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Assessing the dispersal and exchange of brachyuran larvae between regions of San Diego Bay, California and nearshore coastal habitats using elemental fingerprinting

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ABSTRACT

Marine benthic invertebrate populations found in estuarine or coastal habitats often exchange larvae. However, the dynamics of larval exchange are poorly understood because of difficulties in (1) making synoptic assessments of horizontal and vertical larval distribution patterns over large areas for extended periods of time and (2) determining the origins of field-sampled larvae. This study examines how temporal changes in the vertical and horizontal distribution of crab larvae (i.e., *Pachygrapsus crassipes* and *Lophopanopeus* spp.) affect larval transport. Larval concentration and water velocity data were collected concurrently and were used to estimate larval exchange between regions of San Diego Bay (SDB) and between SDB and nearshore coastal waters. A larval fingerprinting technique was used to distinguish SDB and non-SDB spawned, stage I *P. crassipes* zoeae to quantify larval exchange between SDB and nearshore coastal waters. First order estimates of larval exchange over a tidal cycle between inner and outer regions of SDB and between the bay and nearshore coastal habitats corroborate a net transport of stage I *P. crassipes* zoeae from SDB as inferred from larval behavior. The estimated net larval exchange of *Lophopanopeus* spp. zoeae was into SDB, suggesting retention within the bay through larval development. Trace elemental fingerprinting of stage I *P. crassipes* zoeae revealed bi-directional exchange between SDB and the nearshore coastal environment when the predominant transport predicted from zoeal swimming behavior was out of San Diego Bay. Approximately 5% of stage I *P. crassipes* zoeae sampled in the mid region of SDB originated from outside SDB, while 26% of zoeae sampled at the entrance originated from outside SDB. Combined use of trace elemental fingerprinting and synoptic field sampling techniques will help improve our understanding of larval transport and ultimately the population dynamics of nearshore species.

1. Introduction

A number of laboratory and field studies have shown that the transport of decapod larvae between estuarine and nearshore coastal environments is not a passive phenomenon (Epifanio, 1988; McConaugha, 1988). Some species are retained within embayments throughout larval development (e.g., Cronin, 1982), while others preferentially export

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larvae to coastal waters (e.g., Christy, 1982). The behavioral basis for retentive mechanisms has been best studied for temperate brachyuran crabs (see reviews by Sulkin, 1984; Forward, 1988). The ability of many larvae to exit and return to estuarine habitats has been considered critical for survival (Morgan, 1987, 1995; Morgan and Christy, 1995, 1997). This is the case for estuarine species that release planktonic larvae that develop offshore but recruit to adult populations located within estuaries (Epifanio, 1988).

The study of larval exchange between bay and nearshore coastal habitats has typically involved traditional methods of sampling, such as plankton net tows, plankton pump samples, passive drifters, or settlement collectors (Christy and Stancyk, 1982; Emmerson, 1983; Levin, 1983; Dittel *et al.,* 1991; Wooldridge, 1991; Rowe and Epifanio, 1994; Lago, 1993). These approaches require that scientists infer potential spawning sites and dispersal trajectories from physical oceanographic data (i.e., current directions and speed) coupled with descriptions of larval behavior. For example, recent studies evaluating the exchange of crab larvae between embayments and coastal habitats have examined larval abundance and vertical distribution patterns in relation to tidal and diel phase (e.g., Lochman *et al.,* 1995; Queiroga *et al.,* 1997; Garrison, 1999).

Despite the potential for larval exchange between bay and coastal habitats, there have been few attempts to quantify this exchange (reviewed in Lago, 1993; Rowe and Epifanio, 1994). Estimating net larval exchange has been hindered by inherent limitations of sampling equipment used to concurrently assess temporal and spatial (vertical and horizontal) distribution and abundance of zooplankton and hydrographic features (e.g., water velocity). Zooplankton nets and pumps provide accurate estimates of larval concentration, but these approaches require time to deploy and retrieve equipment, concentrate and preserve samples, and transit between sample stations. As a result, an adequate number of samples cannot be collected to assess the temporal and spatial abundance of planktonic organisms at the resolution required to make accurate, integrated estimates of flux. For larvae that originated (i.e., spawned) from either bay or coastal populations, our inability to determine larval origin confounds attempts to quantify larval exchange since individuals may experience bi-directional exchange into or out of embayments, during consecutive tidal phases, prior to settlement.

Due to the above limitations, studies characterizing bay-ocean exchange have been restricted to species that are assumed only to migrate into or out of embayments during specified stages of larval development (Emmerson, 1983; Levin, 1983; Beckley, 1984; Lago, 1993; Rowe and Epifanio, 1994). Flux studies have typically focused their attention on tidal inlets that connect to nearshore coastal waters by way of a narrow ($<$50 m) and shallow ($<$5 m) channel (Christy and Stancyk, 1982; Lago, 1993). This is done to reduce the cross-sectional area that has to be sampled to provide accurate estimates of larval abundance and water velocity flow fields. Depth-stratified samples collected at one station over a designated period of time are used to calculate depth-specific flux estimates, which in turn are extrapolated to the cross-sectional area of the estuarine channel. The assumption

made by these studies is that larval abundance and velocity fields are uniform in cross-section.

The inability to track larval exchange between adult populations of species that inhabit both bay and coastal habitats has limited our understanding of larval exchange processes. Past efforts to track invertebrate larval dispersal have involved direct visual observations of short lived planktonic larvae (Olson, 1985), the use of applied dyes, calcium carbonate or trace element markers (Levin, 1990; Levin *et al.,* 1993; Anastasia *et al.,* 1998), and size variation of newly recruited individuals (Gaines and Bertness, 1992). In recent years, the elemental composition of fish otoliths have been used to track fish migration and address questions about fish life histories (Northcote *et al.,* 1992; Kalish, 1990), recruitment sites (Gillanders and Kingsford, 1996), rearing sites (Kennedy *et al.,* 1997), stock mixing (Edmonds *et al.,* 1989, 1991) and migration (Campana *et al.,* 1995; Campana and Gagné, 1995). A similar trace elemental fingerprinting technique has been developed to distinguish San Diego Bay (SDB) from non-SDB spawned stage I *P. crassipes* zoeae (DiBacco and Levin, 2000).

DiBacco *et al.* (2001) documented temporal and spatial (horizontal and vertical) distributions of *P. crassipes* and *Lophopanopeus* spp. zoeae over a tidal cycle at two sampling sites in SDB. A subset of these larval concentration estimates are combined with concurrently sampled water velocity measurements of the present study to test the hypothesis that heterogeneous vertical and horizontal distributions of brachyuran larvae have a significant effect on larval flux estimates between the inner- and outer regions of SDB and between SDB and nearshore coastal waters. Elemental fingerprints were analyzed for a subset of stage I *P. crassipes* zoeae collected at both sampling sites in SDB to test the hypothesis that zoeae sampled within the bay originated from inside SDB. The observed vertical migratory behavior of stage I *P. crassipes* zoeae relative to tidal phase suggests that the predominant transport of most newly spawned zoeae is out of SDB (DiBacco *et al.,* 2001). The presence of non-SDB hatched, stage I *P. crassipes* zoeae within SDB would reveal an alternative scenario for the dispersal of newly released larvae. A broader objective of this study was to begin to develop a methodology to evaluate net larval transport using analytical techniques to concurrently assess temporal and spatial variations in water velocity flow fields, larval distribution, and larval origins.

2. Materials and methods

a. Study site and organisms

This study took place in San Diego Bay, a crescent shaped embayment with an approximate axial length of 25 km (Fig. 1). The tidal range from mean lower-low water to mean higher-high water is about 1.7 m with extreme tidal amplitudes of about 3 m during spring tidal phase (Chadwick and Largier, 1999). The exchange of brachyuran larvae between inner- and outer-regions of SDB was examined at the Coronado Bay Bridge (CBB) sampling transect, while the exchange between SDB and the nearshore coastal environment was examined at the San Diego Bay Entrance (SDBE) transect (Fig. 1).

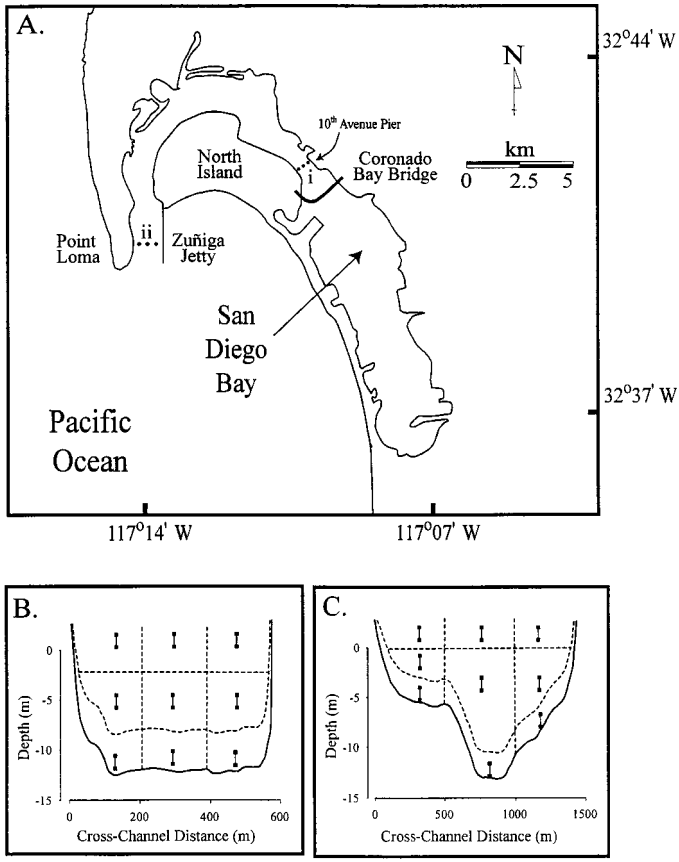

Figure 1. Chart of San Diego Bay study area. (A) Sampling transects were located (i) near the Coronado Bay Bridge (CBB) and (ii) at the San Diego Bay Entrance (SDBE). Dots indicate positions of eastern, middle and western stations within each transect. Cross-sectional views of bottom topography are shown for sampling transects at (B) CBB (looking northwest) and (C) SDBE (looking approximately north). Dashed lines demarcate larval and water-velocity sampling bins at high tide. Zero meter depth corresponds to a mean lower-low water tidal height. Vertical lines with square ends within each sampling bin represent approximate depth and location of integrated pump samples.

Negligible freshwater inflow results in sluggish circulation and a marked increase in average residence time estimates toward the back of the SDB basin (Chadwick and Largier, 1999; Largier *et al.,* 1996, 1997).

The exchange of planktonic larvae was examined for stage I *Pachygrapsus crassipes* zoeae sampled at the CBB and SDBE sampling sites. Stage I zoeae made up about 99% of all *P. crassipes* zoeae sampled; therefore, any reference to *P. crassipes* zoeae in the remainder of this paper refers to the first stage of larval development. Adult *Lophopanopeus bellus diegenisis* and *Lophopanopeus frontalis* co-occur in SDB, but their larvae have

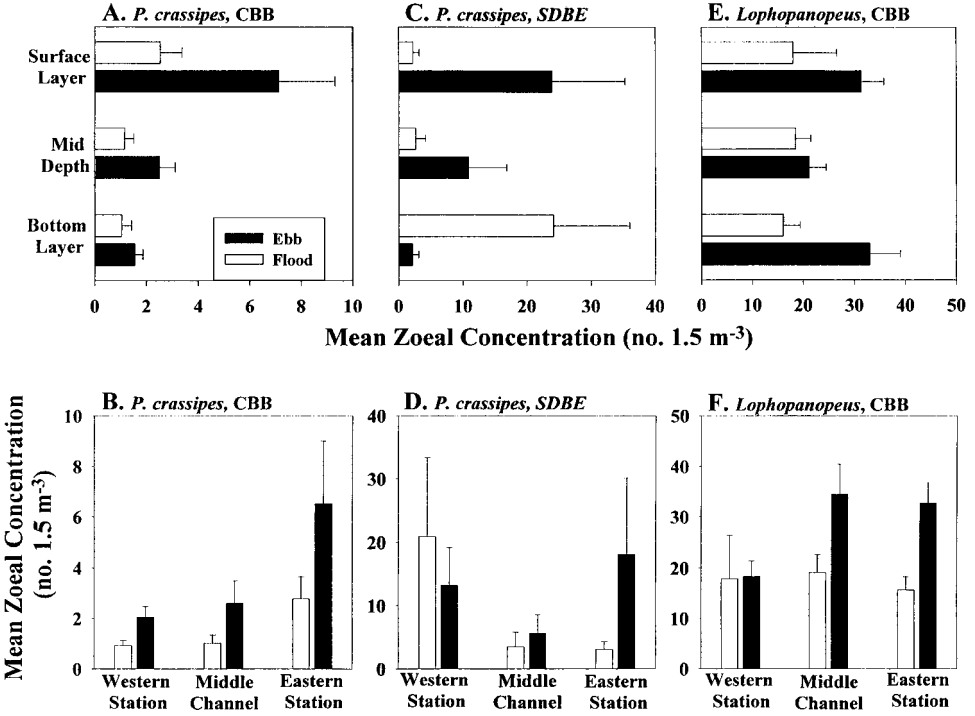

Figure 2. Mean (±1 SE) vertical and horizontal larval concentration estimates of stage I *Pachygrapsus crassipes* zoeae sampled at the (A, B) Coronado Bay Bridge (CBB; 21–22 July 1997) and (C, D) San Diego Bay Entrance (SDBE; 18–19 August 1997) sampling sites. Mean vertical (E) and horizontal (F) larval abundance estimates for combined stage I and post-stage I *Lophopanopeus* spp. zoeae sampled at the CBB. The sediment-water interface was sampled at the SDBE site only.

not been distinguished taxanomically (Ricketts *et al.,* 1985). Stage I and post-stage I *L. bellus diegenisis* and *L. frontalis* zoeae were combined in our analysis since larvae of these two species could not be distinguished and since none of the larval stages exhibited vertical migratory behavior (DiBacco, 1999). Since greater than 97% of all stage I and post-stage I *L. bellus diegenisis* and *L. frontalis* zoeae were sampled at the CBB site, only larval exchange estimates between inner and outer regions of SDB are presented. The temporal and spatial distributions of *P. crassipes* and *Lophopanopeus* spp. zoeae have been described in detail by DiBacco *et al.* (2001) using data collected from four field sampling trips. Larval abundance data used to make net larval exchange estimates (summarized in Fig. 2) represents two of the four field sampling trips that were conducted concurrently with physical oceanographic cruises that provided tidal velocity data.

b. Sample collection

Plankton samples and physical oceanographic data were collected concurrently during two consecutive full moon, spring tidal periods. All samples were collected along a 600-m

transect located at the CBB site (18:00h, 21 July 1997 to 11:00h, 22 July 1997) and a 1400-m transect at the SDBE site (17:00h, 18 August 1997 to 11:00, 19 August 1997) (Fig. 1). Each sampling transect was divided into three lateral sections (eastern, mid-channel and western stations), approximately equivalent to one third of the total width, and three vertical layers (Fig. 1B and C). Vertical layers defined for the two sampling sites differed since the channel depth varied between the two sites. The channel depth at the CBB site was 10 to 12 m (Fig. 1B) while the SDBE channel depth varied between 6 to 12 m (Fig. 1C). At the CBB site, surface, mid-depth and bottom layers were defined as (1) the surface to a depth of 4 m, (2) the bottom of the surface layer to 4 m above the bottom, and (3) the bottom to 4 m above the bottom, respectively (Fig. 1B). At the SDBE site, the surface, mid-depth and bottom layers were defined as (1) the surface to 2 m deep, (2) the bottom of the surface layer to 2 m above the bottom, and (3) the bottom to 2 m above the bottom (Fig. 1C).

Zooplankton samples were collected at depths of 0.5 to 2.5 m, 5 to 7 m, and 0.5 to 2 'meters above the bottom' (mab) at the CBB site, not including the sediment water interface (Fig. 1B). At the SDBE site, zooplankton samples were collected at 0.5 to 2 m, 5 to 7 m, and less than 2 mab, including the sediment water interface. The targeted depth-sampling interval at the western station of the SDBE site, where the channel shoals to 6 m on low tide, was 2 to 4 meters (Fig. 1C).

The CBB and SDBE transects were sampled repeatedly through approximately 1.5 tidal cycles to determine the temporal and spatial (vertical and horizontal) distribution and abundance of brachyuran larvae. Only larvae sampled from slack flood through the subsequent ebb and flood tidal phases, a complete semi-diurnal tide, were used to estimate net larval exchange. The collection of zooplankton samples at both sampling sites commenced in the late afternoon, during late-flood tide and continued through subsequent ebb and flood tidal phases into the following morning. The night-time tidal cycle was targeted since several preliminary field investigations yielded few *P. crassipes* zoeae, our original target species, in the water column during daytime sampling, but many in nighttime samples (DiBacco, 1999).

Zooplankton samples were collected from a 7-m boat using an Ebara AC pump (0.5 horsepower, 115V motor) fitted with a two-inch 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^3 min^{-1}, 300 L min^{-1}) and used to standardize plankton abundance per unit volume of water sampled. Individual pump samples were typically 5 minutes in duration, which corresponded to approximately 1.5 m^3 of filtered seawater. Therefore, larval abundance estimates presented in this paper (see Results) have been standardized to a pumped water volume of 1.5 m^3. This provides an accurate representation of the actual number of larvae sampled per station. The entire transect, consisting of 9 sample stations, required about 75 minutes to complete, which allowed 8 to 9 transects to be sampled during one semidiurnal tide.

Seawater was sieved through a partially submerged plankton net (300-μm mesh) to

prevent damage to organisms during pump outflow. The net was washed down with seawater to concentrate the samples for storage in 500-ml, acid washed polyethylene bottles. Samples were stored on ice until they could be transported to the lab where they were held at 5°C. If samples were not sorted within 24 hours, they were frozen in liquid nitrogen and thawed just prior to sorting. *Pachygrapsus crassipes* and other crab zoeae were sorted and identified to the lowest possible taxa with the aid of a dissecting microscope.

Water velocity flow fields were mapped from a separate research vessel (RV *ECOS*) conducting cross-channel acoustic Doppler current profiling transects concurrent with plankton surveys. During each survey, currents were measured using a RD Instruments 1.2 MHz, narrow-band acoustic Doppler current profiler (ADCP) mounted downward looking in a transducer well aboard the RV *ECOS*. The ADCP was operated in a bottom tracking mode with a ping rate of 6 Hz and a 20 ping averaging period, giving an estimated short-term velocity precision of about 3 cm sec^{-1} (RD Instruments, 1988; Geyer and Signell, 1990). The overall sampling rate, including water column averaging and bottom tracking, was about 0.1 Hz. The horizontal resolution of the flow measurements was about 10 m; based on a vessel speed of about 2 knots (1 m sec^{-1}) maintained while conducting transects. The vertical resolution of the ADCP was one meter.

ADCP transects were repeated at 15 to 30 min intervals throughout the sampling period. The ADCP transects were repeated 110 and 60 times at the CBB and SDBE sample sites, respectively. Shallow water on the western side of both the CBB and SDBE transects limited sampling to within about 200 m of the shore, while at the eastern end of the transects the research vessel typically approached within about 100 m of the shore.

c. Data analysis and larval exchange estimates

Analysis of variance (ANOVA) and *a posteriori* Student *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 m^{-3}) were log $(x + 1)$ transformed and percent data were arcsine transformed to satisfy assumptions of normality (Kolmogorov-Smirnoff) and homogeneity of variance (Bartlett's test or Scheffe's test). Student *t* alpha levels were Bonferroni adjusted to reduce the likelihood of Type I errors (Sokal and Rohlf, 1994).

The eastern, middle and western regions of each transect sampled served as replicates for each depth 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.

Water velocities were extrapolated to the surface and bottom at 10 m horizontal intervals for each transect. An approximate 1.5-m range near the surface and above the bottom could not be resolved by the ADCP. The surface layer was extrapolated freely, while the bottom layer was extrapolated using a log profile. The log profile was matched to the velocity at the

deepest measurement point, and assumed a roughness element of 10 cm based on previous estimates of Chadwick and Largier (1999).

Throughout this paper, we refer to 'sectional larval exchange estimates' as larval exchange estimates for each of the 9 cross-sectional sampling bins (Fig. 1B and C) and to 'net larval exchange estimates' as the sum of site-specific sectional larval exchange estimates (Eq. 1). Net larval exchange was calculated as,

$$Net\ LarvalExchange_{site} = E = \sum_{t=1}^{n} \sum_{b=1}^{9} [C_{tb} \overline{V}_{tb} T_{tb} A_{tb}] \quad (1)$$

where E is the site-specific net flux of brachyuran larvae over one complete 12.4-h semidiurnal tide; C_{tb} is the sampling bin- (b) and transect- (t) specific concentration of larvae sampled; $\overline{V}_{tb}$ is the bin-averaged instantaneous velocity during the period of time required to sample the transect in question (T_{tb}); and A_{tb} is the bin- and transect-specific cross-sectional area.

Net larval exchange estimates provided in this study are first order approximations of net larval transport because of limitations in extrapolating localized larval density estimates to the cross-sectional area of our sampling transects. Sectional larval exchange and net larval exchange estimates provide an effective means to assess how temporal changes and spatial (vertical and horizontal) heterogeneity in the distribution of crab larvae can influence net larval transport. In a study of larval weakfish, Rowe and Epifanio (1994) made no attempt to extrapolate 'unit' (i.e., sectional) flux measurements made at one station in Delaware Bay to the cross-sectional area of the estuary. Instead, they interpreted vertically stratified sectional flux estimates as general indicators of larval weakfish transport within the estuary. Similarly, we use vertically and horizontally stratified sectional flux estimates of brachyuran zoeae presented here to characterize transport between inner and outer regions of SDB and between SDB and nearshore coastal waters.

d. Elemental fingerprinting

The use of naturally occurring trace elements and pollutants as viable tags to distinguish SDB versus coastal origins for planktonic larvae sampled *in situ* was developed concurrent with the present study (DiBacco and Levin, 2000). Trace element fingerprinting and discriminant function analyses were used to identify the origins and characterize the exchange of *P. crassipes* zoeae between inner and outer regions of SDB and between SDB and the nearshore coastal environment. Elemental analyses of larvae were carried out in solution. The trace element composition of individual *P. crassipes* larvae was analyzed with an Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES; Perkin-Elmer, Optima 3000XL). External standards were used to calibrate the instrument at the beginning of each analytical session. A blank (1% HNO_3) and 4 to 5 standard solutions spanning expected concentration ranges (0, 25, 50, 100 and 200 μg kg^{-1} for the Al, Cu, Sr, Mn and Zn matrix; 0, 1, 5, 10 and 20 μg g^{-1} for the Ca and Mg matrix) were run at the start of each analytical session. The blank intensity was subtracted from standard and sample

intensities to obtain net intensities and concentrations. Blanks spiked with defined concentrations of standards were used to monitor instrument drift every 5 samples (15 minutes of instrument operation time).

Discriminant function algorithms were developed from trace element composition data for stage I *P. crassipes* zoeae of known origin (reference samples) collected from 7 locations along an axial transect of SDB, 5 neighboring embayments, and 3 San Diego coastal sites (DiBacco and Levin, 2000). Discriminant function analyses distinguished stage I *P. crassipes* zoeae spawned from SDB populations from zoeae originating from outside the bay, including neighboring embayments and exposed coastal habitats. A validation of classification algorithms indicated that they correctly identified 93 percent of SDB larvae and 96 percent of non-SDB larvae tested.

3. Results

a. Temporal-spatial distribution of crab larvae

Pachygrapsus crassipes larvae sampled at the CBB and SDBE sampling sites exhibited vertical migratory behavior, but *Lophopanopeus* spp. did not. *Pachygrapsus crassipes* zoeae were significantly more abundant in surface layers (0 to 2 m), compared to mid-depth and bottom layers, during nocturnal ebbing tides (CBB, $F_{2,33} = 5.694, p = 0.008$; SDBE, $F_{2,33} = 4.010$, $p = 0.028$) (Fig. 2A and C) and they were more abundant in the bottom layer during flood tide, but only when the sediment-water interface was sampled (SDBE, $F_{2,30} = 7.453$, $p = 0.002$) (Fig. 2C). When the sediment-water interface was not sampled, at the CBB site, the bottom layer (0.5–2 meters above the bottom) did not differ in zoeal density from surface and mid-depth layers during flood tide ($F_{2,42} = 1.742, p = 0.188$) (Fig. 2A). This suggests that *P. crassipes* zoeae may aggregate on the bottom during flood tide, a behavior that should minimize transport back into the bay.

Lophopanopeus spp. zoeae were uniformly distributed among sampling depths during flood and ebb tidal phases and did not appear to settle on bottom sediments during any phase of the tide (Fig. 2E). There was no difference in the percentage of larvae collected in the bottom layer, regardless of whether the sediment-water interface was sampled ($F_{2,55} = 0.002, p = 0.964$).

Heterogeneous horizontal distributions of *P. crassipes* larvae were observed across eastern, mid-channel and western stations of the CBB ($F_{2,165} = 11.495$, $p < 0.001$) and SDBE ($F_{2,72} = 4.680$, $p = 0.012$) sampling transects (Fig. 2B and D). *Pachygrapsus crassipes* zoeae were concentrated in the eastern side of the CBB transect, especially during ebbing tides (Student t: eastern (E) > mid-channel (M), $p = 0.002$; $E >$ western (W) channel, $p < 0.001$; $M = W$, $p = 0.644$) (Fig. 2B). The concentrations of *P. crassipes* zoeae sampled at the SDBE transect was highest in the eastern and western portions of the channel during ebbing tide and greatest in the western side of the channel during flood tide (Student t: $W > M$, $p = 0.023$; $W = E$, $p = 0.327$; $E = M$, $p = 0.058$) (Fig. 2D).

Concentrations of *Lophopanopeus* spp. larvae also were heterogeneously distributed across stations ($F_{2,165} = 8.705$, $p < 0.001$). Larval density was higher in the eastern and

mid-channel stations of the CBB transect during ebb tide (Student t: $E = M$, $p = 0.900$; $E > W$, $p = 0.005$; $M > W$, $p = 0.007$), but there was no noticeable difference between stations during the flood tidal phase (Fig. 2F).

b. Water velocity estimates

Estimates of velocity flow fields along cross-sectional transects at the CBB and SDBE sampling sites provide a means for quantifying the net tidal exchange of bay and ocean water and for making sectional larval exchange estimates of net larval transport. A temporal summary of vertical and horizontal velocity flow fields beginning at slack flood and progressing through the ebb/flood cycle to the subsequent slack flood are provided for the CBB (Fig. 3A–H) and SDBE sites (Fig. 4A–H).

Cross-sectional velocity estimates observed in CBB sampling transects (Fig. 3) were more homogeneous (horizontally and vertically) than those observed at the SDBE site (Fig. 4). At the CBB site, maximum ebb and flood axial velocities were comparable and were higher in surface and mid-depth layers (ca. 45 cm sec^{-1}) than in the bottom layer (ca. 30 cm sec^{-1}), likely due to friction with the bottom (Fig. 3B–D, F–H). Depth-specific velocity estimates (surface, mid-depth and bottom layers) were comparable across eastern, mid-channel and western stations throughout ebb and flood tidal phases. Like the CBB site, maximum ebb and flood axial velocity estimates observed from SDBE sampling transects were higher in surface and mid-depth layers than bottom layers (Fig. 4). The ebb flow was characterized by strong southward flow within the entrance channel with maximum velocities of approximately 80 cm sec^{-1} (Fig. 4C). Ebb flow velocities tended to be higher in the eastern half of the channel than the western (Fig. 4B–D). Tidal excursion times were not equal. The flood tidal phase was about 20 to 30 minutes longer than the ebb phase. This difference was accounted for when estimating net larval transport. The ebb to flood transition of surface and bottom velocities occurred approximately in phase during our sampling period (but see Chadwick and Largier, 1999). The flow reversed from ebb to flood initially along the eastern and western shorelines (Fig. 4E). As the flood flow continued to develop, velocities within the entrance's central channel increased to a maximum of about 60 cm sec^{-1} (Fig. 4G).

c. Net larval exchange estimates

i. Pachygrapsus crassipes. The present study and DiBacco *et al.* (2001) represent a limited number of studies that have sampled the sediment-water interface while considering the vertical distribution of meroplankton (see also Prytherch, 1928; Carricker, 1951). The presence of zoeae on the bottom during flood tide has obvious implications for larval behavior on net transport. However, larval behavior at the sediment water interface requires further consideration before definitive assumptions about its effect on net transport can be made. For example, since plankton pump samples provide only a snapshot of larval distribution, it is difficult to determine whether zoeae sampled on the bottom remain there

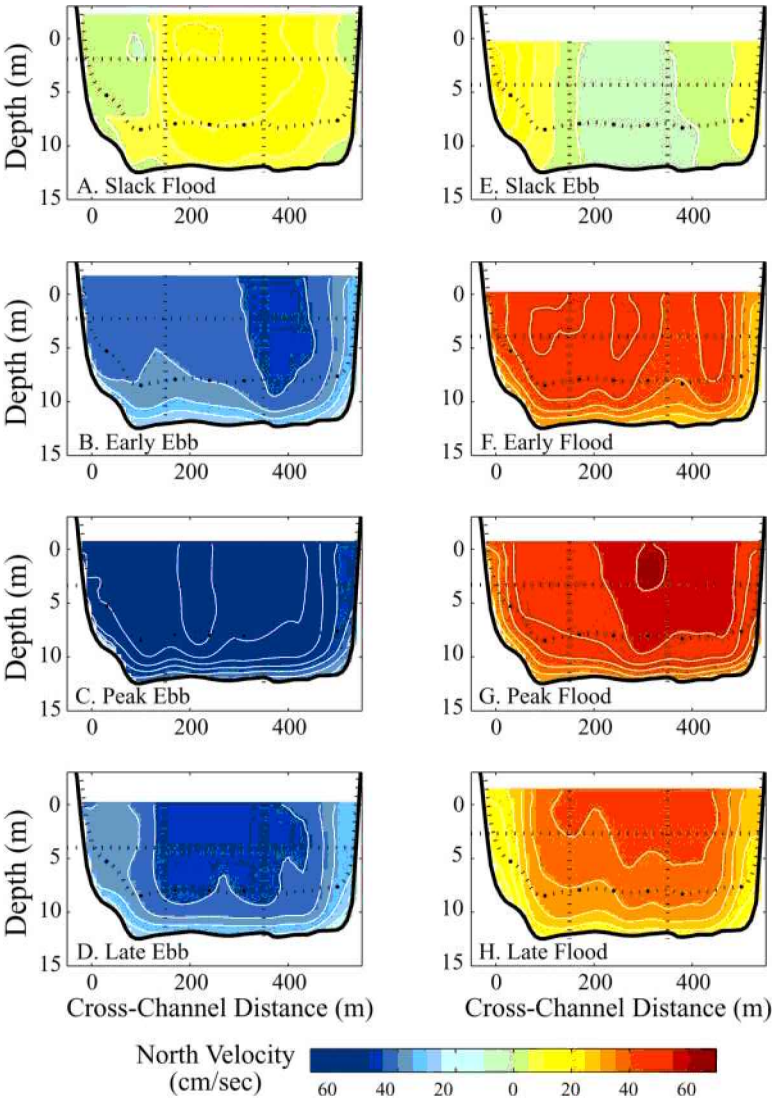

Figure 3. Cross-sectional time series plots of flow velocity at the Coronado Bay Bridge sampling transect (21–22 July 1997). Sections are shown looking approximately northwest, out of San Diego Bay, with the 10th Avenue Pier on the right (E, east) and North Island on the left (W, west). Sections correspond to (A) slack flood, (B) early ebb, (C) peak ebb, (D) late ebb, (E) slack ebb, (F) early flood, (G) peak flood, (H) late flood. The 0-m depth corresponds to a mean lower-low water tidal height.

throughout the flood tidal phase or whether the larvae intermittently migrate between the benthos and the water column. To accommodate these scenarios in larval behavior, two estimates of *P. crassipes* zoeal exchange at the SDBE site where the sediment water interface was sampled (see Results and Discussion) are provided here. One estimate

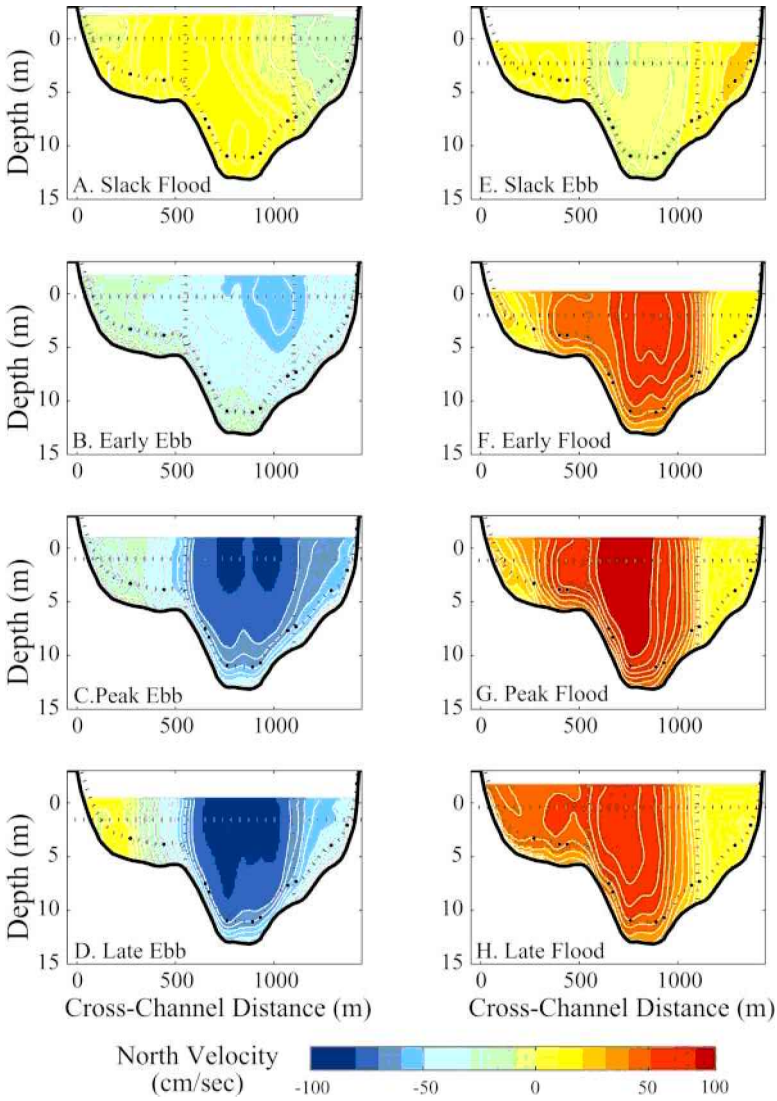

Figure 4. Cross-sectional time series of flow at the San Diego Bay Entrance sampling transect (18–19 August 1997). Sections are shown looking approximately north into San Diego Bay with Point Loma on the left and Zuñiga Jetty on the right. Sections correspond to (A) slack flood, (B) early ebb, (C) peak ebb, (D) late ebb, (E) slack ebb, (F) early flood, (G) peak flood, (H) late flood. The 0-m depth corresponds to a mean lower-low water tidal height.

represents larval exchange conducive with zoeae that occupy the bottom 2 meters of the water column during flood tide, thus experiencing transport into the bay during flood tide at velocities estimated *in situ* with the ADCP. The second estimate (see Discussion) assumes

Table 1. Larval exchange estimates (no. ind.) between (A) inner and outer regions of San Diego Bay (SDB) for stage I *Pachygrapsus crassipes* zoeae and combined stages of *Lophopanopeus* spp. zoeae and (B) between SDB and nearshore coastal waters for stage I *P. crassipes* zoeae. Larval exchange measurements were made over a complete semi-diurnal tidal cycle (12.4 hr) at the Coronado Bay Bridge (CBB; 21–22 July 1997) and San Diego Bay Entrance (SDBE; 18–19 August 1997) sites (see Fig. 1). Sectional larval exchange estimates are provided for vertical (surface, mid-depth, and bottom layers) and horizontal (eastern, mid-channel, western stations) sampling bins (see Fig. 2) during ebb and flood tidal phases. Net larval exchange estimates over a complete semidiurnal tide are provided at each site. Negative values indicate net exchange from inner to outer regions of SDB at the CBB site and out of SDB at the SDBE site. The sediment-water interface was not sampled at the CBB site (bottom, 0.5–2 meters above the bottom). The sediment-water interface was sampled at the SDBE; *P. crassipes* zoeae sampled in bottom layer are assumed to occupy and experience larval transport at flood tide velocities estimated for the bottom 2 meters of the water column.

Sample site, species	Sample depth	Ebb tide, western station	Ebb tide, mid-channel station	Ebb tide, eastern station	Flood tide, western station	Flood tide, mid-channel station	Flood tide, eastern station
A. CBB							
P. crassipes	Surface	-3.0×10^5	-1.2×10^6	-2.6×10^6	1.4×10^5	4.6×10^5	6.6×10^5
	Mid-depth	-4.8×10^5	-2.1×10^5	-1.1×10^6	8.4×10^4	2.5×10^5	6.3×10^5
	Bottom	-3.3×10^5	-4.4×10^5	-1.0×10^5	2.7×10^5	9.1×10^4	4.4×10^5
	Larval Exchange			**-6.7×10^6**			**3.0×10^6**
	Net Larval Exchange						**-3.65×10^6**
Lophopanopeus spp.	Surface	-2.5×10^6	-6.0×10^6	-6.9×10^6	8.9×10^6	4.0×10^6	1.8×10^6
	Mid-depth	-2.2×10^6	-3.6×10^6	-2.9×10^6	2.1×10^6	5.4×10^6	4.6×10^6
	Bottom	-2.6×10^6	-5.5×10^6	-3.2×10^6	2.4×10^6	4.7×10^6	2.8×10^6
	Larval Exchange			**-3.5×10^7**			**3.7×10^7**
	Net Larval Exchange						**1.28×10^6**
B. SDBE							
P. crassipes	Surface	-7.2×10^7	-2.4×10^8	-3.1×10^8	7.3×10^6	3.3×10^6	1.1×10^6
	Mid-depth	-3.6×10^7	-1.8×10^8	-9.2×10^7	3.6×10^7	4.7×10^6	7.2×10^5
	Bottom	-6.4×10^5	-3.5×10^5	-1.4×10^5	3.6×10^6	4.8×10^6	2.0×10^5
	Larval Exchange			**-9.2×10^8**			**6.2×10^7**
	Net Larval Exchange						**-8.63×10^8**

that *P. crassipes* zoeae negate transport during flood tide by exploiting the sediment water interface, thus maximizing net larval transport from SDB.

The net larval exchange of *P. crassipes* zoeae, integrated over a semi-diurnal tide, revealed a net transport from inner to outer regions of SDB at the CBB sampling site (3.65×10^6 individuals) and from outer SDB to nearshore coastal waters at the SDBE sampling site (8.63×10^8 individuals) (Table 1).

Station- and depth-specific sectional larval exchange estimates for *P. crassipes* zoeae at the CBB site were highest in surface and mid-depth layers (i.e., sampling bins) of the eastern station during ebb and flood tidal phases (Table 1A, Fig. 5A). Larval exchange

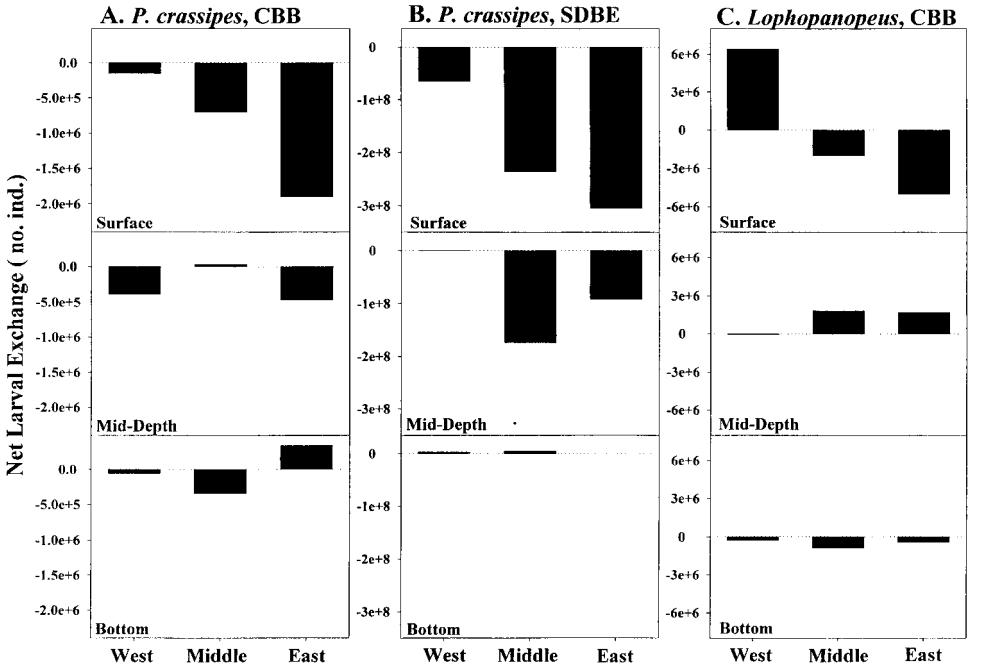

Figure 5. Station- and depth-specific larval exchange estimates for (A) stage I *P. crassipes* zoeae sampled at the Coronado Bay Bridge (CBB; 21–22 July 1997), (B) stage I *P. crassipes* zoeae sampled at the San Diego Bay Entrance (SDBE; 18–19 August 1997), and (C) combined stage I and post-stage I *Lophopanopeus* spp. zoeae sampled at the Coronado Bay Bridge (CBB; 21–22 July 1997). Sectional larval exchange estimates are presented for each sampling bin (defined in Fig. 1B and C). Though *Pachygrapsus crassipes* zoeae were observed to aggregate at the sediment water interface at the SDBE site, larvae are assumed to experience net transport at mean flood tide velocities estimated for the bottom 2 meters of the water column. Larval exchange estimates for larvae that avoid transport during flood tide by settling on the bottom can be estimated by setting flood tide, bottom sectional larval exchange estimates to zero. Adjusted net larval exchange estimates for *P. crassipes* larvae, which settle on the benthos during flood tide, are presented in the discussion. Note the different scales in Figures A and B.

estimates for these sampling bins were on average 1 to 2 orders of magnitude higher than estimates for other sampling bins and corresponded to the higher concentration of *P. crassipes* zoeae (Fig. 2A and B). Mean cross-sectional velocity estimates at the CBB site (Fig. 3) were generally uniform during ebb and flood tidal phases and likely contributed little to spatial differences in sectional larval exchange estimates. The difference in larval exchange estimates for ebb and flood tidal phases revealed a net larval exchange of *P. crassipes* zoeae from inner to outer SDB, with the largest sectional larval exchange estimates in the surface layer of the eastern station (Fig. 5A), where peak larval concentrations were observed (Fig. 2B).

Station- and depth-specific sectional larval exchange estimates for *P. crassipes* zoeae sampled at the SDBE site during ebb and flood tidal phases were more uniform than at the

CBB site (Table 1). This is reflected in a more even distribution of larvae collected among sampling stations at the SDBE site (Fig. 2C and D). Sectional larval exchange estimates were generally higher in surface and mid-depth layers of eastern and mid-channel sampling stations (Table 1B). Larval exchange estimates for sampling stations in the eastern half of the SDBE site were higher than western stations, in part because of higher mean velocity estimates for this region of the channel, particularly during the ebb tidal phase (Fig. 4B–D). Sectional larval exchange estimates were generally from SDB to nearshore coastal waters, and were highest in surface and mid-depth layers, especially in eastern and mid-channel sampling bins (Fig. 5B). Bottom layer sectional larval exchange estimates were several orders of magnitude lower than surface and mid-depth layers (Table 1, Fig. 5B).

ii. Lophopanopeus spp. The net larval exchange for *Lophopanopeus* spp. larvae sampled at the CBB site was from the outer to inner region of SDB (1.28×10^6 individuals). Sectional larval exchange estimates were quite uniform among sampling bins during both ebb and flood tidal phases (Table 1, Fig. 5C), reflecting a relatively uniform temporal and spatial (vertical and horizontal) distribution of *Lophopanopeus* spp. larvae at the CBB site (Fig. 2E and F) as well as uniform mean cross-sectional water velocity estimates (Fig. 3).

d. Origin-specific, bay-ocean exchange of P. crassipes larvae

i. Discriminant function analysis. Discriminant function algorithms, developed to discriminate SDB and non-SDB *P. crassipes* zoeae of known origin (reference zoeae) on the basis of trace element composition (DiBacco and Levin, 2000), were used to distinguish SDB from non-SDB spawned *P. crassipes* zoeae of unknown origin sampled in the present study. Reference zoeae used to develop discriminant function algorithms were collected over a three-month period (12 June to 15 September 1997) overlapping with field studies of the present study. This was done to ensure that inter-annual variations in elemental fingerprints would not confound results presented. A potential weakness of discriminant function algorithms is that they will classify any point (i.e., zoea) in discriminant function (DF) space, regardless of whether or not it is located inside the defined clusters of larvae of known origin. To determine the reliability of the classification algorithms employed here, we plotted DF1 and DF2 values calculated for larvae of unknown origin sampled at CBB (Fig. 6A) and SDBE sites (Fig. 6B) in the same discriminant function space defined by reference zoeae of known origin. The discriminant function space occupied by SDB and non-SDB reference zoeae, described in detail by DiBacco and Levin (2000), is outlined by dotted and dashed lines, respectively (Fig. 6). The points of unknown larvae cluster into two well-defined groups that reflect the distribution of known reference samples of SDB and non-SDB larvae (Fig. 6A, B), indicating that the discriminant function algorithms have captured a significant proportion of the natural variability in larval elemental fingerprints.

ii. Coronado Bay bridge. Trace element analyses indicated that the vast majority of *P. crassipes* zoeae sampled at the CBB site, located approximately 11 km from the bay's

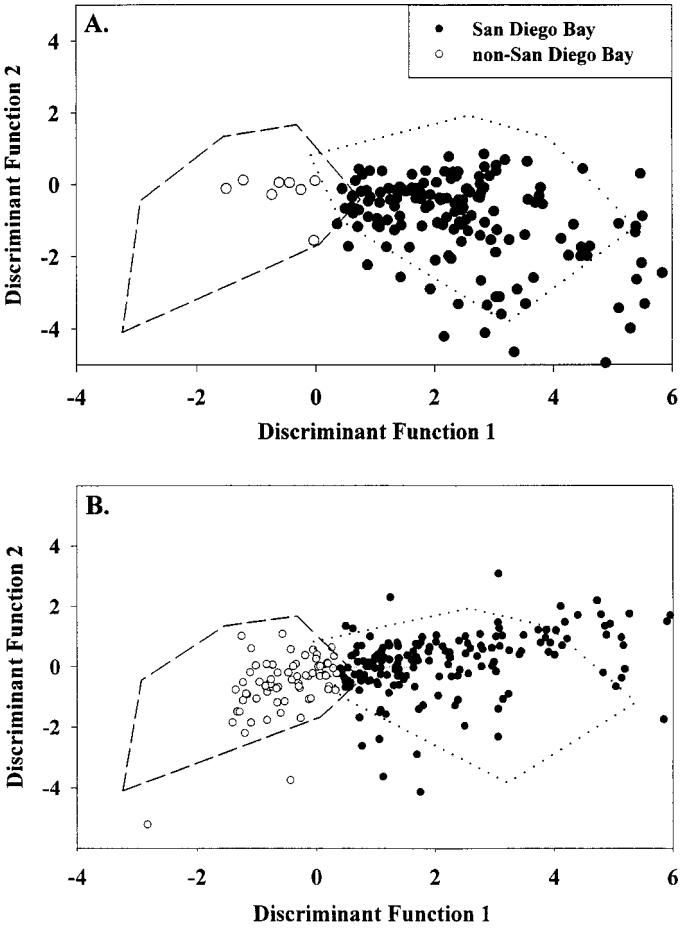

Figure 6. Plot of discriminant function values 1 and 2 (based on trace elemental composition) for zoeae of unknown origin sampled over a tidal cycle at the (A) Coronado Bay Bridge and (B) San Diego Bay Entrance sampling sites. Discriminant function space defined from reference stage I *Pachygrapsus crassipes* zoeae (of known origin) are shown for larvae originating from San Diego Bay (dotted line) and non-SDB (i.e., neighboring embayments and coastal sites; dashed line) sites. Note that most of the points, each of which represents a single larva of unknown origin, cluster within discriminant function space defined by the dotted and dashed lines, with only limited overlap.

entrance, originated within San Diego Bay (Fig. 7). Approximately 89 percent and 98 percent of zoeae sampled during ebb and flood tidal phase, respectively, originated from SDB (Fig. 7). The highest proportion of *P. crassipes* zoeae from SDB were observed in the surface layer during ebb tide conditions (Fig. 7A), while the vertical distribution was comparable between the surface and bottom layers during flood tide, when the sediment-water interface was not sampled (Fig. 7B). The highest proportion of zoeae collected at the

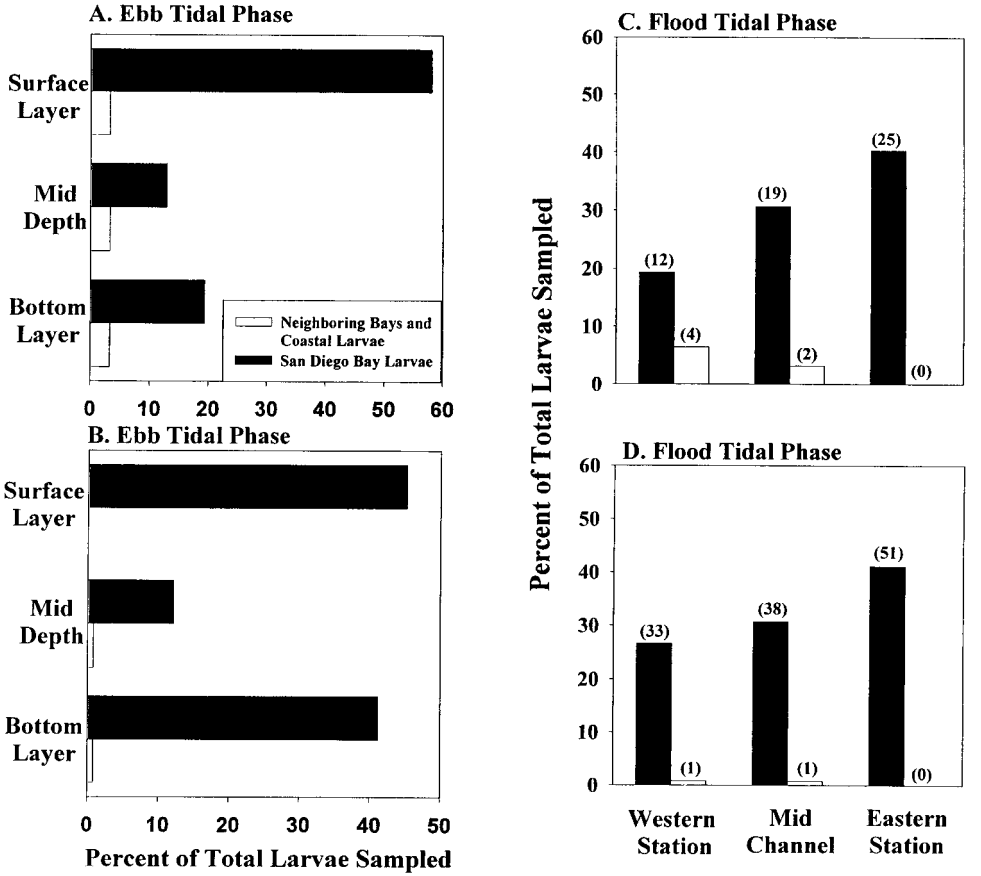

Figure 7. Temporal and spatial distribution of stage I *Pachygrapsus crassipes* larvae sampled at the Coronado Bay Bridge site and originating from San Diego Bay (SDB) or non-SDB populations. Larval origin was determined by trace element fingerprinting and discriminant function analysis (see Methods for details). Vertical distributions are shown for surface, mid-depth, and bottom layers during (A) ebb and (B) flood tidal phase. Horizontal distributions are shown for western, mid-channel, and eastern regions of the sampling transect during (C) ebb and (D) flood tidal phase. The number of larvae analyzed is given in parentheses.

CBB site, which originated from SDB, was sampled in the eastern station; larvae spawned from non-SDB populations were aggregated in the western station (Fig. 7C and D). When net larval exchange of *P. crassipes* zoeae was recalculated with only larvae that originated from SDB (Table 2), net larval exchange remained from inner to outer regions of SDB, but decreased by 0.72%.

iii. San Diego Bay entrance. A large proportion of larvae sampled at the SDBE site originated from non-SDB populations. Approximately 23 percent and 29 percent of *P.*

Table 2. Larval exchange estimates (no. ind.) between (A) inner and outer regions of San Diego Bay (SDB) and (B) SDB and nearshore coastal waters for stage I *P. crassipes* zoeae originating from SDB populations only. Larval origins were determined using trace elemental fingerprinting (see Methods and materials). Larval exchange measurements were made over a complete semi-diurnal tidal cycle at the Coronado Bay Bridge (CBB; 21–22 July 1997) and San Diego Bay Entrance (SDBE; 18–19 August 1997) sites (see Fig. 1). Sectional larval exchange estimates are provided for vertical (surface, mid-depth, and bottom layers) and horizontal (eastern, mid-channel, western stations) sampling bins (see Fig. 2) during ebb and flood tidal phases. Net larval exchange estimates over a complete semidiurnal tide are provided at each site. Negative values indicate net larval exchange from inner to outer regions of SDB at the CBB site and out of SDB at the SDBE site. The sediment-water interface was not sampled at the CBB (bottom, 0.5–2 meters above the bottom). The sediment-water interface was sampled at the SDBE; *P. crassipes* zoeae sampled in bottom layer are assumed to occupy and experience larval transport at flood tide velocities estimated for the bottom 2 meters of the water column.

Sample site, species	Sample depth	Ebb tide, western station	Ebb tide, mid-channel station	Ebb tide, eastern station	Flood tide, western station	Flood tide, mid-channel station	Flood tide, eastern station
A. CBB							
P. crassipes	Surface	-3.0×10^5	-1.2×10^6	-2.6×10^6	1.4×10^5	4.6×10^5	6.6×10^5
	Mid-depth	-4.8×10^5	-1.9×10^5	-1.1×10^6	8.4×10^4	2.5×10^5	6.3×10^5
	Bottom	-2.6×10^5	-4.4×10^5	-1.0×10^5	2.7×10^5	9.1×10^4	3.7×10^5
	Larval Exchange			**-6.6×10^6**			**2.9×10^6**
	Net Larval Exchange						**-3.63×10^6**
B. SDBE							
P. crassipes	Surface	-4.4×10^7	-2.4×10^8	-2.3×10^8	8.7×10^6	1.4×10^6	6.8×10^5
	Mid-depth	-1.8×10^7	-1.5×10^8	-9.1×10^7	3.2×10^7	4.7×10^6	7.2×10^5
	Bottom	-4.6×10^5	-3.5×10^5	-1.4×10^5	3.3×10^6	4.3×10^6	2.0×10^5
	Larval Exchange			**-7.7×10^8**			**5.2×10^7**
	Net Larval Exchange						**-7.1×10^8**

crassipes zoeae sampled at the SDBE site during ebb and flood tide, respectively, originated from populations outside of SDB (Fig. 6B, Fig. 8). The net larval exchange of *P. crassipes* zoeae between SDB and nearshore coastal waters was recalculated for SDB and non-SDB spawned larvae. San Diego Bay spawned larvae were still exported from the bay, but the net larval efflux was reduced from 8.6×10^8 individual zoeae (Table 1B) to 7.1×10^8 individual zoeae (Table 2B) over the sampled semi-diurnal tide, a decrease of 17.7%. The net larval exchange for non-SDB larvae also was out of the bay (1.9×10^7 individuals). The vertical distribution of *P. crassipes* zoeae spawned from SDB and non-SDB populations were similar, with a higher proportion of larvae in surface and mid-depth layers during ebbing tides and a higher proportion in the bottom layer during flooding tides (Fig. 8A and B). Both bay and coastal spawned larvae exhibit the same vertical migratory behavior. The horizontal distribution of SDB and non-SDB spawned larvae were similar with the majority of larvae aggregated in the western station (Fig. 8C and D).

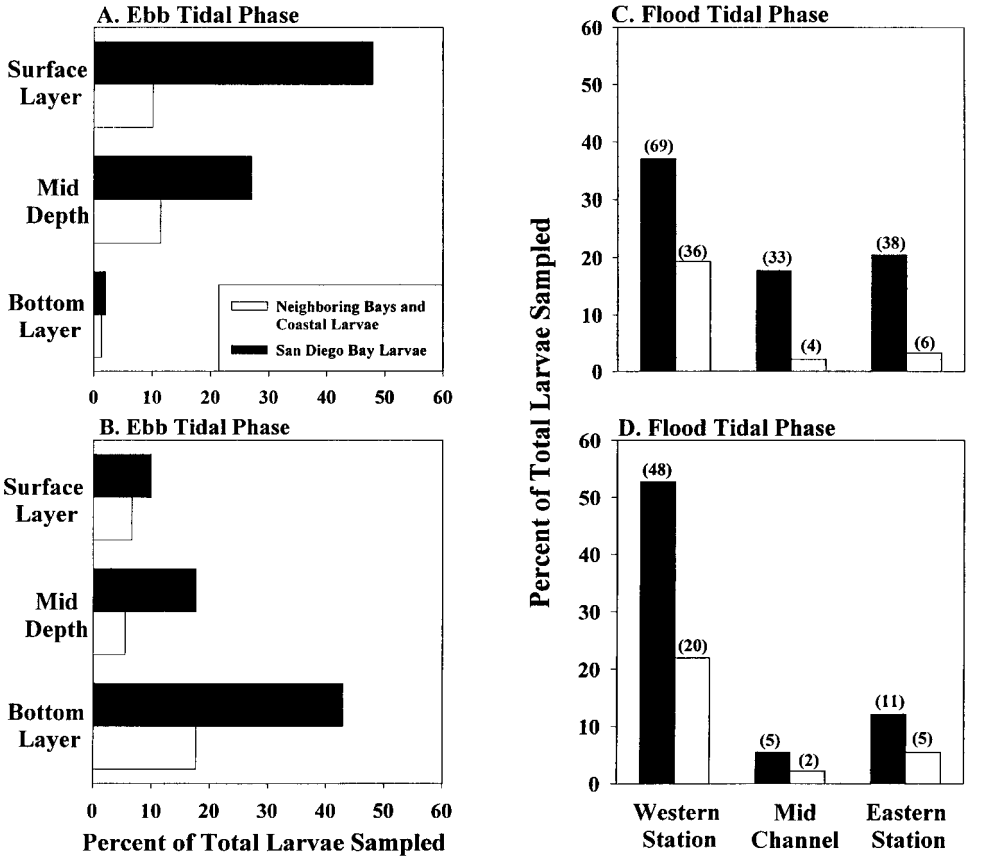

Figure 8. Temporal and spatial distribution of stage I *Pachygrapsus crassipes* larvae sampled at the San Diego Bay Entrance site and originating from San Diego Bay (SDB) or non-SDB populations. Larval origin was determined by trace element fingerprinting and discriminant function analysis (see Methods for details). Vertical distributions are shown for surface, mid-depth, and bottom layers during (A) ebb and (B) flood tidal phase. Horizontal distributions are shown for western, mid-channel, and eastern regions of the sampling transect during (C) ebb and (D) flood tidal phase. The number of larvae analyzed is given in parentheses.

4. Discussion

a. Influence of larval distribution on net transport

Results from this study show that the vertical and horizontal distributions of brachyuran zoeae, as well as their origin, had a significant effect on the net transport of larvae between bay and coastal populations. A number of recent studies have presented evidence that vertical migratory behavior by brachyuran larvae influences net transport between estuaries and nearshore coastal waters (e.g., Queiroga *et al.,* 1994, 1997; Lochman *et al.,* 1995; Rodriguez, 1997; Garrison, 1999). DiBacco *et al.* (2001) and this study observed that stage

I *P. crassipes* zoeae spawned in SDB exhibit vertical migratory behavior, which enhanced net transport from inner to outer regions of SDB and into nearshore coastal waters.

A number of biological (e.g., larval swimming behavior, spawning periodicity) and physical oceanographic processes (e.g., tidal exchange, water velocity) control the vertical and horizontal distributions of larvae. A critical assumption made by earlier studies in estimating net larval exchange or flux was that larval density is uniform across the cross-sectional area of the bay or channel being studied. However, this assumption is rarely tested. The horizontal distributions of both *P. crassipes* and *Lophopanopeus* spp. zoeae was not uniform and is probably influenced by the distribution of adult habitats, which act as point source release sites. *Pachygrapsus crassipes* and *Lophopanopeus* spp. adults inhabit high- and mid-intertidal regions, respectively. As a result, newly hatched zoeae are concentrated close to shore upon release. Tidal currents, especially during peak ebb and flood tidal phase, can effectively entrain newly released zoeae and keep them concentrated close to shore. Even a relatively uniform vertical distribution of larvae may not indicate that the horizontal distribution is homogeneous. *Lophopanopeus* spp. sampled in this study displayed no clear vertical migratory behavior, yet they exhibited heterogeneous densities between horizontal stations (Fig. 2E, F).

There have been no previous attempts to determine the influence of horizontal distribution of brachyuran larvae within coastal embayments on net larval transport. A relatively small number of studies have attempted to support predictions of net transport by quantifying net larval flux for a variety of decapod larvae (Emmerson, 1983; Christy and Stancyk, 1982; Lago, 1993). However, these studies determined larval abundance at one station and extrapolated sectional flux estimates to the whole cross sectional sampling area (discussed in Rowe and Epifanio, 1994).

The heterogeneous distribution of *P. crassipes* zoeae across sampling stations at both the CBB and SDBE sampling transects (Fig. 2) strongly influenced larval exchange estimates. At the CBB site, where cross-channel water velocities were relatively homogeneous, higher *P. crassipes* zoeal concentrations at the eastern station (Fig. 2B) resulted in higher sectional larval exchange estimates at that station (Table 1A). A net larval exchange estimate of *P. crassipes* zoeae at the CBB site extrapolated from mid-channel estimates of larval abundance alone would have been 37.0% lower (ca. 2.3×10^6 individuals) than the larval exchange estimated from all three stations occupied in this study (Table 1A). At the SDBE site, velocity estimates were higher at the mid-channel station, while larval densities were highest in eastern and western stations (Fig. 2D). If extrapolated from mid-channel estimates of larval abundance alone, the net larval exchange of *P. crassipes* zoeae between SDB and nearshore coastal waters would have decreased by 58.3% (ca. 3.6×10^8 individuals). Despite a relatively homogeneous vertical distribution of *Lophopanopeus* spp. zoeae, the net larval exchange extrapolated from mid-channel larval densities would have been an order of magnitude higher (ca. 1.3×10^7 individuals) than the net larval exchange estimated from all 3 stations (Table 1A).

A study considering vertical migratory behavior of *P. crassipes* zoeae conducted at the

CBB and SDBE sites revealed that a significant proportion of zoeae aggregated at the sediment-water interface during flood tide (DiBacco *et al.,* 2001). Since water velocity approaches zero at the sediment-water interface, *P. crassipes* zoeae that aggregate on the bottom and remain there during flood tide would minimize or avoid transport into SDB, thus enhancing net larval exchange from inner to outer regions of SDB and ultimately into coastal waters. At the SDBE site, where bottom layer samples collected in this study included the sediment water interface, net larval exchange estimates (Table 1 and 2) were recalculated with the assumption that *P. crassipes* larvae sampled in the bottom layer during flood tide experienced no net transport. This resulted in a seaward net larval exchange estimate that increased by approximately 6% (8.8×10^8 individuals) for *P. crassipes* zoeae that exploited the sediment water interface during flood tide. This suggests that larval behavior at the sediment-water interface may enhance net larval transport of *P. crassipes* zoeae from SDB and may be an important consideration for other larvae that facilitate or retard transport from embayments using vertical migratory behavior. However, larval behavior at the sediment water interface requires further consideration before definitive conclusions about its effect on net transport can be made.

Larval exchange approximations presented here may be maximal rates since they were estimated during spring tidal phases (full and new moon) when ovigerous *P. crassipes* tend to release zoeae en masse (DiBacco, 1999). Also, tidal exchange or tidal excursion between inner and outer regions of SDB and between the bay and nearshore coastal waters is greater during spring tides (Chadwick and Largier, 1999). This means that a larger volume of water is exported during ebb and imported during flood tidal phases and that seawater constituents (i.e., larvae) are transported over a greater horizontal distances during spring tidal conditions. Spring tides should result in a larger net transport per tidal cycle for *P. crassipes* zoeae, which enhance net transport by migrating into the water column on ebbing tides and into the benthic boundary layer on flooding tides. Finally, interannual and seasonal variability in the timing and magnitude of spawning events for ovigerous *P. crassipes* has been documented (Boolootian *et al.,* 1959). Larval exchange estimates would be expected to vary with the reproductive condition of ovigerous *P. crassipes* during the sampling period.

b. Bay-ocean larval exchange: Insights from elemental fingerprinting

Trace elemental fingerprinting of newly hatched *P. crassipes* zoeae revealed (1) a significant exchange of larvae between SDB and nearshore coastal waters at the entrance of SDB and (2) the presence of non-SDB *P. crassipes* zoeae at the CBB site, approximately 11 km from the mouth. Transport out of SDB was predicted from *P. crassipes*' vertical migratory behavior relative to tidal phase, but approximately 26% of larvae sampled at the entrance of SDB during flood and ebb tidal phases originated from populations located outside the bay. This represents potential for significant exchange between SDB and non-SDB crab populations.

The observed bi-directional exchange of larvae, which was revealed by elemental

fingerprinting, could be explained by the leakage of larvae between bay and coastal habitats if larval migration and tidal phase are not synchronized. This has been suggested for crab larvae that experience a lag between the time the tide turns and active migration to a new depth in the water column (Epifanio, 1988). In this study, 65%, 28% and 6% of *P. crassipes* zoeae sampled during ebb tide were in surface (0.5 to 2 m), mid-depth (5 to 7 m) and bottom layers (<2 meters above the bottom), respectively, while 12%, 16% and 72% were sampled in surface, mid-depth and bottom layers during peak flood tide. Zoeae transported into SDB or spawned within the bay that do not exhibit vertical migratory behavior are likely to be retained within the bay through development, as was the case for *Lophopanopeus* spp.

The transport of non-SDB larvae into the bay may be aided by bay-specific flow dynamics (Dyer, 1997). In bays with narrow inlets, like SDB, tidal exchange is often characterized by an ebb-flood asymmetry in which the ebb flow exits the bay as a jet, while the flood flow is drawn in from a radial sink, a process referred to as "tidal pumping" (Fischer *et al.,* 1979). This could act as a source for the influx of coastal spawned zoeae as well as zoeae recently exported from SDB. The efficiency of the tidal pumping mechanism for transporting larvae from coastal waters into the bay may be enhanced by eddy-like features observed to form along the eastern boundary outside of the SDB entrance (Chadwick and Largier, 1999). Hendricks and Christensen (1987) showed that approximately 25% of the variability in non-tidal residual flow in the region southeast of Point Loma, outside SDB, was explained by an eddy mode circulation. Circulating eddies at the mouths of embayments have been suggested to act as potential traps which concentrate larvae just outside the bay's entrance (Pattiaratchi, 1994). As the tide turns to flood, water in this region is some of the first to be drawn into the bay. Once inside the bay, larvae that do not exhibit vertical migratory behavior conducive with net transport from the bay or do not migrate at all will likely be retained within SDB. Larval transport simulations using a validated hydrodynamic model of SDB predicted that larvae that do not exhibit tidally timed vertical migratory behavior would be retained within the bay (DiBacco *et al.,* 2001). This was observed in situ for *Lophopanopeus* spp. zoeae, which do not migrate vertically and which were retained within SDB though all stages of zoeal development (DiBacco *et al.,* 2001).

An analysis of current measurements about 10 km SSW of Point Loma indicate northward flow (up-coast) about 31% of the time and southward flow (down-coast) about 68%, with typical longshore flow speeds between 5 to 20 cm sec^{-1} (Hendricks and Christensen, 1987). These data suggest that *P. crassipes* populations located both north and south of SDB could have contributed the non-SDB larvae that were sampled in the bay.

c. Significance of bay-ocean exchange

The effect of temporal changes in the vertical distribution of decapod larvae on net transport has been well documented, especially for brachyurans found within estuaries. This study revealed that the horizontal distribution of larvae also has a significant effect on

net larval transport estimates. Although recent improvements in equipment have allowed estimates of larval exchange rates, more efficient methods for assessing temporal and spatial plankton distribution patterns will further improve estimates of net larval transport. Such methods include moored, automated, serial, zooplankton pumps (MASZP) designed for making time series collections of planktonic larvae *in situ* (Butman, 1994) and continuous underway plankton-sampling systems which can effectively provide nearly-synoptic, integrated abundance estimates over a large area (Checkley *et al.,* 1997).

In addition to the temporal-spatial distribution of larvae, the distribution of adult source and hydrodynamic processes of SDB had an effect on net transport and bay-ocean exchange of larvae. Knowledge of *P. crassipes* zoeal origins allowed more accurate larval exchange measurements to be made and provided insights into potential exchange of larvae between bay and coastal populations. Since most *P. crassipes* zoeae leave SDB and complete development in coastal waters before re-entering and recruiting to adult populations, it will be necessary to consider the dispersal and fate of post-stage I zoeae and megalopae in future research. The ability to accurately assess larval exchange rates and to discriminate larval origins offers the potential for improved understanding of many aspects of larval dynamics in estuarine and nearshore ecosystems. Larval exchange between bay and coastal populations, and among populations within bays, may greatly influence larval survivorship, gene flow and the ability of populations to be self-sustaining.

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