

2006

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Original Publication Citation

Yannicelli, B., Castro, L. R., Valle-Levinson, A., Atkinson, L., & Figueroa, D. (2006). Vertical distribution of decapod larvae in the entrance of an equatorward facing bay of central Chile: Implications for transport. *Journal of Plankton Research*, 28(1), 19-37.

doi:10.1093/plankt/fbi098

Vertical distribution of decapod larvae in the entrance of an equatorward facing bay of central Chile: implications for transport

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Received April 27, 2005; accepted in principle July 25, 2005; accepted for publication November 3, 2005; published online November 23, 2005

Communicating editor: K.J. Flynn

Two short biophysical surveys were carried out in order to assess how the decapod crustacean larvae vertical distribution and circulation patterns in an equatorward facing embayment (Gulf of Arauco, 37° S; 73° W) influenced larval transport into and out of the Gulf. The embayment is located at the upwelling area of south central Chile and features a deep (~60 m) and a shallow (~25 m) pathway of communication with the adjacent coastal ocean. Profiles of zooplankton, temperature, salinity, dissolved oxygen and current velocity were measured during a 22-h period at the shallow entrance to the gulf. In addition, three zooplankton profiles were carried out at the deep entrance to the gulf on the basis of observed changes in hydrographic structure. At the shallow entrance to the gulf, current velocities showed a clear semidiurnal tidal signal, with stronger ebb than flood at the surface and stronger flood at depth. Decapod larval abundances showed a bimodal distribution through time, with a maximum during night-time ebb, and a smaller, second peak at day-time ebb. Larval transport in and out of the Gulf depended on larval vertical distribution and the timing of higher densities. Export was reduced when larvae deepened during ebbing tides or when larvae remained deeper throughout the day. Export was enhanced when larger numbers of individuals occupied ebbing surface waters. At the deep entrance, two groups of crustacean larvae were found associated with two different water types: a surface high oxygen water and a deeper suboxic equatorial subsurface water. A group of larvae that originates in the shelf area appeared entering the Gulf in the deeper waters of this entrance but was absent from the shallower one. Larval vertical distribution in the two layer circulation at the embayment entrances can enhance or preclude retention within the bay. The motion of these layers was determined remotely by upwelling dynamics and modified by local wind (sea breeze) and tides. Overall, high frequency processes (semidiurnal tides, diurnal fluctuations) superimposed onto others of lower frequency (3–8 d period of wind-driven upwelling), may contribute significantly to variations in the transport of individuals from bays in upwelling areas.

INTRODUCTION

It has been recognized that the heterogeneity of coastal topography creates hydrodynamic circulation features that affect the transport of inert particles and plankton (Archambault *et al.*, 1998; Archambault and Bourget, 1999). Because gulfs and bays have higher residence

times than the adjacent open coast, they have been identified as nursery areas in continental shelves under the influence of different physical forcing. This is particularly evident at embayments in upwelling regions, where high vertebrate and invertebrate larval concentrations have been reported (Pedrotti and Fenaux, 1992; Castillo *et al.*, 1991; Graham *et al.*, 1992; Wing *et al.*,

1998). In these upwelling regions, an increase in plankton concentration occurs even in open gulfs, particularly downwind of headlands. Upwelled water at headlands frequently intrudes into the adjacent embayment, where cyclonic re-circulation increases the residence time and facilitates retention and concentration of organisms (Graham and Largier, 1997).

In conjunction with water circulation features, specific larval behaviour might enhance or preclude their retention. Decapod crustacean larvae can regulate their vertical position in the water column following diverse environmental cues and/or endogenous biological rhythms (Forward *et al.*, 1997). This ability allows the use of depth-varying current fields to regulate horizontal position in dissimilar environments as has been shown in tidally dominated estuaries (Epifanio, 1988; Queiroga *et al.*, 1997), as well as in buoyancy-driven and in wind-forced continental shelf waters (Wing *et al.*, 1998; Epifanio and Garvine, 2001). Therefore, the combination of physical forcing and specific animal behaviour is believed to determine the fate of meroplankton in an embayment like the Gulf of Arauco.

The Gulf of Arauco ($37^{\circ}10' \text{ S}$ – $36^{\circ}45' \text{ S}$) is the largest equatorward facing bay in south central Chile where southerly (S) to southwesterly (SW) upwelling favourable winds dominate from mid-spring through late summer. During this season, large concentrations of chlorophyll *a* (Chl *a*) and zooplankton have been measured in the gulf in the past decades (Castillo *et al.*, 1991; Castro *et al.*, 1993). Djurfeldt (Djurfeldt, 1989) proposed that a wind-induced subsurface advection of the nutrient-rich equatorial subsurface waters (ESSW) into the gulf through Boca Grande (BG) (Fig. 1) and mixing due to an internal

wave breaking at the head of the gulf during upwelling reversals was responsible for the high productivity of the gulf. More recently, Parada *et al.* (Parada *et al.*, 2001) and Valle-Levinson *et al.* (Valle-Levinson *et al.*, 2003) have proposed that the diel wind pattern and tidal regime would lead to recirculation processes that would also enhance Chl *a* and plankton concentrations.

To date, few studies have addressed questions on meroplankton transport mechanisms in the highly productive upwelling area of south-central Chile. A subsurface transport of mesopelagic organisms to the shelf and gulf during the upwelling season has been suggested to result from the diel vertical migration of larvae embedded in the two layer wind-driven circulation (Castro *et al.*, 1993; Vargas and Castro, 2001; Landaeta and Castro, 2002). In the adjacent Concepción Bay ($36^{\circ}40' \text{ S}$), an increase in crustacean larval abundance has been observed during flooding tidal currents and a decrease during southerly (upwelling favourable) winds (Carbajal, 1997). However, coupled bio-physical studies directed to understand the interaction between crustacean larvae vertical distribution and circulation patterns in determining transport to or retention in coastal environments have not been carried out yet in this area.

During the second week of December 2000, a field study aimed to characterize the wind-induced influence in the general circulation of equatorward facing bays in eastern boundary currents was carried out in the Gulf of Arauco. This study was conducted within that framework. We selected groups of decapod larvae in order to (i) assess the relationship between the pattern of larval abundance with diurnal and semidiurnal environmental cycles and (ii) infer how the larval vertical distribution and the prevailing circulation influenced their transport into and out of the gulf during upwelling favourable winds through the small entrance to the Gulf of Arauco. At the deeper entrance to the Gulf we sought to determine what groups of larvae prevailed at surface or subsurface waters and their relationship with adult habitat depth range and life history.

METHOD

Study site

The Gulf of Arauco is located in the area of widest continental shelf in the Chilean coast. A large change in coastal orientation and an enhancement of coastal upwelling occurs at the western cape of the gulf (Punta Lavapie; Fig. 1). The presence of Santa Maria island in the west, divides the gulf in two openings: Boca Chica (BC), a narrow and shallow opening on the west, and Boca Grande a wider and deeper one in the north where

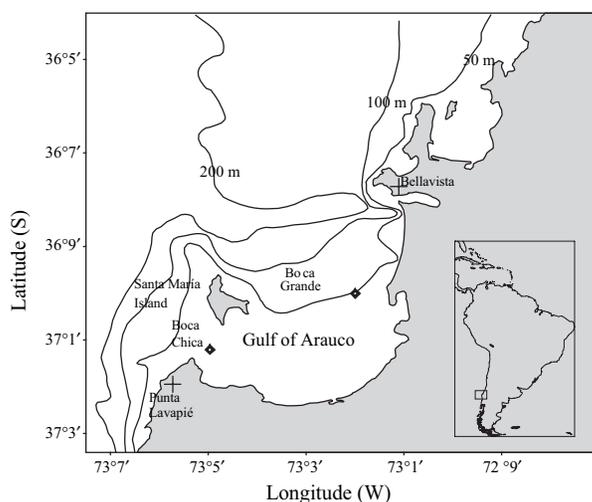


Fig. 1. Gulf of Arauco at Central Chile, and location of sampling stations Boca Chica and Boca Grande.

most water exchanges with the adjacent ocean. Although the bathymetry is smooth within the gulf, the narrow and deep BioBio submarine canyon cuts the shelf from east to west just a few kilometres to the north of the gulf. The BioBio river, the largest in the region, discharges mainly during winter, so no important fresh-water buoyancy forcing was expected during this study. Tides are semidiurnal with a fortnight cycle (amplitude range from 0.5 to 1.5 m in neap and spring tides, respectively).

Boca Chica survey

An intensive 22-h hydrographic and biological sampling was conducted at Boca Chica over a fixed, 17-m deep station, on 8 and 9 December 2000. This survey sought to assess the daily pattern of abundance of larvae and the interaction between the diel larval vertical distribution and the prevailing flow patterns during an active upwelling period. The survey was originally intended to collect data during two semidiurnal tidal cycles (25 h). However, unfavourable weather conditions hindered completion of the full period. Sampling was carried out onboard the R/V *Kay-Kay* of Universidad de Concepción. The boat remained anchored during sampling. Currents were measured with RD Instruments 307 kHz workhorse acoustic Doppler current profiler (ADCP). The ADCP was positioned at 1 m below the surface, pointing downward. Water velocity data were collected at 5-s intervals (pings) and averaged over 30 min at vertical resolutions (bin size) of 1 m. Water velocity was decomposed into east (u) and north (v) components. Positive signs corresponded to eastward and northward flow. Profiles of temperature, conductivity and dissolved oxygen were also obtained every 30 min with a Sea Bird SBE-19 conductivity-temperature-depth recorder with an oxygen sensor (CTDO). These data were converted to salinity and density and further processed to 1-m bins using the manufacturer's software (Seasoft). Additional field data included winds at Punta Lavapie ($37^{\circ}10' S$, $73^{\circ}35' W$) recorded every 10 min and solar radiation, collected at Bella Vista (Fig. 1). These data were averaged every 30 min. Sea surface temperature (SST) and SeaWifs images were also available. To identify diurnal and semidiurnal harmonic constituents of current velocity in u , we fitted a sinusoidal function:

$$u = A_c + A_s \cdot \sin\left(\frac{t}{2} + f_s\right) + A_d \cdot \sin\left(\frac{t}{4} + f_d\right)$$

for depth averaged u , and also for u at 5-, 10- and 15-m depths, where t is local time, f_s and A_s are phase and amplitude of semidiurnal oscillation, f_d and A_d the respective parameters for diurnal component and A_c accounts for the mean current. The semidiurnal fluctuation is given by $t/2$ (approximately equal to the more familiar form $2 \times \pi \times$

$t/12$) and the diurnal fluctuation by $t/4$ ($\sim 2 \times \pi \times t/24$). We fitted functions for averaged u in order to analyse the main flow cycles explaining variability at Boca Chica and for u at every depth in order to determine whether cyclic behaviour was maintained through the water column. The semidiurnal component had a 12-h period (only longer time series would allow the separation of different semidiurnal tidal components). The diurnal component had a 24-h period, and it would reflect diurnal fluctuation other than those due to diurnal tide, since diurnal tide was negligible in the area during the period sampled (Valle-Levinson *et al.*, 2003).

Zooplankton samples were collected at three fixed depths ($d_1 = 5$, $d_2 = 10$ and $d_3 = 15$ m) with a 1 m² mouth Tucker trawl net (300- μ m mesh), equipped with a calibrated flow meter. The Tucker trawl medium net was opened and closed from the deck, so at each sampling time and depth, it was towed, opened at a desired depth and allowed to drift for approximately 10 min, then closed and retrieved. Filtered volume ranged from 50 to 100 m³ per sample, which represented between 10 and 50 times larger volumes than those usually reported in studies with comparable objectives. Zooplankton sampling began at 17:15 h (on the 8 December) and continued until 14:40 (9 December). Profiles (each constituted by 5-, 10- and 15-m depth samples) were conducted at approximately 2-h intervals. A total of 12 zooplankton profiles were obtained (Table I). Once the zooplankton samples were on board, they were preserved in 5% formalin buffered with Borax, for later analyses. In the laboratory, samples were fractionated and subsamples were used for analysis under a

Table I: Sampling schedule followed at Boca Chica

| Tow | Local time | Light | Tidal phase |
|-----|-------------|-------|----------------|
| 1 | 17:15–17:45 | D | F |
| 2 | 18:55–19:25 | D | F |
| 3 | 20:55–21:25 | N | High water (F) |
| 4 | 22:45–23:15 | N | E |
| 5 | 1:02–1:32 | N | E |
| 6 | 2:53–3:23 | N | Low water (E) |
| 7 | 4:45–5:15 | N | F |
| 8 | 6:35–7:35 | D | F |
| 9 | 8:40–9:10 | D | High water (F) |
| 10 | 10:35–11:30 | D | E |
| 11 | 12:50–13:20 | D | E |
| 12 | 14:40–15:10 | D | Low water (E) |

D, day (solar radiation > 0); E, ebbing tidal phase; F, flooding tidal phase; N, night (solar radiation = 0). High and low water are followed by an 'F' or 'E' to indicate their inclusion as a flooding or ebbing phase in variance analysis.

stereo-microscope following standard procedures (Boltovskoy, 1981). Zoeas of Brachyura, Anomura and Thalassinidea (Crustacea, Decapoda) were separated.

Target species

Larval behaviour might differ among crustacean species, even among larval stages within a species. Therefore in the present study we analysed several taxa with different characteristics (both at the larval and adult stages) to compare individual patterns in the same hydrodynamic setting. We included in our study species with different life cycles (adult habitats type and depth range, and larval developmental times). In addition, abundance and

frequency of occurrence should be enough to allow statistical analysis. The degree of detail in taxonomic identification was constrained by the availability of larval descriptions (Wehrtmann and Báez, 1997), compared to the high diversity of decapod crustaceans in the area (Retamal, 1981). The analysis included several species and also groups of species (belonging to the same genus or family) when it was not possible to identify individual species, and adults were known to present similar depth range. The use of groups of similar species is useful when the components share certain characteristics (Wing *et al.*, 1998). The list of species and their characteristics are presented in Table II. In addition to groups and species

Table II: Decapod crustacean larvae identified at Boca Chica (BC) and Boca Grande, average density (individuals/100 m³) out of non-zero samples for each site and frequency of occurrence (number of positive samples out of the 35) at BC

| Species/group and family | Infraorder | Mean density | Frequency | Mean density | Adult habitat type | Larval stages |
|--|---------------|--|------------|---|--------------------|-------------------------------------|
| | | (individuals /100 m ³) Boca Chica | Boca Chica | (individuals /100 m ³) Boca Grande | | |
| <i>Cancer</i> spp. (Cancridae) | Brachyura | 706 | 35 | 48 | Ro S/D | 5 (Quintana, 1981) |
| <i>Neotrypaea uncinata</i> (Callianassidae) | Thalassinidea | 584 | 33 | 271 | Mu S | 5 (Aste, 1982) |
| <i>Pagurus</i> spp. (Paguridae) | Anomura | 208 | 35 | 62 | S | 4 (Lavados, 1982) |
| <i>Pinnixa</i> spp. (Pinnotheridae) | Brachyura | 147 | 33 | 22 | Co S | |
| Porcellanidae | Anomura | 117 | 35 | 14 | Ro I | 2 (Saelzer <i>et al.</i> , 1986) |
| <i>Blepharipoda spinimana</i> (Albuneidae) | Anomura | 54 | 33 | 6 | Sa I | |
| <i>Pinnotheres politus</i> (Pinnotheridae) | Brachyura | 51 | 34 | 3 | Co S | 5 (Saelzer and Hapette, 1986) |
| <i>Halicarcinus planatus</i> (Hymenosomatidae) | Brachyura | 37 | 31 | 2 | S | 2 (Boschi <i>et al.</i> , 1969) |
| <i>Pisoides edwardsi</i> (Majidae) | Brachyura | 14 | 29 | 3 | S | 2 (Faguetti, 1969a) |
| <i>Emerita analoga</i> (Hippidae) | Anomura | 4 | 29 | 34 | Sa I | 5 (Johnson and Lewis, 1942) |
| Grapsidae | Brachyura | 6 | 23 | 3 | I | 5 |
| <i>Callichirus garthi</i> (Callianassidae) | Thalassinidea | 8 | 17 | 30 | Mu S | 5 (Aste, 1982) |
| <i>Pleuroncodes monodon</i> (Galatheaidae) | Anomura | 5 | 21 | 50 | D | 8 (Faguetti and Campodonico, 1971a) |
| <i>Talipes</i> spp. (Majidae) | Brachyura | 0 | 0 | 2 | S | 2 (Faguetti and Campodonico, 1971b) |
| <i>Libidoclaea granaria</i> (Majidae) | Brachyura | 0 | 0 | 4 | D | 2 (Faguetti, 1969b) |

The habitat type and depth range of adult species is also shown: D, deep; Co, commensal; I, intertidal; Mu, muddy bottoms; Ro, rocky bottoms; S, subtidal; Sa, sandy bottoms. Also, number of stages during larval development (when it has been described).

identified (Table II), individual stages of *Neotrypaea uncinata* were recognized (Aste, 1982).

Boca Chica data analysis

At Boca Chica, larval concentration at each profile (i) and depth (d) was expressed as density N_{id} (number of individuals per 100 m³). In this analysis only, taxa present in over 65% of samples were included (Table II). In order to identify whether organisms density fluctuations throughout the day followed a semidiel and/or diel pattern, we averaged density for each profile, to obtain \bar{N}_i , and fitted a sinusoidal function to the log ($\bar{N}_i + 1$), similar to the one used for current measurements:

$$\log(\bar{N}_i + 1) = A_c + A_s \cdot \sin\left(\frac{t}{2} + f_s\right) + A_d \cdot \sin\left(\frac{t}{4} + f_d\right)$$

where t is local time, f_s and f_d (in hours) are phases of semidiel and diel oscillations, A_s and A_d are the corresponding amplitudes and A_c (1/m³·h) is a constant that accounts for the mean larval concentration. The logarithm of mean density was taken since zooplankton samples displayed a log-normal distribution and least square procedures used to estimate model parameters rely on normally distributed residuals. When the model as a whole did not apply to data, but just one of the terms (semidiel or diel), we removed the non-significant cyclic component and re-calculated the percentage of variance explained by the semidiel (12-h period) or diel (24-h period) component. Both phase and amplitude parameters of the diel and/or semidiel components had to be significant in order to be included in the model and considered indicative of the presence of such a cycle. Once the parameters of the regression were estimated (a least squares procedure was followed with both Excel Solver and STATISTICA packages), the time and magnitude for expected maxima during the 24-h cycle were calculated. The rationale behind this approach is that if organism density fluctuates conspicuously according to a natural physical cycle, we could expect a density curve to follow the cycle despite smaller scale variability. Therefore, density could be modelled as a continuous non-linear function of time. Our short Eulerian study allowed us to perform this type of analysis because of the large sampling unit (filtered volume) and a 2-h time resolution. The successful fitting of parameters allowed estimation of the expected time of largest concentration. The approach of using continuous trigonometric functions to describe cyclic biological changes has recently been used for analysing seasonal plankton abundance patterns and tendencies, for longer time series robust methods have been developed (Dowd *et al.*, 2004). For consistency with physical and biological

literature, we will refer to diurnal and semidiurnal physical oscillations and diel, semidiel biological oscillations referring to 24- and 12-h oscillations respectively.

In order to identify whether vertical distribution of organisms during this study followed a semidiel and/or diel pattern we first calculated the weighted mean depth (WMD) for each profile (i):

$$WMD_i = \frac{\sum_{d=1}^3 (N_d \times D)}{\sum N_d}$$

where D stands for sampled depth, and a two-way analysis of variance (ANOVA) was performed to test the effects of factors: light (day light, no light) and tidal phase (ebb, flood). Our design was orthogonal but unbalanced (Table I). The timing of some profiles coincided with slack tides (high and low waters) so the level ‘ebb’ in fact included ebbing plus low water, and the level ‘flood’ referred to flooding plus high water. The categorical division of a continuous phenomenon (such as taxon by taxon displays of temporal changes in WMD) might be rather arbitrary; hence, we also applied the previously described harmonic function to the weighted mean depth distribution. The analysis and visualization of data supplied by the trigonometric function fitting complemented that of the two-way ANOVA.

Transport depends on the quantity of organisms present in a given water parcel and the magnitude and direction of flow they are subject to. In this study, tidal signals on current velocity were superimposed on other signals so even ebbing tides could result in positive (inflowing) velocities at some depths. In order to understand how larvae were being transported we estimated the larval flux (LF) for each depth and profile as the number of larvae crossing a one m² section per hour:

$$LF_{id} = \frac{N_{id} \cdot u_{id}}{100}$$

where u_{id} is the east velocity component (m h⁻¹) at each profile (i) and depth (d). We analysed whether the LF at profile ($\sum LF_d$ for each profile i) depended on light or tidal phase with a two-way ANOVA. Factor levels were defined as in the previous analysis on mean weighted depth, except that we did not include data for slack tides.

If the water velocity at any given time differs between depths, larvae might gain or lose velocity by concentrating at the bottom, middle or surface layers (Queiroga *et al.*, 1997). The larval velocity relative to the water column (relative larval velocity) provides a quantification to understand whether LF results from net gain or loss of velocity. For each profile, the vertically integrated net

larval velocity (LV_i) in m h^{-1} was calculated following Queiroga *et al.* (Queiroga *et al.*, 1997):

$$LV_i = \frac{\sum N_{id} \cdot u_{id}}{\sum N_{id}}$$

We averaged u_5 , u_{10} and u_{15} for each tow (AV_i), and we calculated the difference between LV_i and AV_i which resulted in the relative larval velocity (RLV_i). We did not perform statistical analysis in this last index, but used it as a descriptive tool.

Boca Grande surveys

In order to identify groups of crustacean larvae that were potentially associated with the previously described two-layer wind-driven circulation in the gulf at Boca Grande (Fig. 1), an adaptive stratified sampling strategy was followed. The depth and width of the strata sampled for zooplankton was determined after CTDO and ADCP data inspection at the station, which allowed the identification of thermocline, oxycline, water types and changes in flow direction. Current velocity, water temperature, conductivity and dissolved oxygen concentration, were measured with the same instruments as in Boca Chica, along transects from Coronel to Santa Maria Island on five different dates between 4 and 10 December. In the middle of the Boca Grande transect, zooplankton was collected by means of Tucker trawl (300- μm mesh) oblique tows on three different dates (4, 6 and 10 December). Organisms were collected at three or four adaptive strata (Table III). Physical data are reported only for the stations where zooplankton was collected. Zooplankton samples followed the same preservation and processing routine

as those from Boca Chica. Number of individuals was first standardized to 100 m^3 and then the number of individuals per 100 cubic meter were multiplied by the depth of the corresponding stratum (and divided by 10) to obtain individuals per 10 square meter (m^2). We used these units to express our data because we were interested in the quantity of individuals that were subject to a given condition and water mass (e.g. flow direction, oxygen level).

Boca Grande data analysis

It has been reported that ESSW characterized by low oxygen, high salinity and low temperatures are found below the surface in the Gulf of Arauco during the upwelling season (Djurfeldt, 1989; Valle-Levinson *et al.*, 2003). Therefore we used low oxygen concentrations ($<2 \text{ mL/L}$) as an indicator of deeper waters. In order to assess whether individual species were associated with a water type we performed a quotient analysis (q) following Van der Lingen *et al.* (Van der Lingen *et al.*, 2001). Samples from the three sampling dates were sorted into four classes of oxygen concentration. We calculated the mean oxygen concentration for each stratum and samples were sorted in classes: 0–1, 1–2, 3–4 and $>4 \text{ mL/L}$. Class 2–3 mL/L was left aside because no sample had that average dissolved oxygen concentration. For each species, observed frequencies (f) in each class (i) were calculated by adding up the number of individuals per 10 m^2 of all samples that fell within class i . For each oxygen class, f_i was divided by the total number of individuals per 10 m^2 caught in Boca Grande to find the percentage frequency of occurrence (pf_i) of individuals within a class. Also, the number of samples (s) within each class was determined, and the percentage frequency of samples (ps_i) within a class was calculated. Estimates of q were determined between those two quantities (pf_i/ps_i) because values of q over 1 have been used as indicative of environmental preference (Van der Lingen *et al.*, 2001).

We also aimed to identify groups of species that behaved similarly regarding vertical distribution, so we produced a similarity matrix for species, using oxygen classes as samples, and the quotient pf_i/ps_i as raw data. Similarity was calculated with the Bray Curtis Index on the untransformed quotient, and species were clustered with a complete linkage procedure.

RESULTS

Overall, the wind regime throughout the period was dominated by northward upwelling winds with diurnal variations. Winds increased in intensity during daylight hours, being highest near local sunset (Fig. 2a). Satellite

Table III: Sampling schedule followed at Boca Grande and sampled strata

| Date | Time | Strata |
|-----------------|-------|--------|
| 12 April 2000 | 19:50 | 0–6 |
| 12 April 2000 | 19:50 | 6–18 |
| 12 April 2000 | 20:10 | 18–30 |
| 12 April 2000 | 20:40 | 30–40 |
| 12 June 2000 | 12:30 | 0–18 |
| 12 June 2000 | 12:30 | 18–25 |
| 12 June 2000 | 12:45 | 25–35 |
| 12 October 2000 | 13:10 | 0–5 |
| 12 October 2000 | 13:10 | 5–20 |
| 12 October 2000 | 13:40 | 20–25 |
| 12 October 2000 | 14:15 | 25–40 |

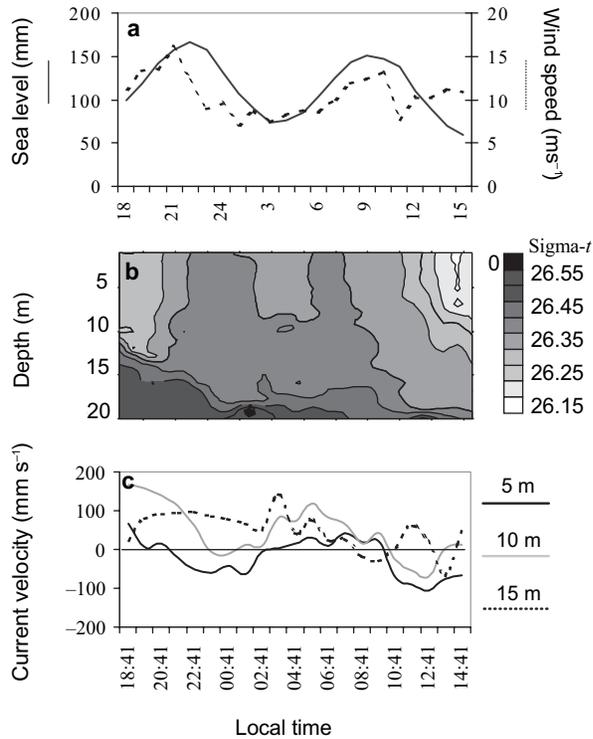


Fig. 2. Time and depth distribution of physical variables during the 22-h sampling at Boca Chica. (a) predicted sea level (mm) and wind intensity ($\text{m}\cdot\text{s}^{-1}$); (b) sigma- t depth/time section; (c) E-W current component (u) at 5-, 10- and 15-m depth.

images (SST and colour, not shown) indicated an active upwelling centre off Punta Lavapie and high Chl a concentrations inside the gulf and along the coast of the entire region.

Boca Chica

Current velocities (in u) during the 22-h sampling at Boca Chica showed a semidiurnal tidal signal of $\sim 10 \text{ cm s}^{-1}$. Strongest outflow appeared at the surface (negative A_c ; Table IV), and strongest inflow occurred at mid and bottom depths (positive A_c ; Table IV and Fig. 2c). Together, semidiurnal and diurnal constituents explained

over 90% of u variability throughout the day (Table IV). At 5- and 10-m depth, the semidiurnal amplitude was larger than the diurnal amplitude, while at 15-m depth, it was the amplitude of the diurnal component that dominated u variability. Maximum outflow (negative velocities) coincided with biological profiles 5 (night) and 11 (day) (Table I), approximately midnight and noon, respectively. Maximum inflow (positive velocities) appeared at profiles 2 (afternoon) and 8 (morning). Surface and mid-depth temperature and density (as sigma- t ; Fig. 2b) showed diurnal variability with surface heating and deepening of the pycnocline during daylight hours. At 15 m, temperature and oxygen concentration increased while density decreased during the sampling period. Vertical gradients, however, were relatively weak (Fig. 2b) but not correlated with wind speed (Valle-Levinson *et al.*, 2003).

Cancer spp. (Cancridae), *N. uncinata* (Callianassidae), *Pagurus* spp. (Paguridae), *Pinnixa* spp. (Pinnotheridae) and Porcellanidae presented the highest densities at the shallow Boca Chica (Table II). The larval density of several taxa fluctuated throughout the day following a bimodal pattern (Table V; Fig. 3aI, cI, iI, jI and kI), with a peak larval abundance at the night ebbing tide. The harmonic model fitted to *Pagurus* spp., Porcellanids, *Blepharipoda spinimana* and *Halicarcinus planatus* showed a good agreement with data (Table V). Larger densities for these taxa were estimated to occur past midnight and a smaller secondary peak before midday. Both peaks were coincident with ebbing tides: the local maximum negative velocities for u at 5- and 10-m depth and integrated velocity (Table IV). During night hours, they were more abundant during late ebb, while during the day they mainly peaked at early ebb. *Emerita analoga* also presented two peaks of density at ebbing tides, without diel variability (Table V; Fig. 3jI). For *N. uncinata* (Fig. 3fI) and *Pisoides edwardsi* (Fig. 3eII) only the diel component was significant and both peaked at night ebb. Overall abundance of *N. uncinata* individual stages decreased with stage (Fig. 4), and they mostly followed the same pattern, except zoea IV that also showed a significant second

Table IV: Parameter estimates for the sinusoidal function fitted to u current velocity component

| Depth | f_s | f_d | A_s | A_d | A_c | H (min) | H (min) | VE (%) |
|---------|--------------------|--------------------|---------------------|---------------------|--------------------|-----------|-----------|--------|
| Average | 4.83 (0.13) | 2.09 (0.2) | 47.3 (6.4) | 32.7 (6.18) | 15.1 (4.48) | 0.13 | 12.06 | 94 |
| 5m | 4.71 (0.13) | 13.3 (0.81) | 60.4 (7.2) | 10.9 (9.1) | -19.8 (5.3) | 0.0 | 12.56 | 80 |
| 10m | 4.75 (0.07) | 2.7 (0.16) | 81.61 (6.08) | 38.7 (5.8) | 51.7 (4.3) | 0.3 | 12.0 | 93 |
| 15m | 5.4 (3.13) | 1.77 (0.27) | 3.77 (13.4) | 48.45 (11.5) | 47.48 (8.3) | | 11.86 | 54 |

Results for average velocity, 5-, 10- and 15-m depth and SE are given within parentheses. $H(\text{min})$, real-time estimates for the minima (maximum negative) velocities according to the fitted model; VE, percentage of variance explained by the fitted model. Bold values are significant at the 0.05 level.

Table V: Parameter estimates of sinusoidal function fitted to mean organisms density for each tow over the 22-h sampling at Boca Chica (BC) and SE (within parentheses)

| Species | f_s | A_s | f_d | A_d | A_c | H (max) | H (max) | VE (%) |
|-----------------------------------|---------------------|---------------------|--------------------|--------------------|--------------------|-----------|-----------|--------|
| <i>Cancer</i> spp. | -0.64 (0.93) | -0.18 (0.17) | 0.03 (0.4) | 0.4 (0.17) | 3.77 (0.12) | | | 55.6 |
| <i>Neotrypaea uncinata</i> | | | 1.26 (0.22) | 0.72 (0.15) | 2.92 (0.11) | 1.24 | | 73.7 |
| <i>Pagurus</i> spp. | -1.23 (0.48) | -0.25 (0.11) | 0.76 (0.32) | 0.37 (0.11) | 2.72 (0.08) | 0.34 | 10.25 | 72.7 |
| <i>Pinnixa</i> spp. | -0.7 (1.99) | -0.06 (0.12) | 0.27 (0.25) | 0.52 (0.12) | 2.53 (0.08) | | | 76.7 |
| Porcelanids | -0.92 (0.37) | -0.4 (0.14) | 0.78 (0.32) | 0.48 (0.13) | 1.95 (0.1) | 0.78 | 9.9 | 75 |
| <i>Blepharipoda spinimana</i> | 1.74 (0.22) | 0.68 (0.14) | 0.88 (0.26) | 0.59 (0.14) | 1.91 | 1.32 | 11.5 | 86.8 |
| <i>Pinnotheres politus</i> | -0.58 (0.95) | -0.11 (0.1) | 0.25 (0.22) | 0.51 (0.1) | 1.64 (0.07) | | | 81.4 |
| <i>Haliscarcinus planatus</i> | 0.93 (0.38) | 0.53 (0.2) | 1.36 (0.4) | 0.51 (0.2) | 1.22 (0.14) | 2.3 | 13.98 | 67.4 |
| <i>Pisoides edwardsi</i> | | | 1.32 (0.2) | 0.59 (0.12) | 0.86 (0.08) | 2.14 | | 75.9 |
| <i>Emerita analoga</i> | -0.8 (0.3) | -0.44 (0.13) | | | 1.76 (0.09) | 23.59 | 11.02 | 57.5 |
| Grapsids | -0.85 (0.6) | -0.14 (0.08) | 0.61 (0.34) | 0.26 (0.07) | 0.71 (0.06) | | | 68.6 |
| <i>Neotrypaea uncinata</i> stages | | | | | | | | |
| I | | | 1.39 (0.31) | 0.49 (0.15) | 2.75 (0.11) | 1.85 | | 56 |
| II | | | 1.62 (0.26) | 0.69 (0.19) | 2.19 (0.13) | 0.93 | | 60 |
| III | | | 1.5 (0.16) | 0.95 (0.16) | 1.6 (0.12) | 0.41 | | 80.6 |
| IV | -1.68 (0.41) | -0.4 (0.16) | 1.53 (0.15) | 1.02 (0.17) | 1.37(0.12) | 1.33 | 12.88 | 87.2 |
| V | | | 1.29 (0.11) | 1.32 (0.15) | 1.12 (0.11) | 2.25 | | 90 |

Significant parameters ($P < 0.05$) are indicated as boldface values, $n = 12$. $H(\max)$, estimated local time of maximum organisms abundance; VE, percentage of variance explained.

peak at day ebb (Table V). Table V shows that it was not possible to identify reliable cyclic components in *Cancer* spp. (Fig. 3hI) and *Pinnixa* spp. (Fig. 3bI) which showed a less clear bimodal pattern and Grapsids and *Pinnotheres politus* that were spread through the day (Fig. 3dI and 3gI, respectively).

The mean weighted depth at profile varied during the day for different species. *B. spinimana* was significantly deeper in the water column during ebbing tides, while *H. planatus* was significantly shallower at ebb (significant ANOVA for factor tidal phase at $\alpha = 0.05$; Fig. 3iII). *Pinnixa* spp was significantly shallower during night hours (significant ANOVA for factor day/night at $\alpha = 0.05$; Fig. 3bII). The significant harmonic function adjusted for Porcelanids and *Pagurus* spp indicated that they were shallower in the water column during night hours (Fig. 3aII and cII); however, day–night differences were not significant with ANOVA analysis. Although *N. uncinata* appeared shallower during night hours, no significant differences were found between night and day *WMD* (Fig. 3fII). Individual stages of *N. uncinata* tended to be shallower during night (ebb) though the probability was only lower than 0.1. *N. uncinata* stages IV and V showed an overall trend to be deeper than earlier stages (Fig. 4). Although *P. politus* showed a significant interaction between tide and day/night cycle

factors, the plot of *WMD* against time shows no clear pattern through the day, except that they were shallower during night-ebb (Fig. 3gII). Grapsids showed a clear diel cycle though it was not in phase with the categories defined for ANOVA analysis (Fig. 3dII). They were shallower at evening high water and deeper at morning high water. *E. analoga*, *Cancer* spp and *P. edwardsi* showed no distinguishable changes in vertical distribution though the day (Fig. 3jII, hII and eII, respectively). Taking the average mean weighted depth for each species shows that *Pinnixa* spp. was the deepest followed by Porcelanids, *H. planatus*, *P. politus* and *B. spinimana*, and *N. uncinata*, *Pagurus* spp, *Cancer* spp and *E. analoga* were the shallowest species (Fig. 3).

Except for *B. spinimana*, *H. planatus*, *E. analoga* and *N. uncinata*, there was a significant effect of tidal phase on *LF* (Table VI): inflow was larger during floods and negative fluxes appeared during day and night ebb, when the relative larval velocities were negative (Fig. 3a through hIII). Among the group of organisms that showed significant effect of tidal phase, *P. edwardsi* and Porcelanids did not show negative flux (outflowing) during night ebb (Fig. 3aIII and eIII). For Porcelanids, *Pinnixa* spp. and Grapsids that showed a conspicuous deepening in the water column during day hours, the relative larval velocity at day ebb was

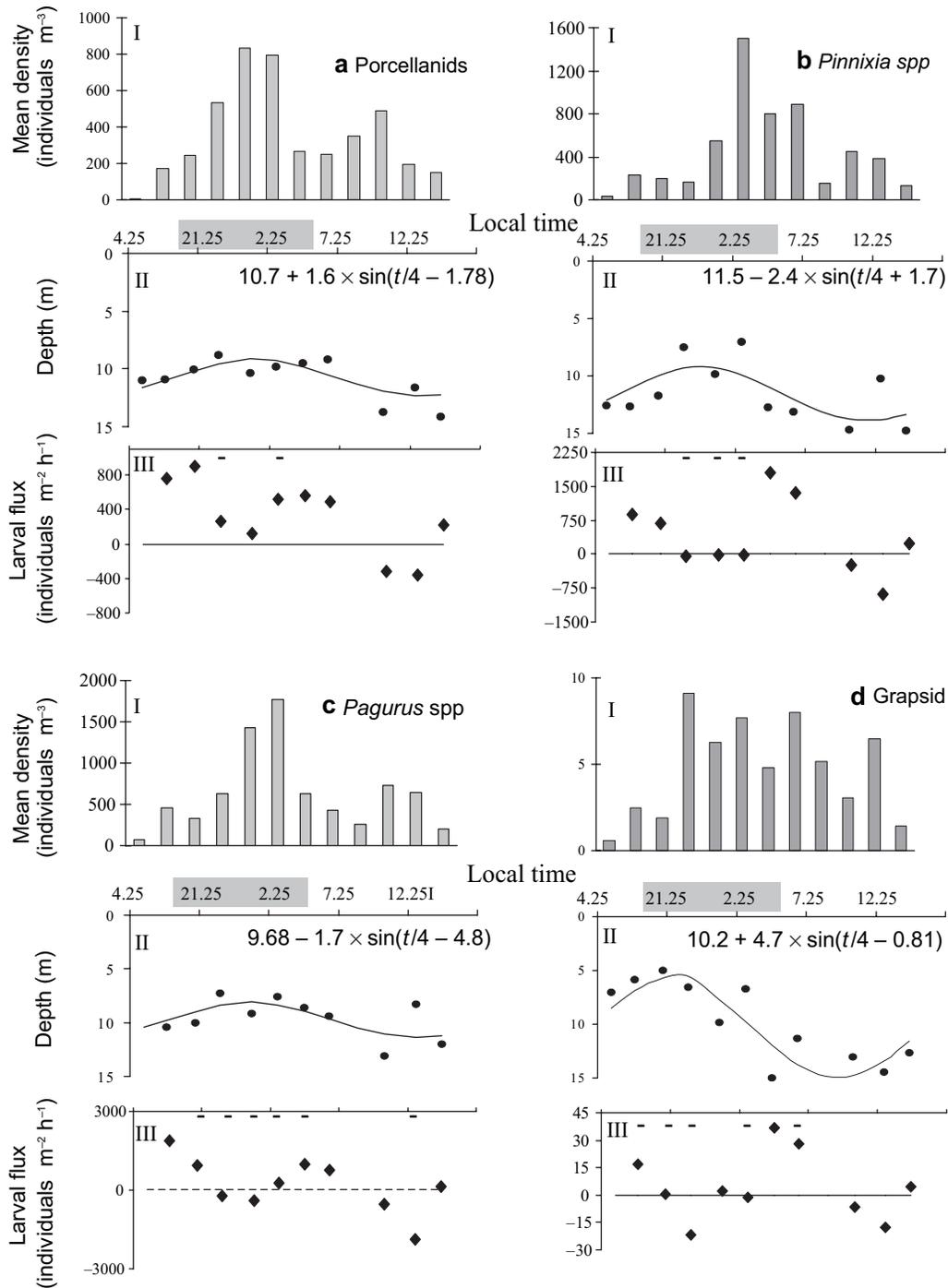


Fig. 3. Larval densities, mean depths and flux in Boca Chica during 22-h sampling. For each species (indicated from **a** through **k**), the upper graph (I) refers to the average species density (individuals $\cdot 100 \text{ m}^{-3}$) for each profile, undertaken at the specified local time. The middle graph (II) shows the mean organism depth (m) at each profile (dots) and fitted sinusoidal model (black line) when parameters were significant. Significant models are shown. Otherwise the mean depth throughout sampling is drawn. In the bottom graph (III), the larval flux at profile (individuals $\text{m}^{-2} \text{ h}^{-1}$) is plotted as dots, horizontal line indicates the 0. Negative signs in the bottom (III) graph of each species, indicates hours of larval negative relative velocity. Gray shadows over local time indicate night hours.

positive despite the absolute negative flux at this time (Fig. 3a, b and dIII). For *B. spinimana*, larger inflow occurred during night ebb. *E. analoga* showed a negative

relative velocity during most of the sampling period despite showing strong negative flux only during day ebb. *N. uncinata* stages from I through IV showed

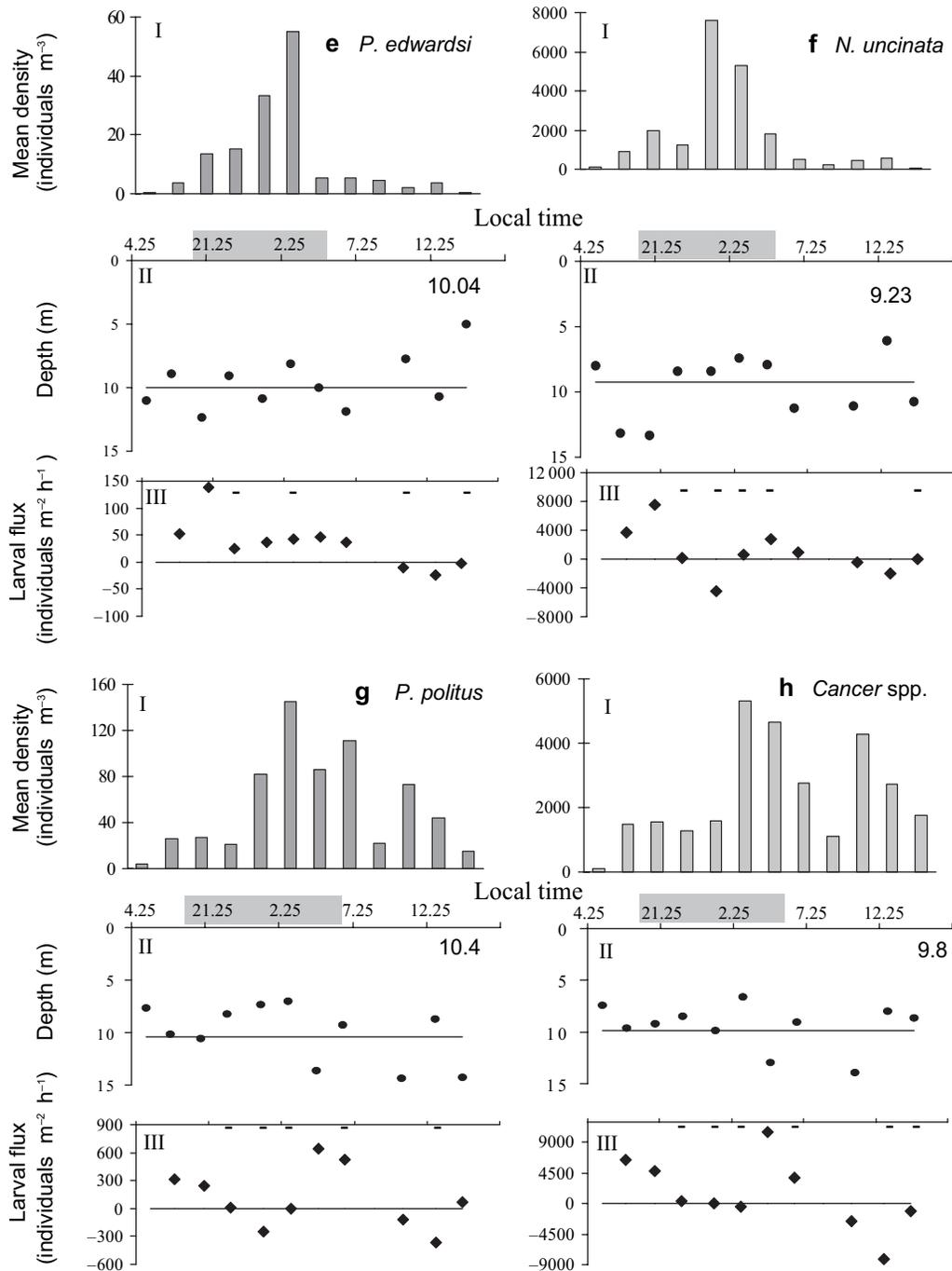


Fig. 3. continued

the same outflowing pattern during both night and day ebb although only for stage III the tidal phase had a significant effect (Table VI). *N. uncinata* V remained inflowing throughout the day (data not shown), although significant larger inflow occurred during flood and night hours (Table VI).

Boca Grande

The thermocline and halocline were well defined at Boca Grande in the three sampling occasions (Fig. 5). In general, hydrographic vertical gradients were much steeper than those at Boca Chica. The thermocline and the oxycline coincided between 10 and 20 m (Fig. 6a-c).

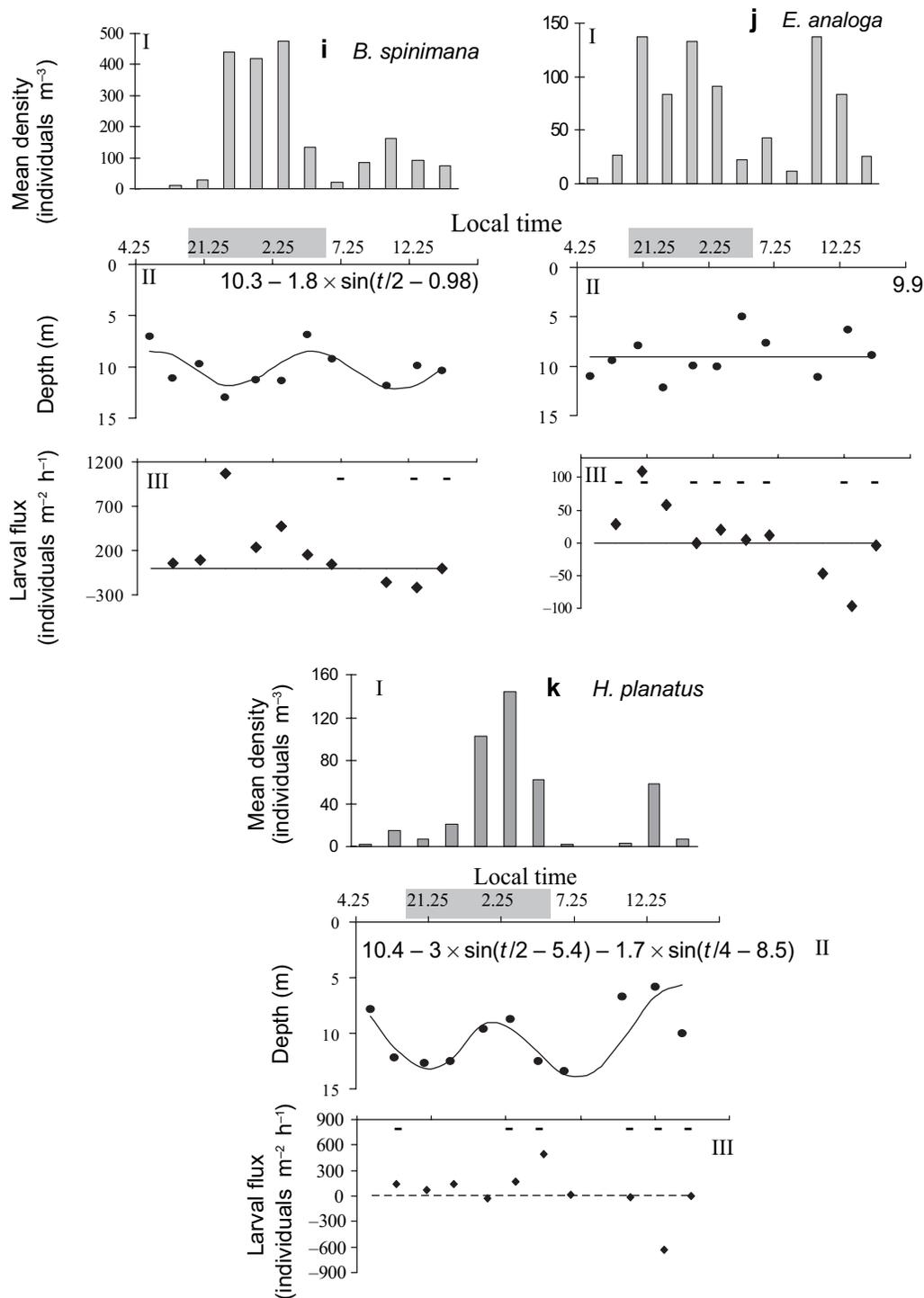


Fig. 3. continued

The upper layer temperature reached 14°C from atmospheric heating and surface water was well oxygenated. The lower layer, in contrast, was <10°C and <1 mL L⁻¹. These water characteristics are typical of the ESSW

(Strub *et al.*, 1998; Sobarzo *et al.*, 2001). These hydrographic conditions were indicative of an active upwelling situation. At the time of biological sampling, surface flow was downwind (positive *v*: towards the N)

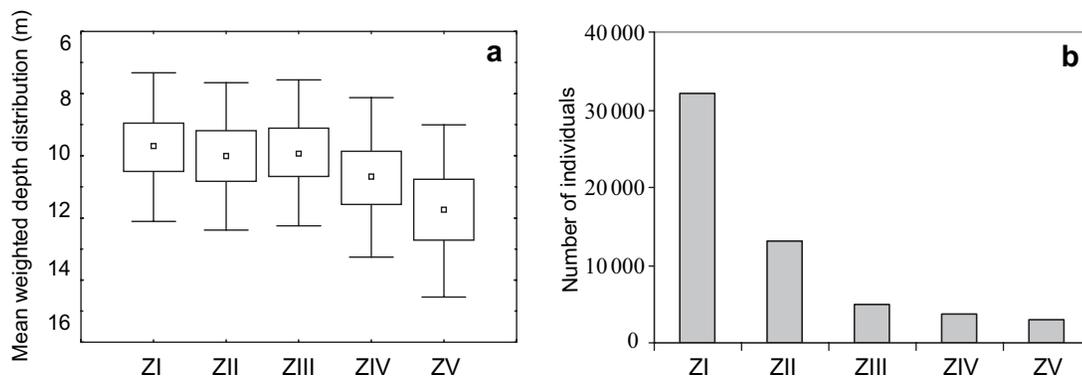


Fig. 4. *Neotrypaea uncinata* development stages. (a) Average *Neotrypaea uncinata* stages mean weighted depth through the 22-h sampling at Boca Chica (small squares), SE (large squares) and standard deviation (error bars); (b) stage composition of *N. uncinata* total abundance.

Table VI: Summary of results for two-way analysis of variance (ANOVA) on mean larval flux at profile (individuals·m⁻²·h⁻¹) for factors: (i) light level (day and night) and (ii) tidal phase (ebb/flood), n = 10

| Species/group | Ebb/flood | | Day/night | | Interaction | |
|-----------------------------------|-----------|--------------|-----------|---------------|-------------|--------------|
| | F | P | F | P | F | P |
| <i>Cancer</i> spp. | 28.49 | 0.01 | 7.8 | 0.06 | 0.001 | 0.97 |
| <i>Neotrypaea uncinata</i> | 5.31 | 0.1 | 0.02 | 0.88 | 0.12 | 0.74 |
| <i>Pagurus</i> spp. | 11.64 | 0.04 | 0.24 | 0.65 | 1.14 | 0.36 |
| <i>Pinnixa</i> spp. | 45.33 | 0.006 | 5.35 | 0.10 | 0.08 | 0.78 |
| Porcelanids | 45.65 | 0.006 | 5.8 | 0.09 | 8.86 | 0.058 |
| <i>Blepharipoda spinimana</i> | 0.23 | 0.66 | 2.9 | 0.18 | 1.86 | 0.26 |
| <i>Pinnotheres politus</i> | 29.5 | 0.012 | 1.71 | 0.28 | 0.16 | 0.71 |
| <i>Haliscarcinus planatus</i> | 3.9 | 0.14 | 3.56 | 0.15 | 0.009 | 0.93 |
| <i>Pisoides edwardsi</i> | 24.1 | 0.01 | 9.99 | 0.051 | 7.9 | 0.07 |
| <i>Emerita analoga</i> | 1.8 | 0.26 | 2.8 | 0.19 | 5.44 | 0.1 |
| Grapsids | 18.88 | 0.02 | 0.79 | 0.43 | 0.38 | 0.57 |
| <i>Neotrypaea uncinata</i> stages | | | | | | |
| 1 | 5.95 | 0.09 | 0.011 | 0.92 | 0.24 | 0.65 |
| 2 | 3.35 | 0.16 | 0.73 | 0.45 | 0.07 | 0.8 |
| 3 | 11.23 | 0.04 | 0.52 | 0.52 | 0.55 | 0.51 |
| 4 | 8.27 | 0.06 | 1.01 | 0.38 | 0.36 | 0.59 |
| 5 | 164 | 0.001 | 517 | 0.0001 | 111 | 0.001 |

Bold values are significant at the 0.05 level.

while subsurface flow was mainly upwind (negative *v*: towards the S) (Fig. 5e).

At Boca Grande, larval highest concentration was not as high as in Boca Chica (Table II). However, *L. granaria* was found at this entrance and not at Boca Chica, and *P. monodon* comprised a larger proportion of total organisms. Taxa showed marked differences in vertical distribution in the water column (Fig. 6 for contrasting examples). *Cancer* spp. were either more

abundant at surface waters (higher temperature, higher oxygen) or in the thermocline. *Emerita analoga* peaked at the thermocline also. *Pleuroncodes monodon* was always more abundant in low oxygen, deeper waters, and *N. uncinata* showed differences for all stages (Fig. 6d and e). Late stages were found deeper than early stages. It is important to note that sampling at Boca Grande was always during daylight hours (6 and 10 December) or twilight (4 December).

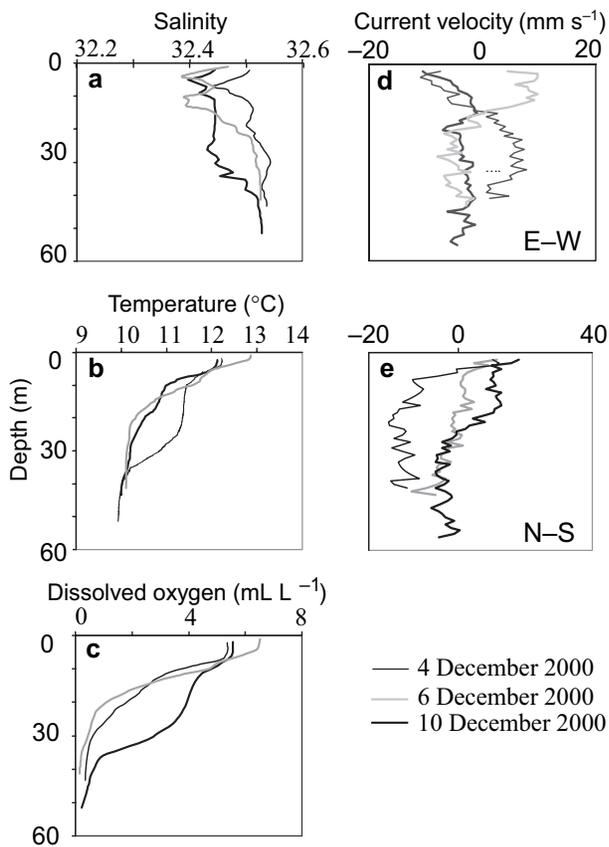


Fig. 5. Hydrographic profiles at Boca Grande (BG) during 4, 6 and 10 December 2000. (a) Salinity; (b) temperature; (c) oxygen concentration; (d and e) N-S (v) and E-W (u) current velocity components.

Cluster analysis (Fig. 7) yielded two groups. One group comprised those species/groups that mainly occupied depths above or at the pycnocline (i.e. *Cancer* spp. and *E. analoga*), of high oxygen and mainly downwind flowing waters. A second group was made of organisms that appeared at depth (e.g. *Callichirus garthi*, *P. monodon*, *Talipeus* spp., *L. grenaria*) in low oxygen, upwind flowing waters. For group one (*B. spinimana*, *Cancer* spp., *P. edwardsi*, *E. analoga* and *P. politus*) quotient q was greater than one in well oxygenated waters. While for group 2 the quotient q was greater than one in less oxygenated deeper waters (Table VII).

DISCUSSION

The results obtained with this sampling snapshot shed some insights into the role of tidal and wind-driven larval advection at the shallow and deep entrance of the equatorward facing Gulf of Arauco and the LF dependence on larval vertical distribution. At the shallow entrance, peak larval densities coincided with ebbing tides (especially night ebb) and LF was driven by tidal oscillations superimposed on a pattern of outflowing surface waters and inflowing deep

waters. Most groups were outflowing during ebb and inflowing during flood. However, LF was related to species vertical distribution: those that remained deeper experienced larger inflow (mean u was 47 mm s^{-1} at 15-m depth over the 22-h period) and those that dwelled in shallower waters were influenced by larger outflow (mean u was -20 mm s^{-1} at 5-m depth). Also for those groups that showed differences in vertical distribution between ebbing/flooding periods, average flux was independent of tidal oscillations. At the deep entrance, the regional wind-induced upwelling dynamics dominated the exchange pattern of two different water types, one above the pycnocline, outflowing from the gulf at the flanks, and another low oxygen water below the pycnocline, inflowing (Valle-Levinson *et al.*, 2003). Larvae were vertically segregated into these water types. The last finding supports the hypothesis related to a subsurface transport of organisms into the gulf during upwelling events.

Boca Chica

At Boca Chica, net flow was westward (outflow) at the surface and eastward (inflow) at the subsurface. This pattern was also found by additional current measurements taken in transects across this entrance (reported by Valle-Levinson *et al.*, 2003) during the same week, so it seems to be a typical condition for the Boca Chica entrance during upwelling periods. In the nearby Concepción Bay ($36^{\circ}40' \text{ S}$, $73^{\circ}02' \text{ W}$), a two layer circulation also develops under upwelling winds (Sobarzo *et al.*, 1997; Valle-Levinson *et al.*, 2004). Despite Boca Chica shallowness, intense southerly (upwelling) winds and net water inflow at Boca Grande, outflow at Boca Chica was hardly found throughout the water column at any given time. The bidirectional water exchange pattern, which might be the result of regionally forced Ekman dynamics and/or curvature effects related to the presence of a nearby headland (Valle-Levinson *et al.*, 2003) has a decisive influence on larval advection through Boca Chica. Larvae with deeper distribution were influenced mainly by positive relative velocity, and influx (e.g. Porcellanids), and those that dwelt shallower experienced mainly negative relative velocity (e.g. *E. analoga*). Also, the semi-diurnal water velocity modulation had an influence on larval advection. Many groups experienced outflux during ebb and influx during flood. However, the amplitude of the semi-diurnal constituent was larger at surface (5 m) and subsurface (10 m), than at 15-m depth, where the amplitude of a diurnal cycle dominated the u variability. Organisms with vertical migrations would be subject to different amplitudes of semi-diurnal fluctuations that, in this shallow entrance, could be the result of overtides (Valle-Levinson *et al.*, 2003). In the nearby Concepción Bay, which has the same geographical orientation with two

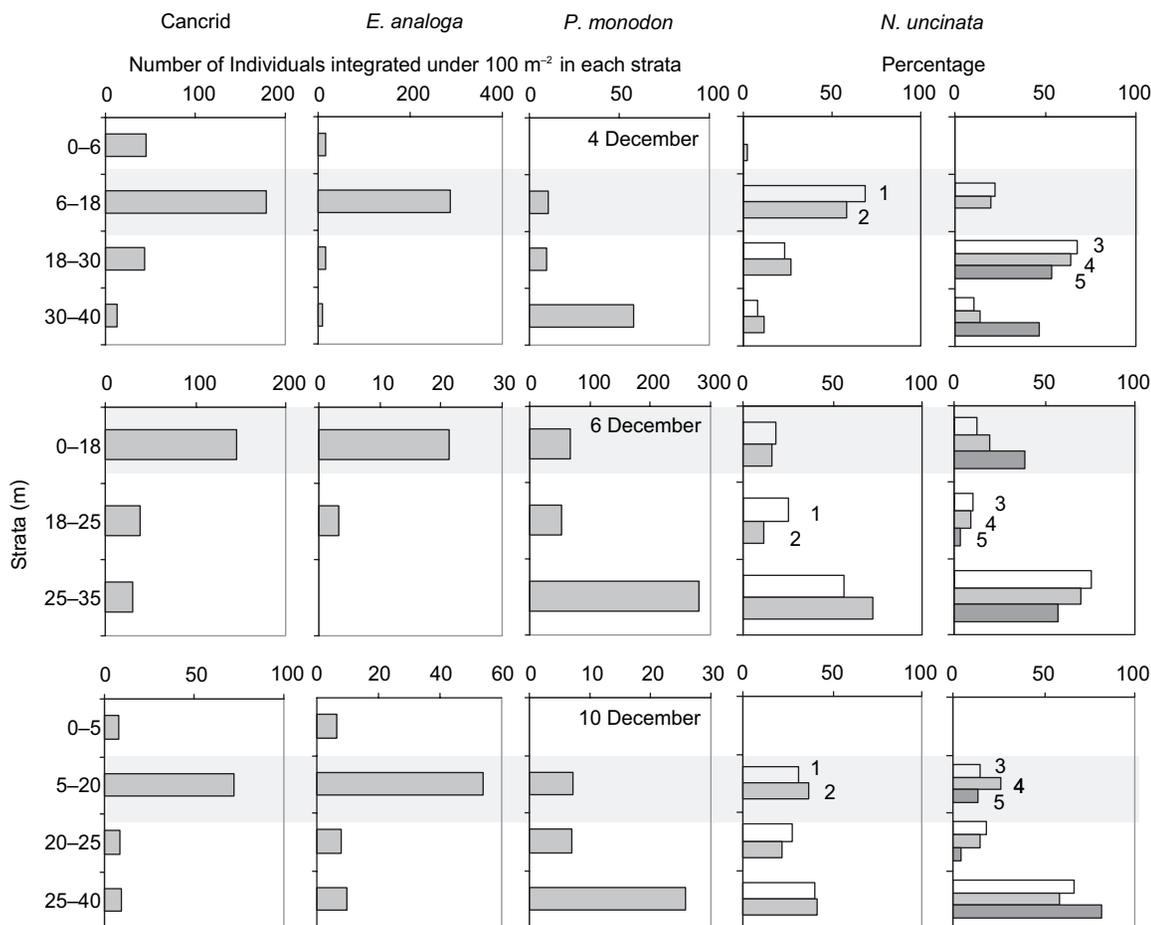


Fig. 6. Vertical distribution of larvae at Boca Grande during 4, 6 and 10 December 2000. Abundance at each strata (individuals-100 m⁻²) is shown for Cancrid, *Emerita analoga* and *Pleuroncodes monodon* larvae (first three columns) and depth percentage of *Neotrypaea uncinata* stages I through III and IV-V (columns 4 and 5, respectively). Shaded areas, thermocline at sampled date.

openings as the gulf of Arauco, semidiurnal tides also exert a larger influence on the flux through the smaller and shallower opening (Valle-Levinson *et al.*, 2004).

Several organisms showed two peaks of density and had a semidiel periodicity in phase with tidal currents. A coupling between meroplanktonic larval density fluctuation and tidal cycles has been reported in channels (Drake *et al.*, 1998), estuaries (Garrison, 1999), tidal flats (Levin, 1986) and bays (Belgrano and Dewarumez, 1995; Carbajal, 1997). Such coupling has been associated with larval hatching and tidal cycle synchronization (Levin, 1986; McConaughy, 1988), larval transport and larval active behaviour. For example, some larvae are found in the water column when they leave the water-bottom interface during ebbing tide (DiBacco *et al.*, 2001). In this case, zoeas from different stages were included in the analysis so larval hatching synchronization was excluded as a general explanation for the observed pattern. For those species with bimodal distribution over time (except *E. analoga*), densities were

always higher at night. However, outflow comprised a larger part of the water column during day ebb and not all groups peaked in surface outflowing waters. Therefore it seems that the advective effect of ebbing tides plus the availability of larvae, should be responsible for the observed density patterns.

B. spinimana in particular showed semidiel and diel density peaks. They were found deeper in the water column during ebbing tides. Deepening during ebbing tides resulted in positive larval relative velocity in which case *LF* did not follow the semidiurnal tidal cycle. The vertical distribution of this group translated into influx toward the gulf. Active swimming during flooding phases has been described in megalopas of estuarine species (Forward *et al.*, 1997) and has been related to re-invasion of coastal habitat. *B. spinimana* is an intertidal species, the larva itself is big in relation with most of the other studied taxa. The capacity to deal with currents that vary in a small depth range is consistent with the fact that offshore larval distribution

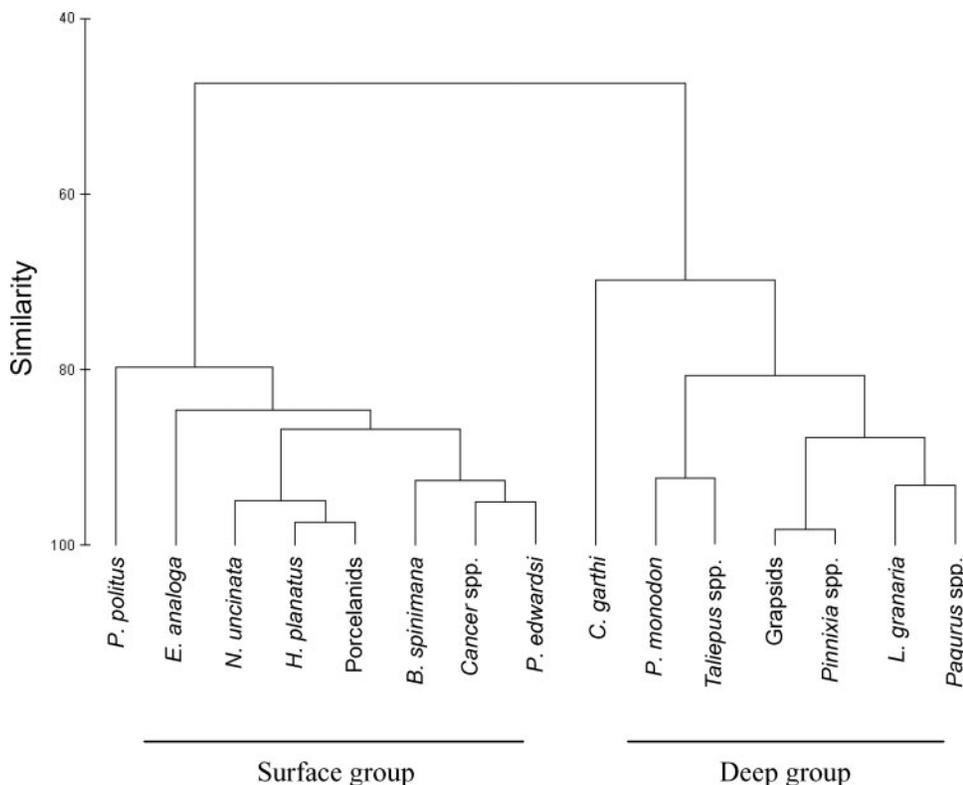


Fig. 7. Results of cluster analysis that grouped species from Boca Grande based on their oxygen quotient (q) over three sampling occasions and different strata. We used the Bray–Curtis index for constructing the distance matrix and a complete linkage procedure for clustering species.

Table VII: Quotient (q) for species collected at Boca Grande in different oxygen concentration ranges

| Species | Range of oxygen concentration (mL·L ⁻¹) | | | |
|-------------------------------|---|------|------|------|
| | 0–1 | 1–2 | 3–4 | >4 |
| <i>Cancer</i> spp. | 0.51 | 0.49 | 1.74 | 1.25 |
| <i>Neotrypaea uncinata</i> | 0.77 | 1.66 | 1.76 | 0.46 |
| <i>Pagurus</i> spp. | 0.76 | 2.18 | 0.70 | 0.75 |
| <i>Pinnixia</i> spp. | 0.92 | 3.36 | 0.63 | 0.07 |
| Porcelanids | 0.39 | 1.59 | 1.38 | 0.97 |
| <i>Blepharipoda spinimana</i> | 0.16 | 0.63 | 1.03 | 1.80 |
| <i>Pinnotheres politus</i> | 0.00 | 1.26 | 1.43 | 1.40 |
| <i>Halicarcinus planatus</i> | 0.38 | 1.21 | 1.98 | 0.87 |
| <i>Pisoides edwardsi</i> | 0.99 | 0.48 | 0.79 | 1.38 |
| <i>Emerita analoga</i> | 0.11 | 0.31 | 3.78 | 0.62 |
| Grapsids | 0.99 | 3.12 | 0.64 | 0.13 |
| <i>Pleuroncodes monodon</i> | 2.77 | 0.37 | 0.18 | 0.40 |
| <i>Taliepus</i> spp. | 1.94 | 0.44 | 1.10 | 0.53 |
| <i>Libidoclaea granaria</i> | 1.49 | 1.90 | 0.17 | 0.60 |

is restricted to coastal waters and large concentrations have been found within the gulf of Arauco (unpublished data).

Daily fluctuations in vertical distribution, their amplitude and the mean depth of occurrence had an influence on organisms flux through Boca Chica. For example, the

deepening of *Pinnixia* spp. and Porcellanids during day hours resulted in a reduction of out flux from the gulf (positive relative velocity) and the opposite during night hours. *Pagurus* spp., which also was shallower during night hours, was closest to surface among the mentioned species and experienced larger outflux than them. Porcellanids (whose mean depth distribution was deeper) remained inflowing during night ebb. *Pinnixia* spp. was the deepest of the three, but the amplitude of diel cycle was larger, so outflow occurred during night ebb. In this environment, larval displacement between waters flowing in opposite directions at Boca Chica would reduce net inflow or outflow. Larvae of the genus *Pinnixia* have been found to be exported from mixed estuaries, concentrated in surface waters during night ebb, but later, daily migration would induce their retention within the inner shelf (McConaugha, 1988). In the California current, *Pinnixia* spp. are also strong vertical migrators and tend to distribute downwind with respect to non-vertical migrators such as *Cancer* spp. (Wing *et al.*, 1998). In this case, larvae were found shallower during night time (enhancing outflow) but they were found deeper during the rest of the day, resulting in inflow to the Gulf of Arauco. Since currents diurnal variability is not related to tidal influence in this area, day/night cycle and diurnal fluctuations could remain in phase, in contrast with the phase of day/night cycle and semidiurnal fluctuations that changes along time. The maintenance of phase for different cycles is necessary to enhance/reduce transport if behaviour is triggered by one factor (e.g. light) and transport by the other (e.g. daily currents fluctuations) (Criales *et al.*, 2005).

The vertical distribution during the time of higher abundance had an important effect on *LF*. For example, *P. edwardsi* and *N. uncinata*, both showed one peak of abundance and neither had a significant temporal change in vertical distribution. However, *P. edwardsi* remained deeper during night hours (when larger numeric densities were found) resulting in positive fluxes, while *N. uncinata* remained above their mean distribution depth during night hours, resulting in negative relative velocities and export from the gulf during those hours. In addition, there was a tendency for late stages of *N. uncinata* to be deeper in the water column, and stage V kept inflowing during night ebb. There is no information in the literature regarding larval vertical distributions of the species involved in this study; however, it has been shown that early stages of the thalassiniid *Callinassa californiensis* occurs in surface ebbing flows in estuaries and their megalopa in inflowing waters (Johnson and Gonor, 1982). We did not include their megalopa in this study, but even later stages of *N. uncinata* gained influx by being positioned deeper in the water column. In a two layer circulation pattern

characteristic of upwelling periods, ontogenetic shifts in mean distribution depth could result in early export of larvae, enhanced offshore distribution of intermediate stages and later re-invasion of the coastal habitat where they must settle.

When larval density peaks did not occur in phase with either the diurnal or semidiurnal cycle, *LF* became independent of tidal cycle. Such effect of the density pattern throughout the day on *LF* is exemplified by *E. analoga*. It peaked during early ebbs without diel modulation and such a density pattern resulted in a flux independent of tidal phase. The concentration of larvae around two semidiel peaks, soon after high water could be the result of continuous hatching. In addition, no temporal change in vertical distribution could be distinguished for *E. analoga*, although its shallowness resulted in negative relative velocities spread throughout the day. Experiments conducted with *E. analoga* from the California Coast have shown a behavioural response to the interactive effect of pressure and light that would position larvae in surface layers (Burton, 1979). Its surface distribution plus long larval development result in a widespread horizontal distribution (Sorte *et al.*, 2001). Species like *E. analoga*, which show little capacity to regulate their horizontal distribution through vertical migrations, could be favoured by enhanced hatching during downwelling periods. In fact, a peak hatching period occurs during upwelling reversal in south central Chile (Contreras *et al.*, 1999).

When organisms showed neither a clear pattern of abundance nor a vertical distribution pattern, *LF* followed the tidal cycle, as exemplified by *P. politus* and *Cancer* spp. Estuarine pinnotherids have been reported outflowing during ebbing tides (Garrison, 1999). *Cancer* spp. was among the shallower species in this study. *Cancer* zoeas in the California current also dwell in surface waters and tend to be more widespread in the horizontal plane than vertically migrating larvae (Wing *et al.*, 1998). There is wide evidence that *Cancer* spp. megalopas in different systems do migrate daily (e.g. Hobbs and Botsford, 1992; Kringel *et al.*, 2003), but results regarding larvae are contrasting (Shanks, 1996; Wing *et al.*, 1998). In our case, the pooling of all stages and the four species of *Cancer* that live in the area (with adults from very different depth ranges) could influence in the lack of daily pattern observed, in addition to the lack of neuston sampling.

In summary, *LF* at Boca Chica followed tidal currents except for groups that showed deeper distribution during ebbing than flooding (*B. spinimana*) and a shallow species whose peak density occurred during early ebb (*E. analoga*). In addition, shallow mean depth at night enhanced export of larvae. The vertical patterns observed suggest at least certain control of depth by organisms; however, it is not possible to speculate from our short time series,

whether vertical fluctuations emerge from endogenous behaviour, responses to external stimuli or are influenced by other factors such as wind stress and vertical mixing. In this case, ebbing flows coincided almost entirely with night time (except at two vertical profiles), so we cannot clearly separate the effects of tides and day–night cycle. In addition, wind intensity was lower during night time, and so was stratification. Nonetheless, whether vertical fluctuations were behaviourally or mechanically generated, larvae experienced bidirectional advection at Boca Chica, with a net inflow probably enhancing retention within the gulf. Again, whether the changes in current field with depth are a result of wind forcing and/or different amplitude of tidal (overtide) currents in Boca Chica, variations in vertical distribution of organisms allow group/species/stage regulation of horizontal transport.

Boca Grande

In Boca Grande, surface waters displayed maximum hydrographic and velocity amplitudes in response to daily heating and sea-breeze wind regime. Below the pycnocline, upwind flow (southward) dominated the core of the flow. The observed pattern was consistent with continental shelf Ekman dynamics plus local modifications (at higher-daily-frequencies) (Valle-Levinson *et al.*, 2003). Therefore, the larval assemblages present in each layer were subject to velocity variations of different frequencies.

During daylight hours at Boca Grande, two groups of larvae were differentiated, those that peaked in abundance at the pycnocline, where flow was minimal (and high to intermediate oxygen concentration) and those in the deep layers where waters were mainly entering the gulf (and low in oxygen concentration). The accumulation of organisms in layers of decreased horizontal advection associated with pycnoclines has been documented for fish larvae and other planktonic organisms (Peterson *et al.*, 1979). Among taxa found in subsurface waters, *P. monodon* and *L. granaria* are especially interesting since adults have a deeper distribution than most of the other groups studied. Garland *et al.* (Garland *et al.*, 2002) found a similar pattern for groups of larvae associated with cold upwelling waters (adults from the shelf) and warm downwelling waters (intertidal and shallow subtidal adults). *Neotrypaea uncinata* (stages IV and V), *P. monodon* and *L. granaria* larvae should approach the coast in upwelling waters and even intrude into the gulf as reported for the larvae of some mesopelagic and demersal fishes (*Maurollicus parvipinnus* and *Merluccius gayi*) (Vargas and Castro, 2001; Landaeta and Castro, 2002). The demersal *M. gayi*, *L. granaria* and *P. monodon* overlap their depth distribution. Therefore our results support

the idea that convergent strategies have evolved in co-occurring populations of benthic invertebrates and demersal fish (Bradbury and Snelgrove, 2001).

One of the particularities of this area is the low oxygen concentration in shallow subsurface waters, which might impose restrictions on vertical migrations for non-tolerant species. Sampling at Boca Grande took place during day hours, when most of the described groups might be at the deepest layers they reach. However, most groups seemed to be excluded from the bottom layer. The deeper influence of ESSW on 10 December compared to 4 December at Boca Grande, might explain the somewhat deeper distribution of the ‘surface’ group during the 10th. This group of organisms in the upper layers might be subject to the more variable hydrography above the pycnocline (Valle-Levinson *et al.*, 2003). However, sampling during 4 December was conducted during evening hours and a possible shift of some organisms in the surface groups towards the surface cannot be discarded.

Results for larval vertical distribution from Boca Chica and Boca Grande were fairly consistent. Larvae that were ‘surface’ larvae at Boca Chica remained as surface or pycnocline larvae at Boca Grande (*Cancer* spp., *E. analoga*, *P. politus*). Those that showed a tendency for deepening during day time at Boca Chica (although not always significantly), such as *Pagurus* spp., Porcellanids, *Pinnixa* spp. and *N. uncinata*, were found at intermediate to lower-intermediate depths at Boca Grande as could be expected for daytime. Also at Boca Grande, a completely different ‘deep’ group of organisms appears, which were less abundant or not present at all at Boca Chica (*P. monodon*, *L. granaria*, *Taliepus* spp.). However, *B. spinimana*, which tended to be deeper at Boca Chica and showed changes in vertical distribution throughout the day, appeared as surface or pycnocline organisms at Boca Grande. There were several aspects to take into account when comparing both entrances. For example, surface strata sampled at Boca Grande sometimes comprised the entire water column at Boca Chica, therefore ‘shallow’ has two different meanings for Boca Chica and Boca Grande, and the scale did have an effect on the definition of preferred depths. *E. analoga*, for example, at Boca Chica did have an overall shallow mean weighted depth distribution, however, organisms density was not significantly different between 5, 10 and 15 m. At Boca Grande, it was clearly a ‘surface to pycnocline’ species. On the contrary, *B. spinimana* had an average mean weighted depth below 10 m at Boca Chica while it was a ‘shallow’ species at Boca Grande. The different scale not only has an effect on the definition of species as shallow or deep, but it reflects the scale at which the pattern of flow in opposite directions occurs at each entrance. While regulating vertical positioning in a range of 10 m at Boca Chica would

expose larvae to opposite fluxes, in Boca Grande such an extent may represent unidirectional flux. In this respect, shallow parts might also allow the exploitation of the benthic-pelagic layer during certain periods of day/tidal cycle. This layer might not be available at Boca Grande because low oxygen waters in the bottom can restrict vertical distribution for certain organisms. In addition, hydrographic stratification was higher at Boca Grande, which could also contribute to the much sharper vertical contrasts found in this entrance.

The overall picture emerging from this study is that high frequency processes (semidiurnal tides, diurnal fluctuations) superimposed onto others of lower frequency (3–8 day period of wind-driven upwelling) may contribute significantly to variations in the transport of individuals from bays in upwelling areas. Larval vertical distribution in the two layer circulation at the embayment entrances can enhance or preclude retention within the bay. From this study, we hypothesize that during upwelling periods, the group of surface dwelling larvae (e.g. *Cancer* spp., *E. analoga*) would be exported offshore from the gulf. A second group (e.g. *Pagurus* spp., Porcellanids and *Pinnixa* spp.) would be retained near-shore; *N. uncinata* would be widespread during the first stages, and later stages should tend to concentrate near-shore. A third group (e.g. *P. monodon*, *L. granaria*) would possibly approach the coast in the subsurface in successive instars from their offshore hatching areas.

ACKNOWLEDGEMENTS

This research was funded by the US National Science Foundation (NSF) under a supplement to project OCE-9812206 and, secondarily, the Chilean national FONDECYT project 1990470 to L.R.C. and the Research Foundation of the Universidad de Concepción. CONICYT also financed a stay for L.R.C. at CCPO (Old Dominion University). B.Y. was supported by the German Academic Exchange Service (DAAD) doctoral scholarship and is presently supported by MECESUP UCO0002. We acknowledge the cooperation of R/V *Kay-Kay* crew at sea. We also thank R. Sanay (ODU), R. Veas (UdeC) and C. Katzenmiller because of their essential work during field sampling. H. Arancibia (UdeC) and W. Schneider also gave technical support with equipments. The comments of anonymous reviewers have largely improved the quality of the manuscript.

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