage I *Pachygrapsus crassipes* zoeae observed in the laboratory swam at an approximate rate of 20 mm s<sup>-1</sup> (DiBacco 1999), comparable with swimming rates reported by Chia et al. (1984), simulated larvae in shallow regions of the bay ( $\leq 7$  m) were assumed capable of traversing the water column during a single 6 min time step. Zoeae in the deepest regions of the bay (15 m) were assumed to complete a vertical migration through the water column within two to three 6 min time steps.

Simulated larvae were released from the Sweetwater Marsh area (see Fig. 1), since this is the largest natural marsh in SDB with the largest expected point-source release of crab larvae in the bay. Also, Sweetwater Marsh is located in the inner half of SDB and provides a rigorous test for the efficiency of larval behavior as a mechanism to facilitate the export or retention of larvae. Simulated larvae were introduced during the nighttime flood to ebb tide transition during spring tidal conditions corresponding to larval survey dates (described below) and mimicking *in situ* larval release patterns observed for ovigerous *Pachygrapsus crassipes*.

**Study organisms.** Temporal and spatial distributions of planktonic larvae of 2 brachyuran families were examined. In southern California, *Pachygrapsus crassipes* adults and larvae are widely distributed in low-energy bays and exposed coastal habitats; ovigerous females and newly hatched larvae are present from late spring to early fall (Ricketts et al. 1985, DiBacco 1999). *P. crassipes* zoeal stages are readily identifiable (Schlotterbeck 1976). *Lophopanopeus* spp. zoeae (*L. bellus diagenensis* and *L. frontalis*) could not be distinguished from one another since zoeal stages of the latter species have not been described (Ricketts et al. 1985). These species co-occur as adults in the low intertidal zone of bays and estuaries from Monterey Bay to SDB and characteristically hatch larvae from late spring through summer (Knudsen 1958, 1959, Morris et al. 1980). The temporal and spatial distribution and abundance of larvae sampled in this study are presented for Stage I *P. crassipes* zoeae and for combined stages of *Lophopanopeus* spp. zoeae. *Lophopanopeus* spp. zoeal stages were combined since statistical results were consistent whether Stage I, Post-Stage I or combined larval stages of development were analyzed.

**Sample collection.** Field-sampled larvae were collected during 4 consecutive new and full moon spring tidal periods between 21 July 1997 and 2 September 1997 (Table 1). Two sampling field trips were conducted at the Coronado Bay Bridge (CBB) site and 2 at the San Diego Bay Entrance (SDBE) site (Fig. 1). Collection of plankton samples started in the late afternoon, during late-flood tide, and continued until high tide the following morning (Table 1). The nighttime tidal cycle was targeted because of sampling constraints (e.g., availability of equipment) and since preliminary field investigations indicated that *Pachygrapsus crassipes* zoeae were present in the water column mainly at night (DiBacco 1999).

Plankton samples were collected at the CBB transect, which consisted of 3 sampling stations located in the eastern, middle and western regions of the 500 m cross-channel transect (Fig. 1). Each station was sampled at 3 water depths: 0 to 2 m, 5 to 7 m, and <2 'meters above the bottom' (mab), typically 8 to 11 m deep. The bottom samples included the sediment-water interface during the September sampling period and from 0.5 to 2 mab during the July sampling dates. The CBB transect was sampled at 1 to 1.5 h intervals between (1) 18:00 h on 21 July and 11:00 h on 22 July and (2) 16:00 h on 1 September and 11:00 h on 2 September.

Larval sample collections at the SDBE transect were conducted along a 1400 m cross-channel transect between Point Loma and Zuñiga Jetty (Fig. 1). Only the eastern station of the SDBE transect was sampled during the 4 to 5 August sampling period because of problems with sampling gear. Eastern, middle, and western regions were sampled on 18 to 19 August. Three depths were sampled at each station; 0 to 2 m, 5 to 7 m, and <2 mab, including the sediment-water interface, typically 9 to 12 m deep.

Plankton samples were collected from a 7 m motorboat using a stainless steel pump (0.5 horsepower, 115 V motor) powered by a portable electric generator (1850 W). The pump was fitted with a 2 inch (~5.1 cm) diameter hose and a vortex impeller that minimized damage to larvae. The pump's outflow was measured for each sampling depth (ca 0.3 m<sup>3</sup> min<sup>-1</sup>) and used to standardize plankton abundance per unit volume of water sampled. Individual pump samples were typically 5 min in duration and corresponded to an approximate volume of 1.5 m<sup>3</sup>. Therefore, larval abundance estimates presented in this paper (see 'Results') have been standardized to a pumped water volume of 1.5 m<sup>3</sup>. This provides an accurate representation of the actual

Table 1. Sampling dates and corresponding lunar phase, sampling location (CBB = Coronado Bay Bridge transect; SDBE = San Diego Bay Entrance transect), stations sampled, station depth, tidal regime, and total number (n) of Stage I *Pachygrapsus crassipes* zoeae and combined Stage I and Post-Stage I zoeae of *Lophopanopeus* spp. larvae (*L. bellus diagenensis* and *L. frontalis*) sampled

Sampling date	Lunar phase	Sampling location	Stations sampled	Station depth (m)	High tide	Low tide	<i>Pachygrapsus crassipes</i> (n)	<i>Lophopanopeus</i> spp. (n)
21–22 Jul 1997 (18:00–11:00 h)	Full	CBB	East-channel Mid-channel West-channel	10–12	22:59 h (2.13 m)	5:50 h (–0.13 m)	198	1768
4–5 Aug 1997 (18:00–11:30 h)	New	SDBE	East-channel	7–12	22:27 h (1.71 m)	5:20 h (–0.01 m)	348	29
18–19 Aug 1997 (17:00–11:00 h)	Full	SDBE	East-channel Mid-channel West-channel	7–12	22:07 h (2.27 m)	4:52 h (–0.31 m)	847	60
1–2 Sep 1997 (16:00–11:00 h)	New	CBB	East-channel Mid-channel West-channel	10–12	21:53 h (1.91 m)	4:28 h (–0.04 m)	371	1903

number of larvae sampled per station. Seawater was sieved through a 300  $\mu\text{m}$  Nitex plankton net that was partially submerged to prevent damage to organisms. The net was washed down with seawater to concentrate samples in 500 ml bottles. Samples were stored on ice until they could be transported to the laboratory, where they were held at 5°C. If samples were not sorted within 24 h, zooplankton was concentrated onto Nitex filters, placed into 50 ml disposable centrifuge tubes, frozen in liquid nitrogen, and thawed just prior to sorting. Crab zoeae were sorted and identified to the lowest possible taxa with the aid of a dissecting microscope.

**Statistical analysis.** Analysis of variance (ANOVA) and a *posteriori* Student's *t*-tests were used to test the effects of tidal and diel phase on the spatial distribution and abundance of sampled brachyuran larvae. Larval concentration data (no.  $1.5\text{m}^{-3}$ ) were  $\log(x+1)$ -transformed and percent data were arcsine-transformed when data did not meet assumptions of normality (Kolmogorov-Smirnov) and homogeneity of variance (Bartlett's test or Scheffé's test). Student's *t* alpha levels were Bonferroni-adjusted to reduce the likelihood of Type I errors (Sokal & Rohlf 1995).

The eastern, middle and western regions of each transect sampled served as replicates for each depth sampled, with the exception of the 4 to 5 August sampling period, when only the eastern portion of the channel was sampled. Before pooling data across horizontal stations, larval concentration estimates were tested (ANOVA) for differences in the cross-channel concentration of larvae. Only stations not differing statistically in larval concentration estimates were combined.

Tidal and diel light cycles were in phase during the spring-tide sampling periods targeted in this study; ebb tides always coincided with nocturnal sampling. Diurnal ebbing tides were never sampled, while flood tides were sampled during nocturnal and diurnal sampling. Thus the different effects of tidal phase and diel phase on the vertical distribution of brachyuran larvae could not be separated and assessed statistically. Since tidal and diel phases were confounded, 2-way ANOVAs were performed to test for effects of tidal or diel phase and sampling depth on the concentration of *Pachygrapsus crassipes* or *Lophopanopeus* spp. larvae.

## RESULTS

### Larval transport simulations

Snapshots of SDB-wide larval transport during TRIM2D model simulations are shown in Fig. 2. Model

simulations predicted that larvae with rhythmic vertical migratory behavior (within 2 m of the surface during ebb tide; within 2 m above the bottom during flood tide) experienced net transport towards the bay's entrance (Fig. 2A–D). Simulations of passive larvae that were uniformly distributed in the water column predicted that larvae would be retained within the inner half of SDB (Fig. 2E–H). Both simulations indicated that larvae were maintained on the eastern side of the channel during the first ebb tide after release. This distribution persisted through subsequent ebb tides for simulated larvae with vertical migratory behavior.

Time-series plots of the relative distribution of simulated larvae released from Sweetwater Marsh indicate that vertically migrating larvae are initially transported from inner to outer regions of SDB and into coastal waters in a matter of 30 to 40 h (Fig. 3A). Simulated larvae that did not exhibit vertical migratory behavior were retained within SDB, with less than 10% dispersing into coastal waters after 70 h (Fig. 3B).

Simulated larvae that migrated onto the bottom during flood tides were transported from SDB more quickly than larvae that migrated only into the bottom boundary layer (within 2 m above the bottom) (Fig. 4). Time-series plots of the percentage of simulated larvae transported into nearshore coastal waters after 70 h showed that approximately twice the number of larvae reached coastal waters if the larvae exploited the sediment-water interface during flood tidal conditions (81%) versus migrating within 2 m of the bottom (41%).

### Species composition and abundance

More than 99% of *Pachygrapsus crassipes* larvae sampled in this study were newly hatched Stage I zoeae. Panopeid larvae consisted of *Lophopanopeus bellus diagenesis* and *L. frontalis*, identified to genera from published descriptions of zoeal development (Knudsen 1958, 1959, Rice 1980, Ingle 1992). The majority of *Lophopanopeus* spp. zoeae sampled (ca 97%) were collected from the CBB site, with about 58% of these larvae in the first zoeal stage of development. There were no significant differences in the concentration of *P. crassipes* zoeae sampled during CBB and SDBE sampling dates (ANOVA,  $F_{3,296} = 1.988$ ,  $p = 0.116$ ) (Figs 5 & 6) or *Lophopanopeus* spp. zoeae sampled during CBB sampling dates ( $F_{1,169} = 0.258$ ,  $p = 0.613$ ) (Fig. 7), therefore species-specific density estimates could be combined across sampling periods for subsequent statistical analyses.

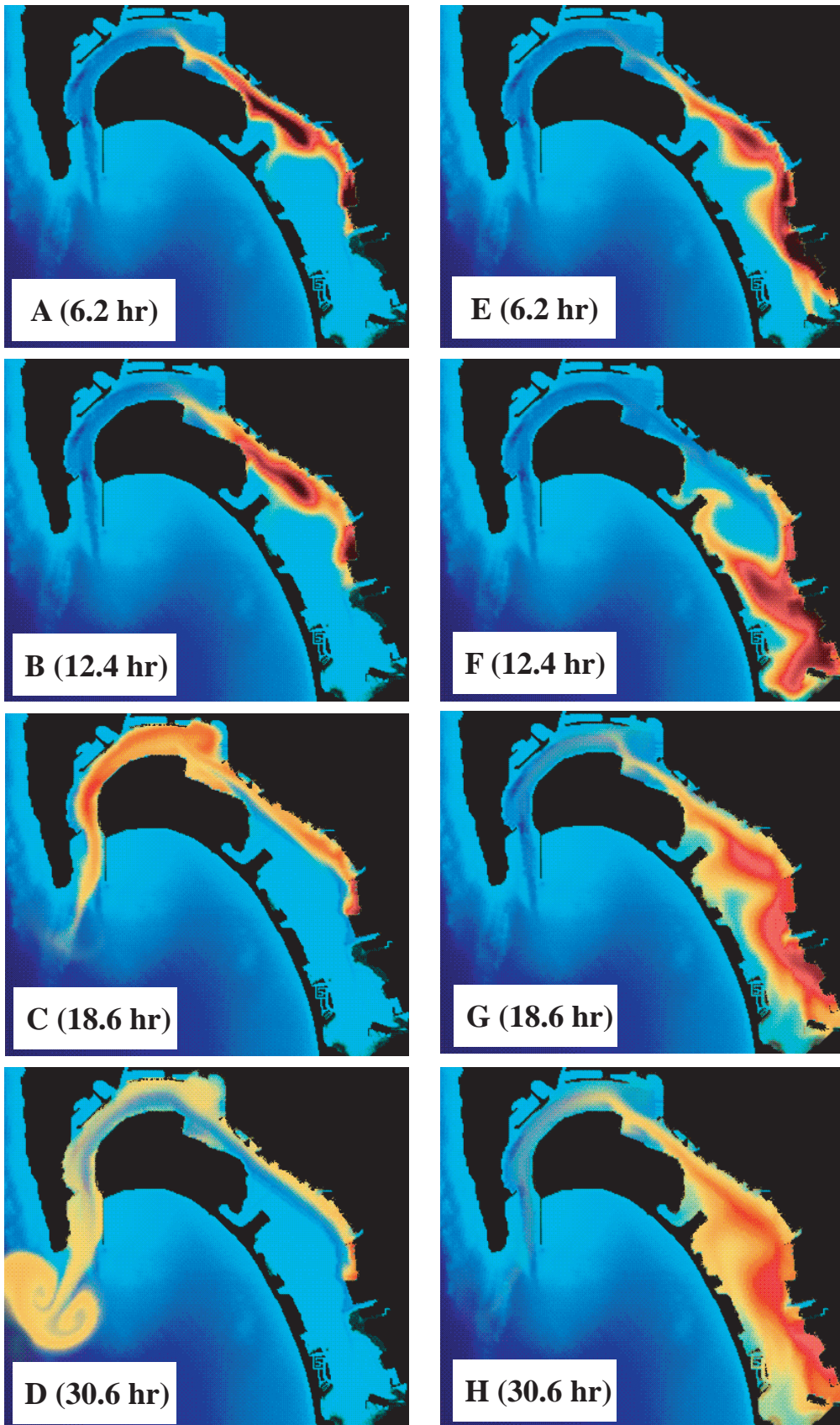


Fig. 2. Tidal residual intertidal mudflat model (TRIM2D) simulations for brachyuran larvae released from identified intertidal and high intertidal habitats off Sweetwater Marsh on the eastern side of San Diego Bay (see Fig. 1 for location of larval release site). Simulated larvae with vertical migratory behavior (A–D) are aggregated in surface layers (within surface 2 m) during flood-tide phases and in benthic layers during ebb tidal phases (within 1 m of bottom). Migratory larvae are concentrated in the eastern half of the channel at the Coronado Bay Bridge site and experience a net transport towards the San Diego Bay entrance. Simulated larvae without vertical migratory behavior (E–G) produce larval distributions concentrated in the back of San Diego Bay. Relative larval abundance is represented by black, red, orange and yellow shading, with red and darker areas indicating higher concentrations, following the initial ebb tide (6.2 h post-release: A and E), flood tide (12.4 h post-release: B and F), ebb tide (18.6 h post-release: C and G), and subsequent ebb tide (30.6 h post-release: D and H)

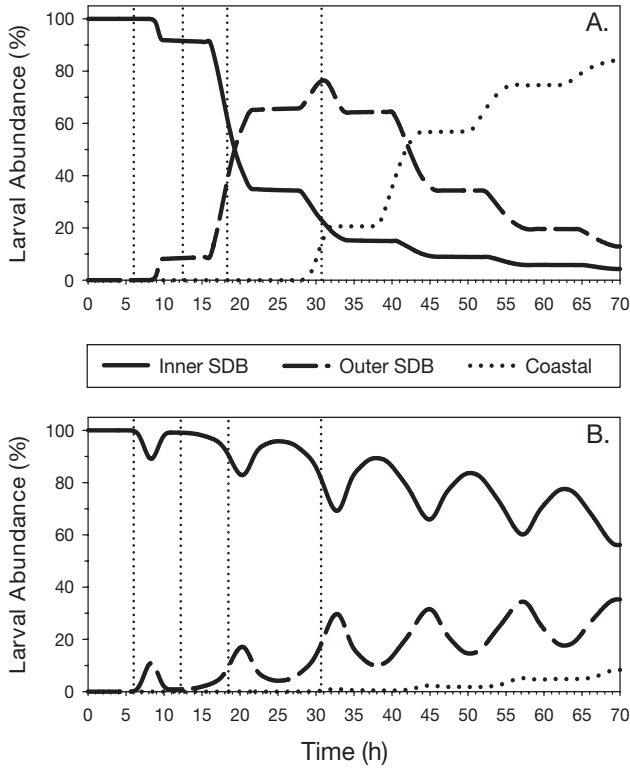


Fig. 3. Time-series plots quantifying relative horizontal distribution of simulated larvae released from Sweetwater Marsh, San Diego Bay (Fig. 2). Relative abundance (%) estimates between inner and outer regions of San Diego Bay and nearshore coastal waters are for larvae (A) with and (B) without vertical migratory behavior. Vertical dotted lines correspond to TRIM2D simulation snapshots in Fig. 2 for 6.2, 12.4, 18.6 and 30.6 h post-release

**Vertical distribution of larvae**

*Pachygrapsus crassipes*

Larval vertical migratory behavior was observed in Stage I *Pachygrapsus crassipes* zoeae hatched in SDB. The concentration of Stage I *P. crassipes* larvae sampled in this study did not vary with tidal phase, diel phase or sampling depth when analyzed independently (Table 2). Significant interaction terms suggest a strong effect of tidal phase and diel phase on the vertical distribution of *P. crassipes* zoeae (Table 2). The highest densities of Stage I *P. crassipes* larvae consistently occurred in the surface sampling layer (0 to 2 m) during nocturnal ebb-tide conditions (Table 3) and in the bottom layer (0 to 2 mab) during diurnal flood-tide conditions (Table 3, Figs 5 & 6). A downward

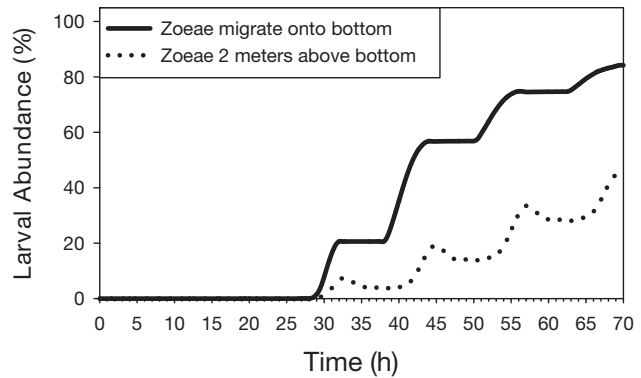


Fig. 4. Time-series plot showing relative abundance (%) of simulated larvae transported from San Diego Bay into near-shore coastal waters. Continuous line: zoeae that maximize transport from San Diego Bay by settling on the bottom during the flood-tide phase; dotted line represents larvae that migrate within 2 m of bottom during the flood-tide phase, but do not settle on the bottom

migration of Stage I *P. crassipes* zoeae is suggested from mean larval concentration estimates collected during the nocturnal-ebb tide to diurnal-flood tide transition of the 4 to 5 August sampling period (see Transects 8 to 15: Fig. 6A). The relative concentration of *P. crassipes* zoeae is highest in the surface layer during late-ebb (Transects 7 to 9), followed by mid-depth during the ebb- to flood-tide transition (Transect 11) and in the bottom layer during flood tide (Transects 12 to 15: Fig. 6A).

Table 2. *Pachygrapsus crassipes* and *Lophopanopeus* spp. Two-way ANOVA comparing effects of tidal phase (T) and sampling depth (Z) or diel phase (D) and sampling depth on larval abundance (log[x+1] transformed) of Stage I *P. crassipes* zoeae and *Lophopanopeus* spp. larvae (all stages combined). Results from the analyses of Stage I and Post-Stage I *Lophopanopeus* spp. zoeae are not presented separately since significance levels of terms were similar to those revealed by the analysis of combined stages of development. Results from a *posteriori* multiple comparisons are given in Table 3

Source	<i>Pachygrapsus crassipes</i>			<i>Lophopanopeus</i> spp.		
	df	F-ratio	p-value	df	F-ratio	p-value
Tidal phase (T)	1	1.551	0.210	1	15.815	<0.001
Depth (Z)	2	2.197	0.114	2	1.391	0.252
T × Z	2	22.299	<0.001	2	2.477	0.087
Error	213			165		
Diel phase (D)	1	2.568	0.111	1	13.971	<0.001
Depth (Z)	2	2.308	0.102	2	1.467	0.234
D × Z	2	25.143	<0.001	2	2.142	0.121
Error	213			165		

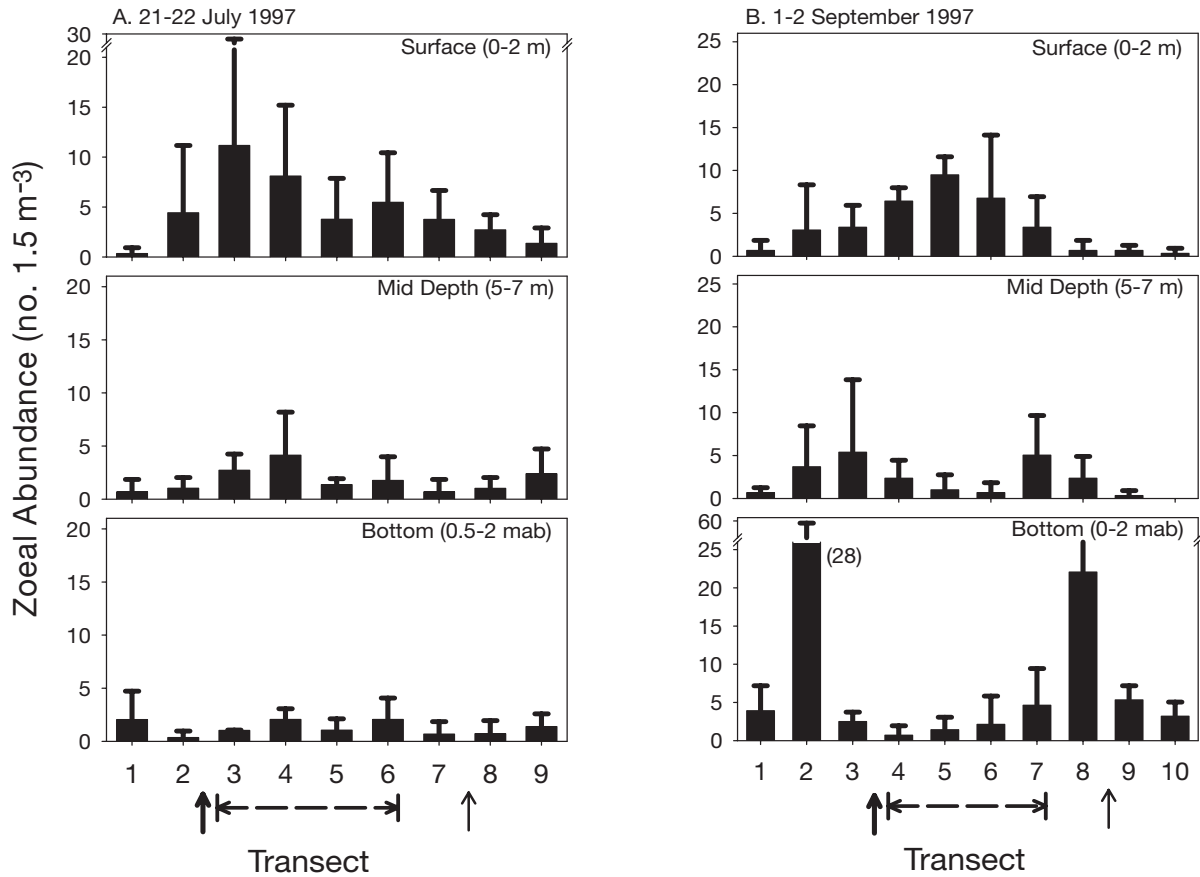


Fig. 5. *Pachygrapsus crassipes*. Temporal and vertical distribution of Stage I zoeae sampled at Coronado Bay Bridge transect on 21–22 July and 1–2 September 1997. Mean zoeal abundance was calculated by averaging depth-specific larval abundance estimates from eastern, middle and western stations for each transect, respectively. Dashed line along the x-axes: ebb-tide phase; thick and thin vertical arrows on x-axes: onset of sunset and sunrise, respectively; numbers in parentheses next to vertical bar in last graph indicates maximum value that exceeds range on y-axis. mab: meters above bottom. Error bars = 1 SD

Table 3. *Pachygrapsus crassipes* and *Lophopanopeus* spp. One-way ANOVA comparing larval abundance estimates (mean ± SD) for surface (T = 0 to 2 m), mid-depth (M = 5 to 7 m), and bottom (B = <2 mab: meters above the bottom) layers sampled during ebb and flood tides during July, August and September 1997 sampling periods. Stage I zoeae were analyzed for *P. crassipes*; Stage I and Post-Stage I *Lophopanopeus* spp. zoeae were combined for the analysis presented; separate analyses of Stage I and Post-Stage I *Lophopanopeus* spp. zoeae failed to identify any statistical differences. Statistically significant multiple comparison results (Bonferroni-corrected Student's *t*-test) are given for each ANOVA that identified significant differences. July 1997 sampling period was not analyzed for *P. crassipes* since the sediment-water interface was not adequately sampled during this period

Sampling date	Tidal phase (T)	Surface	Mid-depth (M)	Bottom (B)	n	F-ratio	p-value	Student's <i>t</i>
<b><i>P. crassipes</i></b>								
4–5 Aug	Ebb	4.06 (3.61)	1.91 (2.79)	1.07 (1.27)	12	4.367	0.038	T > M, B
	Flood	0.71 (0.68)	1.04 (1.09)	5.44 (5.64)	30	3.091	0.060	–
18–19 Aug	Ebb	29.88 (31.3)	13.28 (16.9)	2.31 (3.74)	33	4.010	0.028	T, M > B
	Flood	1.73 (1.63)	2.39 (2.58)	23.63 (39.46)	30	7.453	0.002	T, M < B
1–2 Sep	Ebb	6.52 (2.49)	2.27 (1.99)	2.22 (1.70)	33	5.694	0.008	T > M, B
	Flood	1.47 (1.37)	2.07 (2.14)	10.91 (11.3)	51	12.787	<0.001	T, M < B
<b><i>Lophopanopeus</i> spp.</b>								
21–22 Jul	Ebb	31.33 (8.09)	21.10 (11.3)	33.04 (13.9)	33	1.207	0.312	–
	Flood	18.06 (19.5)	18.48 (6.66)	16.07 (9.45)	42	0.978	0.384	–
1–2 Sep	Ebb	22.60 (10.4)	22.70 (16.3)	32.92 (15.1)	33	1.573	0.223	–
	Flood	12.13 (1.81)	21.97 (8.64)	23.07 (9.28)	51	0.759	0.473	–



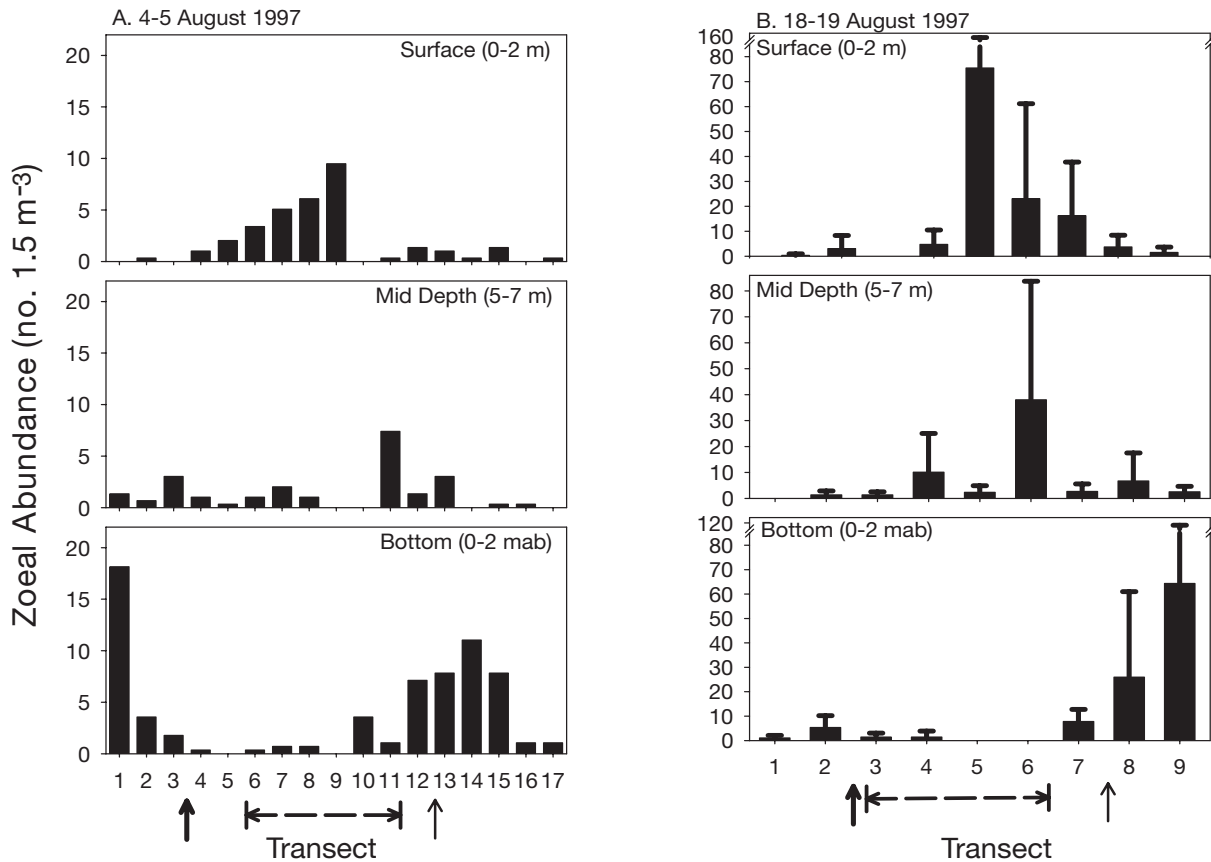


Fig. 6. *Pachygrapsus crassipes*. Temporal and vertical distribution of Stage I zoeae sampled at San Diego Bay Entrance transect on 4–5 August and 18–19 August 1997. No error bars are presented in (A) since only 1 station was sampled on this date. Further details as in Fig. 5

The relative proportion of Stage I *Pachygrapsus crassipes* zoeae sampled in the bottom layer at the CBB site during 21 to 22 July, when the sediment-water interface was not sampled (Fig. 5A), was significantly lower (16.3%) than the proportion of Stage I zoeae sampled in the bottom layer at the same site on 1 to 2 September (51.6%), when the sediment-water interface was sampled (Fig. 5B). The difference in the relative proportion of zoeae found on the bottom between sampling periods is attributable to a larger concentration of larvae collected in the bottom layer during flood-tide conditions, suggesting that a significant proportion of the larvae exploit the sediment-water interface during flood tide (Fig. 5). There was no significant difference in the proportion of *P. crassipes* larvae sampled in the bottom layer during July and September ebb-tide sampling periods (Table 4). Stage I *P. crassipes* zoeae were also concentrated in bottom-layer samples collected at the SDBE site during flood tide conditions of the August sampling periods where the sediment-water interface was sampled (75.7%, 4 to 5 August; 83.2%, 18 to 19 August) (Fig. 6). *P. cras-*

*sipes* larval abundance estimates from the July sampling period were not used in subsequent statistical analyses of vertical distribution patterns since bottom samples underestimated larval concentrations during flood-tide conditions.

#### *Lophopanopeus* spp.

The concentration of *Lophopanopeus* spp. zoeae sampled at the CBB site varied significantly with tidal and diel phase, but neither sampling depth nor the interaction terms were significant (Table 2). *Lophopanopeus* spp. zoeae were significantly more abundant, across all sampling depths, during ebbing tides (Table 2). This distribution corresponds to maximum horizontal transport from the inner region of SDB, where the majority of *Lophopanopeus* spp. zoeae are concentrated, towards the CBB sampling site during ebb tide. Since only nocturnal ebb tides were sampled, this probably explains why diel phase had a significant effect on larval abundance at the CBB site.

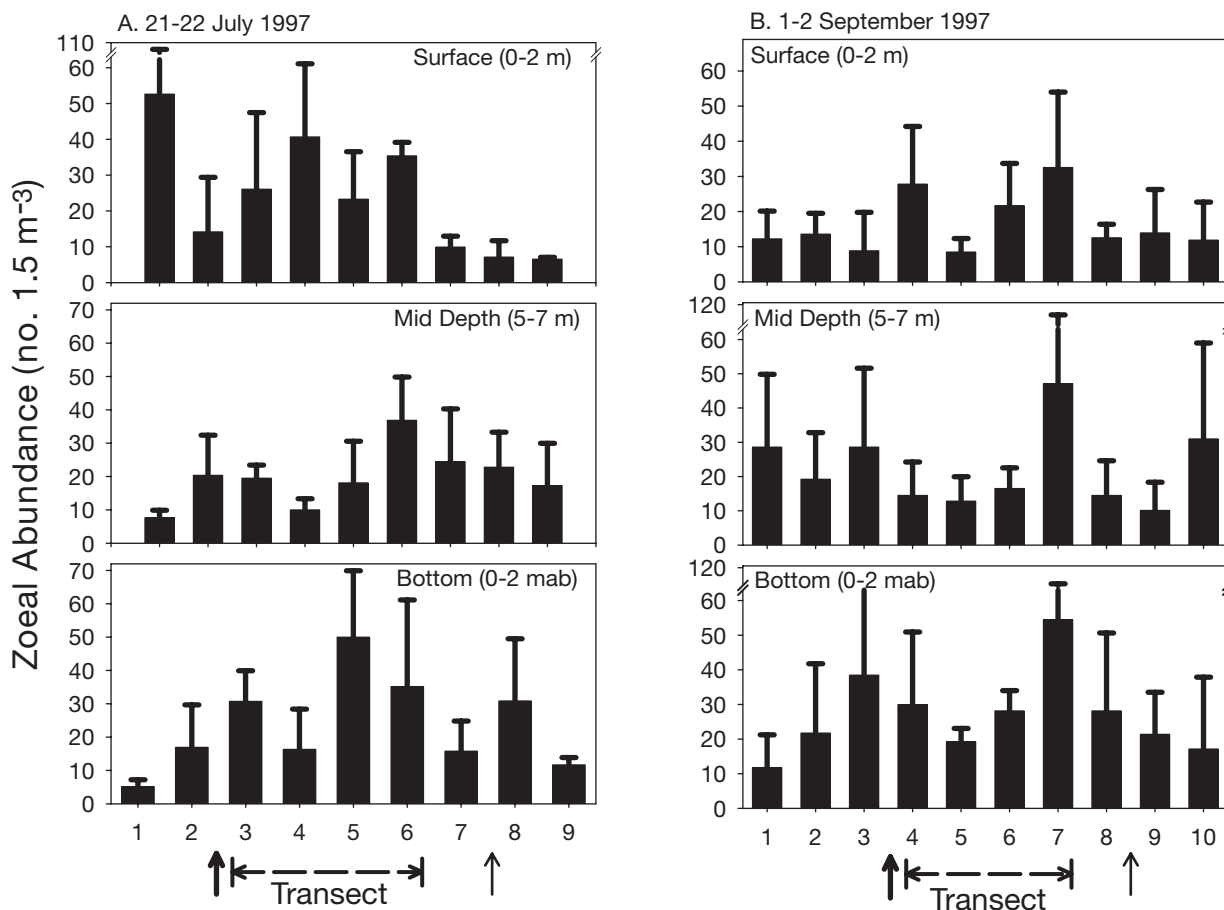


Fig. 7. *Lophopanopeus* spp. Temporal and vertical distribution of zoeae sampled at Coronado Bay Bridge transect on 21–22 July and 1–2 September 1997. Further details as in Fig. 5

Table 4. *Pachygrapsus crassipes* and *Lophopanopeus* spp. One-way ANOVA comparing percent zoeal abundance estimates sampled in the bottom layer for Stage I *P. crassipes* zoeae and combined Stage I and Post-Stage I *Lophopanopeus* spp. zoeae at the Coronado Bay Bridge transect. Sediment-water interface was not sampled during 21–22 July 1997 sampling period (only 0.5 to 2 m above bottom, mab), while samples collected on 1–2 September 1997 included sediment-water interface (0 to 2 m above bottom)

Tidal phase	Sampling date	Sampling depth	% larval abundance	n	F-ratio	p-value
<b><i>P. crassipes</i></b>						
Flood	21–22 Jul	0.5–2 mab	22.0	31	17.096	<0.001
	1–2 Sep	0.5–2 mab	75.5			
Ebb	21–22 Jul	0–2 mab	13.9	22	0.926	0.346
	1–2 Sep	0–2 mab	20.2			
<b><i>Lophopanopeus</i> spp.</b>						
Flood	21–22 Jul	0.5–2 mab	30.5	31	0.012	0.915
	1–2 Sep	0.5–2 mab	40.4			
Ebb	21–22 Jul	0–2 mab	38.7	22	0.241	0.628
	1–2 Sep	0–2 mab	42.1			

*Lophopanopeus* spp. zoeal concentrations never differed between sampled depths, regardless of tidal or diel phase (Table 3), indicating no detectable vertical migratory behavior. *Lophopanopeus* spp. zoeae did not appear to settle on the bottom during any phase of the tidal cycle sampled (Fig. 7). Unlike Stage I *Pachygrapsus crassipes* zoeae, there was no difference in the proportion of *Lophopanopeus* spp. zoeae sampled in the bottom layer, regardless of whether the sediment-water interface was sampled (Table 4).

**Horizontal distribution of larvae**

*Pachygrapsus crassipes*

The distribution of Stage I *Pachygrapsus crassipes* larvae was heterogeneous

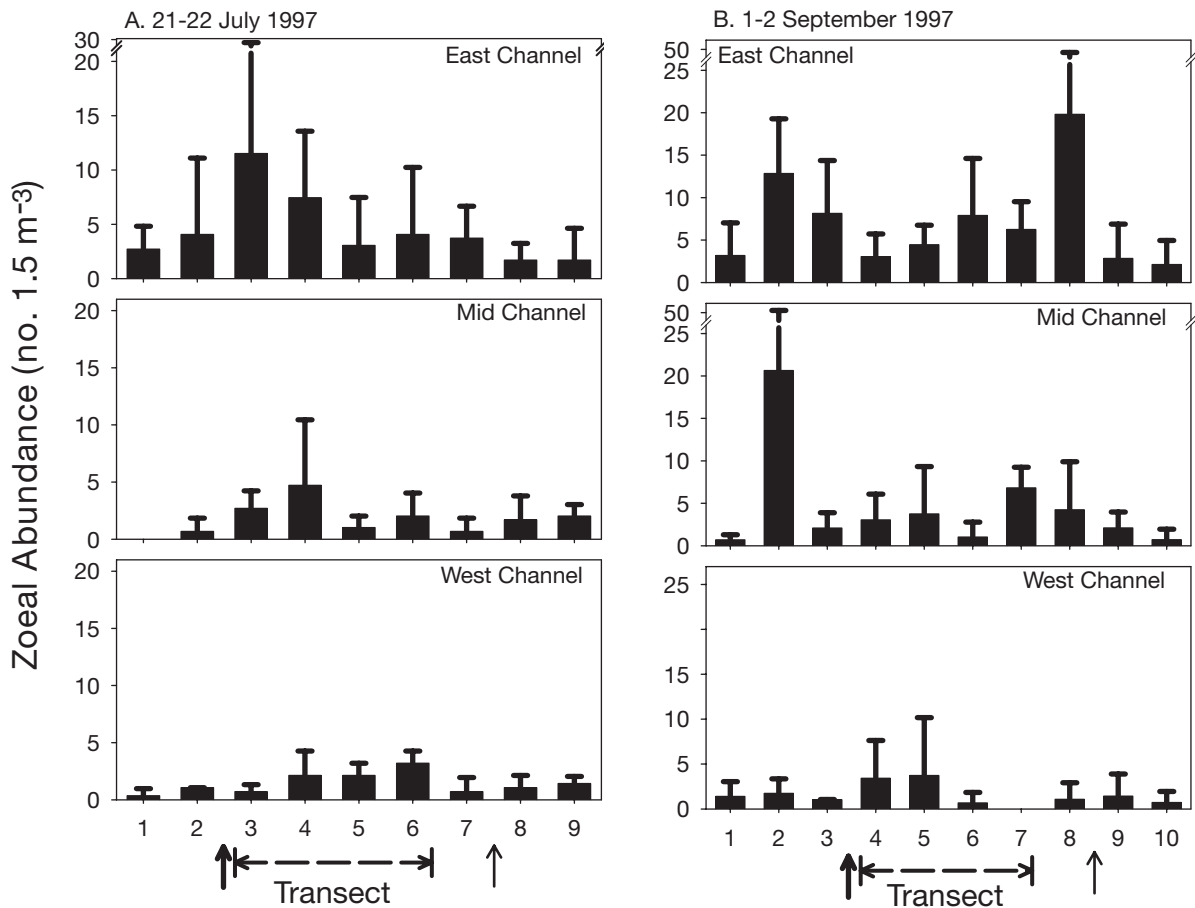


Fig. 8. *Pachygrapsus crassipes*. Temporal and horizontal distribution of Stage I zoeae sampled at Coronado Bay Bridge transect on 21–22 July and 1–2 September 1997. Mean zoeal abundance was calculated by averaging station-specific larval abundance estimates from surface, mid-depth, and bottom layers for each transect, respectively. Further details as in Fig. 5

across sampling stations of the CBB transect (Table 5). Larvae were usually concentrated in the eastern station of the CBB transect (Fig. 8). During ebb tide, larval densities in the eastern station were higher than in the western station (Fig. 8). Larval density estimates for the mid-channel station did not differ from either eastern or western station densities (Fig. 8). During flood tide, Stage I *P. crassipes* larval densities were highest in the eastern station compared to mid-channel or western station densities (Fig. 8). Larval densities were not significantly different between the mid-channel and western stations (Table 5).

At the SDBE site (B, Fig. 1), the average concentration of larvae collected from the eastern station was greater than either the western or mid-channel stations during ebb tide (Fig. 9B); however, none of the station densities differed significantly (Table 5). The distribution of *Pachygrapsus crassipes* larvae was heterogeneous during flood tide (Fig. 9B). The western station had a significantly higher density of Stage I zoeae than

the mid-channel station, but it did not differ from the eastern station (Table 5).

#### *Lophopanopeus* spp.

*Lophopanopeus* spp. zoeae were heterogeneously distributed across the CBB transect (Table 5). Larvae were more concentrated in the eastern and mid-channel stations of the CBB transect (Fig. 10). Similar distribution patterns were observed for both Stage I and Post-Stage I *Lophopanopeus* spp. zoeae sampled during July and September; therefore statistical results for analyses on densities of combined larval stages of development are presented in Table 5. *Lophopanopeus* spp. larval densities were lower at the western station during ebb tides than at either the eastern or mid-channel stations. Mean larval densities sampled during flood tide remained lower at the western station than at either the eastern station or the mid-channel stations (Fig. 10).

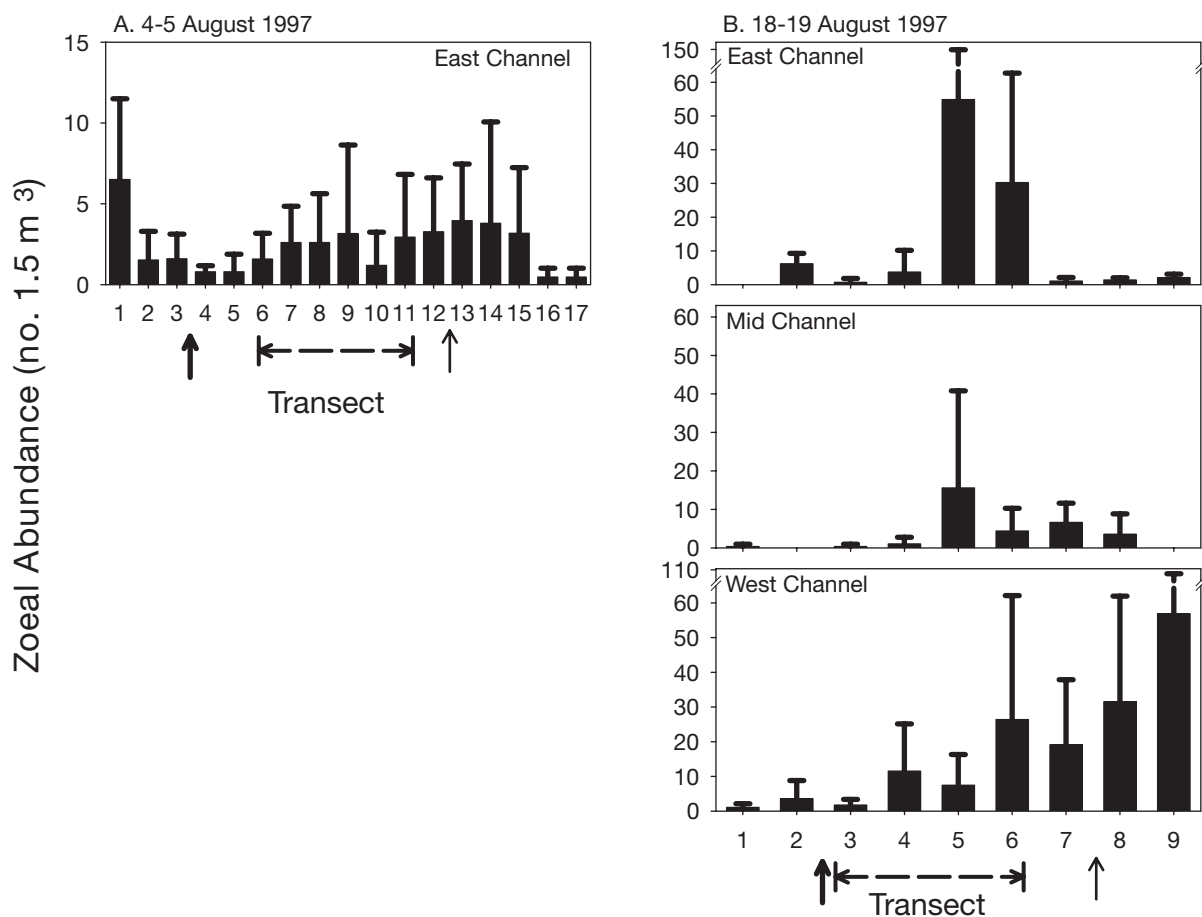


Fig. 9. *Pachygrapsus crassipes*. Temporal and horizontal distribution of Stage I zoeae sampled at San Diego Bay Entrance transect on 4–5 August (only eastern station sampled) and 18–19 August 1997. Further details as in Figs 5 & 8

Table 5. *Pachygrapsus crassipes* and *Lophopanopeus* spp. One-way ANOVA comparing larval abundance estimates (mean  $\pm$  SD) for eastern (E), mid-channel (M), and western (W) stations sampled during ebb and flood tides at Coronado Bay Bridge transect (CBB: 21–22 July 1997, 1–2 September 1997) and San Diego Bay Entrance transect (SDBE: 18–19 August 1997). Larval abundance data for Stage I *P. crassipes* zoeae and Stage I and Post-Stage I *Lophopanopeus* spp. zoeae were analyzed for ebb, flood and pooled ebb and flood tides. Results from pooled *Lophopanopeus* spp. larvae are presented, since the same statistically significant effects were revealed in separate analyses of Stage I and Post-Stage I zoea. Statistically significant multiple-comparison results (Bonferroni-corrected Student's *t*-test) are given for each ANOVA which identified a significant effect of tidal phase on larval abundance. Data from 4–5 August 1997 sampling period were combined with the 18–19 August 1997 data analyzed here since only the eastern portion of the channel and a significantly higher concentration of *P. crassipes* larvae were sampled during the former period. \*0.05 > *p* > 0.01; \*\*0.01 > *p* > 0.001, \*\*\**p* < 0.001

Sampling site	Tidal phase	East	Middle	West	n	F-ratio	p-value	Student's <i>t</i>
<b><i>P. crassipes</i></b>								
CBB	Ebb	5.9 (0.8)	3.1 (0.7)	2.0 (0.1)	69	4.905	0.011	E = M, E > W**, M = W
	Flood	5.5 (3.8)	3.1 (2.9)	1.1 (0.2)	96	7.092	<0.001	E > M*, E > W**, M = W
SDBE	Ebb	12.4 (14.2)	6.9 (6.2)	16.1 (8.4)	42	1.866	0.167	–
	Flood	2.2 (0.2)	1.1 (1.7)	18.9 (24.7)	30	3.380	0.047	E = M, E = W, M < W*
<b><i>Lophopanopeus</i> spp.</b>								
CBB	Ebb	30.2 (3.5)	34.8 (0.4)	16.9 (2.0)	69	5.619	0.006	E = M, E > W**, M > W**
	Flood	20.4 (6.8)	19.9 (1.2)	14.6 (4.7)	96	4.096	0.020	E = M, E = W, M > W*

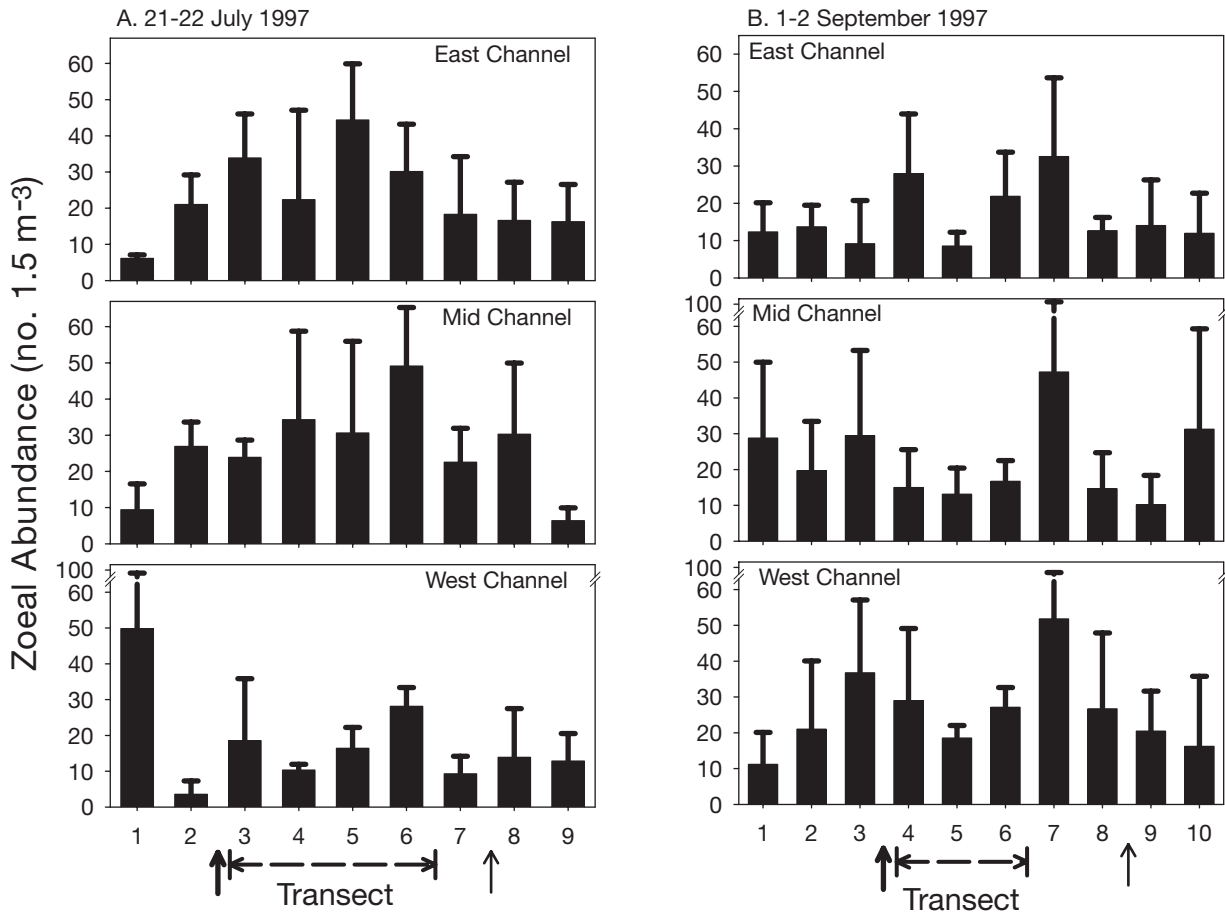


Fig. 10. *Lophopanopeus* spp. Temporal and horizontal distribution of Stage I zoeae sampled at Coronado Bay Bridge transect on 21–22 July and 1–2 September 1997. Further details as in Figs 5 to 8

## DISCUSSION

### Vertical distribution of larvae

#### *Pachygrapsus crassipes*

A large body of laboratory and field evidence suggests that the export or retention of brachyuran larvae spawned in estuaries is not a passive phenomenon. Many brachyuran larvae facilitate their export from or retention within embayments with specific adaptations, such as tidally timed vertical migratory behavior (e.g., Epifanio 1988, McConaugha 1988). Stage I *Pachygrapsus crassipes* zoeae sampled in this study appear to minimize their residence time within SDB by aggregating in surface layers during nocturnal ebbing tides and at the sediment-water interface during flood tide (i.e., selective tidal stream transport). Stage I *P. crassipes* zoeae were observed to burrow to a depth of 2 cm when hatched in the laboratory and raised in still water in aquariums with coarse sand bottoms (DiBacco 1999).

This burrowing behavior has never been examined *in situ* for brachyuran larvae because of sampling limitations. If *P. crassipes* larvae, or other meroplankton, can selectively settle on or burrow into sediments during specific phases of the tide, this would allow them to effectively escape transport by unfavorable tides and currents and would enhance the efficiency of selective tidal stream transport. In an LIE such as SDB, exploiting the bottom layer to avoid retention by flooding tides and currents should be particularly advantageous for species like *P. crassipes* that exploit ebbing tides to exit embayments. TRIM2D simulations suggested that larvae settling on the bottom during the flood-tide phase would be considerably more efficient at exiting SDB than larvae which exploited reduced flows in the bottom boundary layer during flood tide (Fig. 4).

Selective tidal stream transport was highly effective in exporting simulated larvae from SDB (Figs 2A–D & 3A). Field observations revealed a limited proportion of Post-Stage I *Pachygrapsus crassipes* zoeae (<1%) at both the CBB and SDBE sampling sites. Vertical migra-

tion exhibited by Stage I *P. crassipes* zoeae sampled in the field allowed them to exit SDB before molting to subsequent larval stages of development. *P. crassipes* zoeae reared under laboratory conditions at ambient bay temperatures (18 to 20°C) required between 68 and 108 d to develop through all 6 zoeal stages of development, and averaged about 10 to 15 d per larval stage of development (DiBacco 2001). *Lophopanopeus* spp. zoeae exhibited no apparent vertical migratory behavior and were retained within SDB through all larval stages of development.

Numerous studies have examined the vertical distribution of brachyuran larvae relative to tidal and diel cycles and provided evidence for selective tidal stream transport based on reductions in estuarine tidal current velocities within the benthic boundary layer (most recently, Lochmann et al. 1995, Queiroga et al. 1997, Rodriguez et al. 1997, Garrison 1999). Tidally timed rhythmic migrations have been observed for other grapsid crabs which export newly hatched larvae to coastal waters (e.g., *Sesarma cinereum*, *S. reticulatum*: Christy & Stancyk 1982; *S. catenata*: Lago 1993) and for other panopeid species which retain planktonic stages of larval development within estuaries until recruitment to adult populations (e.g., *Rhithropanopeus harrisi*: Cronin & Forward 1979, 1982, Lambert & Epifanio 1982). However, none of these studies have sampled the sediment-water interface to establish the presence or absence of larvae on the bottom (Lochmann et al. 1995). The present study is the first to provide evidence that a brachyuran species, *Pachygrapsus crassipes*, may exploit the sediment-water interface to enhance selective tidal stream transport during larval development. Knowledge of the difference in mean velocities experienced by larvae which settle on the bottom (approaching 0 cm s<sup>-1</sup>) relative to those distributed through a layer above the bottom is needed to evaluate the relative efficiency of vertical migratory behavior. In LIEs such as SDB, *P. crassipes* may reduce its residence time within the bay by reducing transport back into the bay during flood tides.

#### *Lophopanopeus* spp.

Marine invertebrate larvae with limited vertical migratory behavior that are passively distributed by currents will experience limited net transport in an LIE such as SDB because of negligible freshwater inflow and weak seaward residual currents. Limited net transport of passive simulated larvae and field-sampled *Lophopanopeus* spp. zoeae was apparent in SDB. *Lophopanopeus* spp. zoeae were uniformly distributed throughout depth strata sampled in this study without any indication of tidally timed spawning by ovigerous

females or vertical migratory behavior by planktonic zoeae. The persistence of all panopeid larval stages of development at the CBB sampling site (inner SDB), negligible densities at the SDBE site (outer SDB), and model simulation results all suggest that *Lophopanopeus* spp. zoeae are retained in SDB throughout larval development despite the lack of vertical migratory behavior. Residence time estimates for SDB seawater are on the order of 50 d in the vicinity of the CBB site and even higher in the innermost regions of the bay (Chadwick & Largier 1999). *Lophopanopeus* spp. zoeae typically have 4 zoeal stages of development, which are completed in about 5 wk under laboratory conditions (Hart 1935, Knudsen 1958, 1959). This is considerably shorter than the predicted residence times for inner SDB constituents that disperse passively (Fig. 3B). Garrison (1999) reported that tidally timed migration patterns of panopeid larvae in the York River, a partially mixed estuary in Chesapeake Bay, promoted very slow downstream dispersal, yet Post-Stage I panopeid zoeae were not reported in samples.

Zoeae of another panopeid, *Rhithropanopeus harrisi*, have been shown to employ tidally timed, rhythmic migration into surface layers during flood tide and into bottom layers during ebb tide to maintain their position within estuaries (Sandifer 1975, Lambert & Epifanio 1982). This is the reverse of the migration behavior of Stage I *Pachygrapsus crassipes*' zoeae described in this study, which facilitated transport from SDB. Cronin & Forward (1982, 1983) observed that *R. harrisi* might aggregate around depths of no net flow during the ebb-tide phase to avoid transport out of estuaries. The lack of non-tidal residual currents in SDB and the lack of net downstream transport and flushing may preclude the need for rhythmic vertical migration by *Lophopanopeus* spp. zoeae, and perhaps other passive meroplanktonic or holoplanktonic species, to retain larvae within the bay.

#### Horizontal distribution of larvae

The horizontal distribution of newly hatched zoeae may be influenced by the distribution of adult populations. In the case of *Pachygrapsus crassipes*, newly hatched larvae were concentrated in the eastern station of the CBB transect during flood and ebb tides. The eastern side of this region of SDB has both natural (e.g., Sweetwater Marsh) and artificial (e.g., piers and jetties) habitats occupied by adult *P. crassipes*. The opposite shore is sandy (Silver Strand) or has been replaced by concrete docks and boardwalks (North Island) that provide little or no habitat for *P. crassipes*. As a result, most Stage I *P. crassipes* larvae hatched near the CBB sampling site originate from the eastern side of the bay.

Once larvae are released into the water column, physical features can concentrate or disperse them. For example, an intensified ebb-tide current that develops on the eastern side of the channel extending from inside the Coronado Bay Bridge past the CBB site has been documented by Chadwick & Largier (1999). This tidal jet would entrain newly released zoeae and keep them concentrated in the eastern region of the channel, within a few hundred meters from shore. Model simulations predicted that larvae spawned from the eastern side of SDB would remain most concentrated on the eastern side of the channel (Fig. 2). Maximum velocity estimates of this ebb-jet have been reported to be about  $50 \text{ cm s}^{-1}$  in the eastern side of the channel and  $25 \text{ cm s}^{-1}$  in the western side of the channel (Chadwick & Largier 1999). Flood-tide velocities were symmetrical across the channel, with maximum velocities in the middle of the channel ( $40$  to  $45 \text{ cm s}^{-1}$ ) and decreasing velocities closer to shore ( $20$  to  $25 \text{ cm s}^{-1}$   $100 \text{ m}$  from either shore) (Chadwick & Largier 1999). The horizontal distribution of Stage I *P. crassipes* zoeae sampled at the entrance of SDB and tidal velocity estimates reported were more spatially uniform across stations than at the CBB site (Chadwick & Largier 1999).

Differences in the horizontal distribution of Stage I *Pachygrapsus crassipes* and panopeid larvae relative to tidal currents at each site will affect larval exchange between regions of SDB and between SDB and near-shore coastal waters. In the case of panopeid larvae, the vertical distribution, which is uniform, may be less important to net transport than the observed horizontal distribution relative to tidal currents at the CBB site. In contrast to the situation for *P. crassipes*, the eastern and western sides of the inner SDB channel provide some suitable habitat for adult panopeid populations. The more extensive development of military, commercial and recreational piers, which support intertidal mussel communities inhabited by *Lophopanopeus* spp., near the eastern station than the western station may explain the larger concentration of panopeid larvae sampled in the western station of the CBB sampling transect (Fig. 10).

### Significance of bay-ocean exchange

The vast majority of studies considering temporal and spatial distributions of brachyuran larvae have been conducted in partially mixed estuaries where significant freshwater inflow results in non-tidal residual flows and net downstream transport of passive and uniformly distributed constituents. The present study considered the vertical migratory behavior of crab larvae in SDB, an LIE which experiences negligible or no net downstream flow due to limited freshwater

input. Tidal stream transport appears necessary for *Pachygrapsus crassipes* larvae to exit SDB, based on the retention of *Lophopanopeus* spp. larvae (which lacked vertical migration behavior) within SDB through all planktonic stages of development. The efficiency of rhythmic vertical migration in promoting export appears to be enhanced by *P. crassipes*' ability to exploit velocity gradients that approach zero near the sediment-water interface during flood tides. Swimming behavior-mediated retentive mechanisms were not necessary for retention of *Lophopanopeus* spp. larvae within SDB.

A trade-off between nutrition, predation, and physiological stress have been offered as an explanation why certain larvae may be preferentially exported from estuaries while others are retained throughout their development (reviewed by Morgan & Christy 1995, 1997). In a separate study, *Pachygrapsus crassipes* larvae cultured in coastal seawater experienced higher survivorship during zoeal development and yielded a larger percentage of viable megalopae than larvae reared in SDB seawater (DiBacco 2001). Thus, *P. crassipes* larvae leaving SDB for open coastal waters should experience an increased probability of surviving to the megalopal stage of development, the stage that recruits to sedentary benthic populations. Vertical migratory behavior, which can facilitate the export or retention of select crab species during planktonic larval development, can reduce predation pressure and physiological stress associated with coastal habitats, while retention within an embayment throughout planktonic larval development can reduce dispersal from the adult habitat and enhance recruitment.

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