

Larval dispersion of the estuarine crab *Neohelice granulata* in coastal marine waters of the Southwest Atlantic

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ABSTRACT

The estuarine brachyuran crab *Neohelice granulata* export their larvae from the parental intertidal population of the Mar Chiquita coastal lagoon, and probably other populations, to marine waters. The degree of larval dispersion or self-recruitment of populations is unknown. We evaluated the presence of all larval stages of *N. granulata* in coastal waters of Argentina between 37.9° and 35.8° S, at two different spatial scales: a broad scale of tens to hundreds of kilometers from the Río de la Plata estuary in the north, to Mar Chiquita lagoon in the south, and a small scale of hundreds of meters to some kilometers around the mouth of Mar Chiquita, during spring and summer. Additionally, we registered the larval composition and density at San Clemente creek population, in Samborombon Bay (Río de la Plata estuary), every 3 h along a 30-hour period. Evidence indicates that larval release of *N. granulata* is temporally synchronized with nocturnal ebb tides and all development from Zoea I to Zoea IV occur in areas close to the parental population, even with very different oceanographic characteristics. A possible mechanism based on salinity selection and wind-driven transport is proposed for such behavior, and some considerations related to the connectivity of present populations are made.

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1. Introduction

Connectivity among populations of benthic marine organisms with pelagic larval phases is crucial to understand their population dynamics. Adults of many estuarine species (e.g. crabs, shrimps, fishes) are restricted to this patchily distributed environment and show two strategies in relation to larval development: retention of all larval stages in adult habitat or export of first larval stage to more stable marine conditions. Retained larvae must be able to osmoregulate, to cope with variable salinity, and to tolerate extreme temperatures; in addition they should have behavioral responses preventing an involuntary export (Cronin and Forward, 1982; Forward et al., 1982; Strathmann, 1982). Connectivity will be very restricted in species with such strategy and more or less “closed” local populations will arise. The other strategy, export of larvae, was formerly thought mainly as an opportunity for dispersal (Scheltema, 1986), but it is now considered more as a strategy to

prevent potentially stressful physiological and biological conditions present in estuaries (Hovel and Morgan, 1997). The exported larvae face the problem of reentering to the parental habitat or finding an appropriate new habitat to settle, avoiding advection away from suitable sites; there is growing evidence that marine larvae of many invertebrate and vertebrate groups exhibit a variety of behaviors that strongly influence their dispersal (Kingsford et al., 2002; Sponaugle et al., 2002 and references therein). Connectivity among populations with export strategy will depend more on the efficiency of larval behavioral mechanisms and the oceanographic features at a scale relevant to this process, than on the duration of the larval phase or the distance between populations. However, field data on real distances reached by marine larvae during the dispersive process are scarce, particularly regarding crabs (Petrone et al., 2005; Cowen et al., 2006) and the knowledge of the origin of recruiting larvae in marine and estuarine populations has been limited until today because the difficulties in tracking individuals throughout their larval period; only examples of taxa with very short larval periods (hours to some days) are reported (Sweater et al., 2002).

Neohelice granulata is a semiterrestrial crab endemic in Southwest Atlantic warm-temperate coasts. It exclusively inhabits mudflats and salt-marshes between Río de Janeiro, Brazil and San

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José Gulf, Argentina, when they are associated with the halophytes *Spartina* spp. and *Sarcocornia perennis* (Isacch et al., 2006). Adult crabs are not found in coastal marine waters but live in estuaries exposed to low or fluctuating salinities or in hyperhaline marshes and mudflats with no freshwater input or with small rivers of local influence (e.g. San Antonio Bay and Bahía Blanca, Argentina, respectively). Larvae of *N. granulata* are produced between September and March (end of spring and beginning of fall in the Southern Hemisphere) with some inter-annual and inter-population variation (Bas et al., 2008 and references thereof); the normal larval development comprises four zoeal stages and a megalopa but an additional fifth zoea may be observed under extreme environmental conditions (Boschi et al., 1967; Pestana and Ostrensky, 1995; Giménez and Torres, 2002). The complete larval development lasted from 20 to 26 days (salinity 32 and 15, respectively) at 18 °C (Anger and Ismael, 1997; Anger et al., 2008). Zoeae I can tolerate low salinities: they osmoregulated slightly at 15–17, osmoconformed below and above that salinity, and were able to survive hours or days at 5 (Charmantier et al., 2002; Anger et al., 2008). This physiological aptitude was almost lost by zoeae II and III, but it was regained in zoea IV; megalopae are good hypo- and hyper regulators (Charmantier et al., 2002; Anger et al., 2008). In this way, larval physiology seems to have evolved in relation with a development in mixohaline or marine waters, zoeae I are able to hatch in low salinity but must reach mixohaline or marine waters after a period of hours to days.

The physiological plastic responses of *Neohelice granulata* larvae to salinity have been widely studied (see Anger et al., 2008; Bas et al., 2008). On the basis of these plastic responses, Giménez (2003) speculated on the existence of estuarine population networks, each one consisting of a set of estuarine habitats where juveniles, adults, and embryos live (the benthic component) and a coastal cell containing the larval pool (pelagic component). This model implies an export of larvae offshore. Nevertheless, empirical data about the real degree of larval dispersion and the conditions faced by the planktonic larvae are lacking. For these reasons, hypotheses are not testable. In fact, larval dispersion strategy has been studied only partially in two populations: Mar Chiquita coastal lagoon and Bahía Blanca estuary. In Mar Chiquita, where salinity has strong and unpredictable variations, zoeae hatch within the adult habitats, preferably at nocturnal high tides, and are transported rapidly towards coastal marine waters by outflowing ebb currents; later, megalopae reinvade the adult habitat where they settle and metamorphose (Anger et al., 1994; Luppi et al., 2001). Zoeae II, III and IV were never found inside the lagoon, even in the area more influenced by tides (Anger et al., 1994), but it is not known how far larvae are dispersed in the sea. In Bahía Blanca, instead, all larval stages develop inside the estuary (Cervellini, 2001); salinity is never below 15 in this large estuary (120-km long in the main channel) except at the sites of freshwater discharge and it increases to 32–34 at only 10 km away from these sites.

Neohelice granulata offers a very interesting model to study larval dispersion because adults have a patchy distribution, the larval period has a moderate duration and larval behavior is apparently plastic in different oceanographic conditions. The goal of this study was to add new empirical evidences on the larval dispersal of this species in order to find support to the scenario proposed by Giménez (2003), i.e. open populations that include several estuarine habitats connected by offshore larval pools. We first recorded the presence and density of different larval stages in a creek that opens to the mixohaline waters of Río de la Plata in order to evaluate the possibility of larval export in populations of this huge estuary. Afterwards, we analyze the larval dispersion and potential population connectivity by monitoring the abundance of the different larval stages at two spatial scales: a regional scale,

covering an area of about 6900 km² between 36° 22'S and 37° 45'S, and a local scale, covering 16 km² of nearshore waters in the mouth of the Mar Chiquita lagoon.

2. Materials and methods

2.1. Study areas

The area covered by the study was located in Buenos Aires province coastal waters (Fig. 1). The general pattern of coastal currents has a northward direction in autumn–winter and a southward drift during spring and summer (Piola and Rivas, 1997; Palma et al., 2004). North of 38°S, the intensity of such influence seems to be modified by inter-annual variations in wind pattern and river runoff (Lucas et al., 2005; Jaureguizar et al., 2007).

Samborombón Bay is an approximately 100-km long coastal basin within the Río de la Plata, affected by low-amplitude (<1.4 m) semidiurnal tides, which open to the external, mixohaline zone of the estuary (Boschi, 1988). A high number of shallow tidal creeks drain the area where dense *Neohelice granulata* populations live. Creek sediments are fine sands in the external zone of the bay; the silt-clay percentage increases with distance from the sea (Bértola et al., 1993). San Clemente creek (Fig. 1b) is one of the easternmost and deeper tidal channels (36°22'S, 56°45'W) of the area.

The waters of the marine coastal zone (<35 m depth) between Samborombón and Mar Chiquita are homogenous, usually non-stratified, with salinity between 30 and 34 and a bottom characterized by sandy sediments very uniform in grain size and composition (Lucas et al., 2005 and references thereof).

The Mar Chiquita coastal lagoon (37° 45'S, 57° 26'W) covers an area of 46 km² with a 1.2-m maximum depth at low tide (Fasano et al., 1982) opening to the ocean by a narrow channel at its most southern tip (Fig. 1c). Semidiurnal tides (amplitude <1 m) superimposed by variable and often strong winds cause an irregular pattern of water influx and outflux (Anger et al., 1994; Reta et al., 2001). A smooth slope, with a highly mobile and morphologically variable tidal delta characterizes the mouth of this coastal lagoon (Isla, 1980). Alongshore current causes the drift of water and sediments northward in the surf zone.

2.2. Field procedures

Larval export in Samborombón bay: To evaluate the larval export in populations adjacent to the Río de la Plata estuary, nine plankton samples were collected from a permanent station located at the mouth of San Clemente creek, where it opens to Samborombón Bay (Fig. 1b), at approximately 3-hour intervals along a continuous 30-hour period on December 9 and 10, 1999. A 19.5-cm internal mouth diameter mini-bongo net was hauled 200 m with a boat from bottom to surface (channel depth: 1.2–2 m). The content of both twin nets was pooled reaching a final filtered volume of 11.9 m³ for each sample. Conductivity, temperature, and depth were measured *in situ* with an SBE19-CTD. Plankton was concentrated and fixed in 4% formalin solution.

Larval dispersion in coastal marine waters: Samples were collected in oceanographic cruises carried out on board FRV Capitán Canepa between November 17 and 21, December 12 and 16, 1999 and between February 10 and 17, 2000. Eighteen stations distributed in four sections perpendicular to the coast were established between Samborombón Bay and Mar Chiquita lagoon in front of Punta Rasa, Punta Médanos, Faro Querandí and Mar Chiquita (Fig. 1a). Stations in each section were approximately 10 km apart, beginning 1.2–2 km offshore. Depth was variable among stations (4–26 m). A 0.5-m diameter mouth part Hydro-Bios multi net, with five 300 µm meshes was hauled at two depths, and temperature

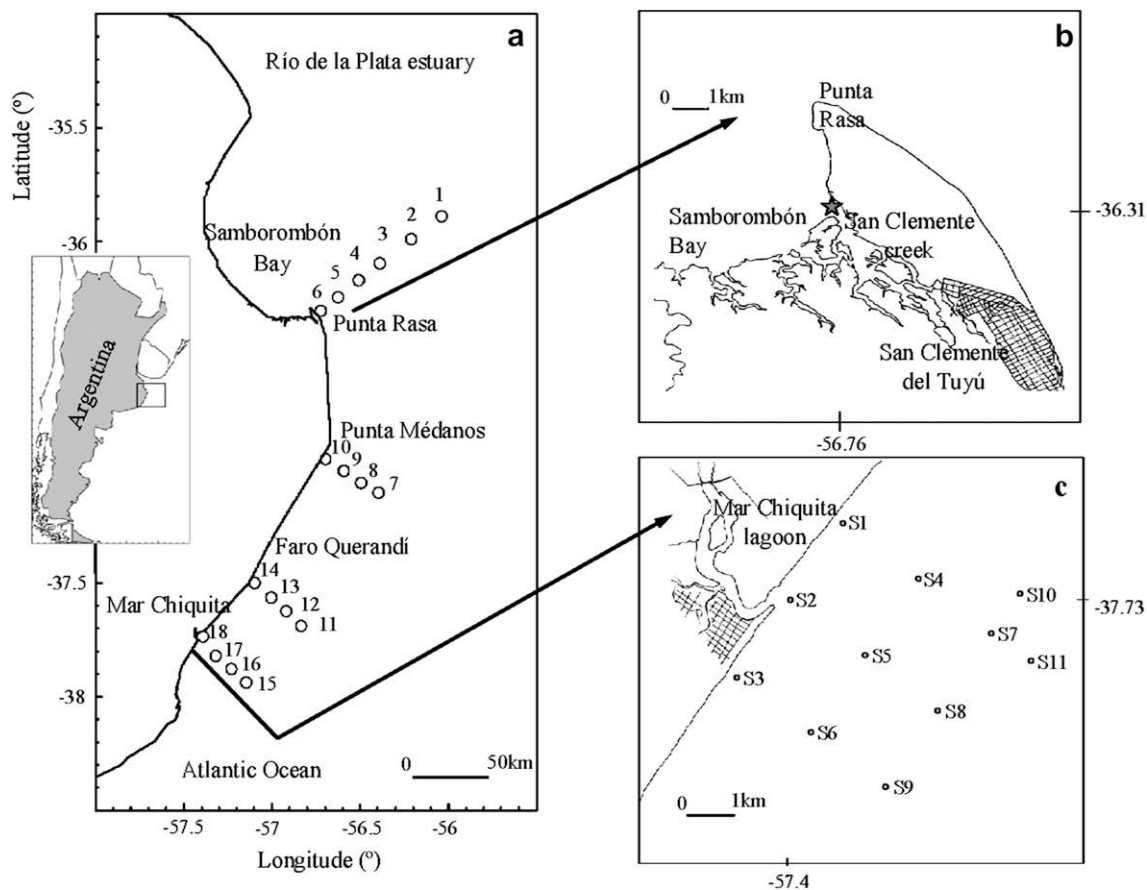


Fig. 1. Study areas: a) sampling sections along the coast of Buenos Aires province between the Río de la Plata estuary and Mar Chiquita lagoon. 1–6: sampling stations at Punta Rasa section. 7–10: sampling stations at Punta Médanos section. 11–14: sampling stations at Faro Querandí section. 15–18: sampling stations at Mar Chiquita section. b) detail of San Clemente creek and Samborombón Bay. Grey star: sampling site; c) detail of the coastal area next to Mar Chiquita lagoon. S1 to S11: sampling stations. Small insert in a): location of the study area in Argentinean coast.

and salinity profiles were recorded by a SBE19-CTD. When a pycnocline or a thermocline was detected, samplings were made at three depth levels. Since nets were not equipped with fluxometer, filtered volumes were estimated by speed and period of hauling. A total of 132 samples with volumes between 100 and 430 m³ were collected. Samples were preserved as previously stated.

Larval dispersion of Mar Chiquita larvae: Beginning at a line near parallel to the coast (250–370 m), plankton was sampled from 9 fixed stations set each 2 km delimiting an area of 16 km² near the mouth of the lagoon (S1 to S9, Fig. 1c). Two extra stations, 1 km eastward and 1 km northward of S7, were added later (S10 and S11, Fig. 1c). Samplings were performed on March 3, and December 30, 2005 and February 13, and April 4, 2006.

Not all stations were sampled each time due to difficult slow navigation with a small rigid boat to collect plankton samples in the splash zone. A total of 49 plankton samples were obtained: 6 from six sampling stations on March 3, 2005; 13 from 7 stations on December 30, 2005; 14 from 7 stations on February 13, 2006 and 16 from 8 stations on April 4, 2006. Sampling was carried out during flood tide in March and during ebb tide in the other months because, although many other attempts were made, these were the only opportunities in which wind and water conditions were good enough for operating.

Samples were collected with the same net used in San Clemente creek. Since the net was hauled 400 m each time but only the content of one of the twin nets was randomly fixed, the volume of samples was 11.9 m³. With the exception of sampling performed on March 3, when a unique sample covering the whole water column

was obtained from each station, two depths, surface and bottom, were sampled in each station by adding to or removing a 20-kg load from the net. Since no CTD was available, salinity, temperature, pH and turbidity were recorded with a multiparameter meter HORIBA U-10 in each station and depth. Samples were preserved as previously stated.

Wind data, recorded every 30 min during the week previous to every plankton sampling were obtained from the meteorological station in Mar Chiquita (Laboratorio de Oceanografía Física, Departamento de Ciencias Marinas, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata).

2.3. Laboratory procedures

In the laboratory, decapod larvae were separated and counted from each complete sample or from an adequate aliquot under stereomicroscope. *Neohelice granulata* were identified (at both specific and larval stage levels) after the description by Boschi et al. (1967). The different larval stages were abbreviated ZI, ZII, ZIII, ZIV and M (zoea I to IV and megalopa, respectively). Larvae of *N. granulata* were quantified as larvae/m³ or larvae/100 m³ and as percentage of total decapod larvae.

2.4. Data analysis

Every wind record was multiplied by their intensity (km/hour) and added according to their direction. Winds from each direction were considered as favorable/unfavorable to nearshore retention

based on Bogazzi et al. (2001) analysis. Favorable winds were those with an onshore component and/or S component, opposite to coastal drift. Unfavorable winds instead, were those with an offshore component and/or N component which could favor advection by coastal drift.

In Mar Chiquita, correlation of larval densities with environmental variables was analyzed with a canonical correspondence analysis (CCA) (Ter Braak, 1986), having temperature, salinity, turbidity, pH and northerly–easterly location into grid as physical factors, and zoeal stages (I to IV) as biological factors. To eliminate seasonal temperature and salinity variations, sample differences were standardized as proportional to the maximal value in each sampling date.

3. Results

3.1. Larval exportation in Samborombón Bay

Temperature along the sampling period varied between 19.3° and 24.6 °C and salinity, between 16.5 and 18.9. Maximal tidal amplitude registered was 1.2 m and salinity varied inversely to tidal height (Fig. 2a). ZI, ZII, ZIII and M of *Neohelice granulata* were

present in all San Clemente creek samples and corresponded to 59–100% of total decapod larvae collected. ZI density varied between 35.7 and 1091 larvae/m³ (Fig. 2b), ZII and ZIII were present at low densities (ZII: 0.07–5 larvae/m³; ZIII: 0.07–3.5 larvae/m³) (Fig. 2c). Zoeae I peaks corresponded to ebb tides and were higher at the highest amplitude nocturnal ebb tide (Fig. 2a, b). ZII and ZIII peaks had no clear correspondence with tidal phase (Fig. 2a, c). Density of megalopae was higher in the nocturnal flood tide (20.4 larvae/m³) than in the next three samplings (2.2–6.4 larva/m³) (Fig. 2c).

3.2. Larval dispersion in coastal marine waters

ZI and M of *Neohelice granulata* never appeared in the samples; only ZII, ZIII and ZIV were present in 14 from a total of 132 samples. They were more abundant in the Punta Rasa section and never appeared in the Faro Querandí section. Decapod larvae other than *N. granulata* were present in 95% of the 132 samples.

In November, larvae appeared only in Punta Rasa and Punta Médanos sections. Punta Rasa section covers the mixohaline zone of the estuary, and shows strong vertical stratification. Salinity ranged between 30.8 and 14.8 and temperature between 16.6 and 20.1 °C (bottom and surface respectively). *Neohelice granulata*

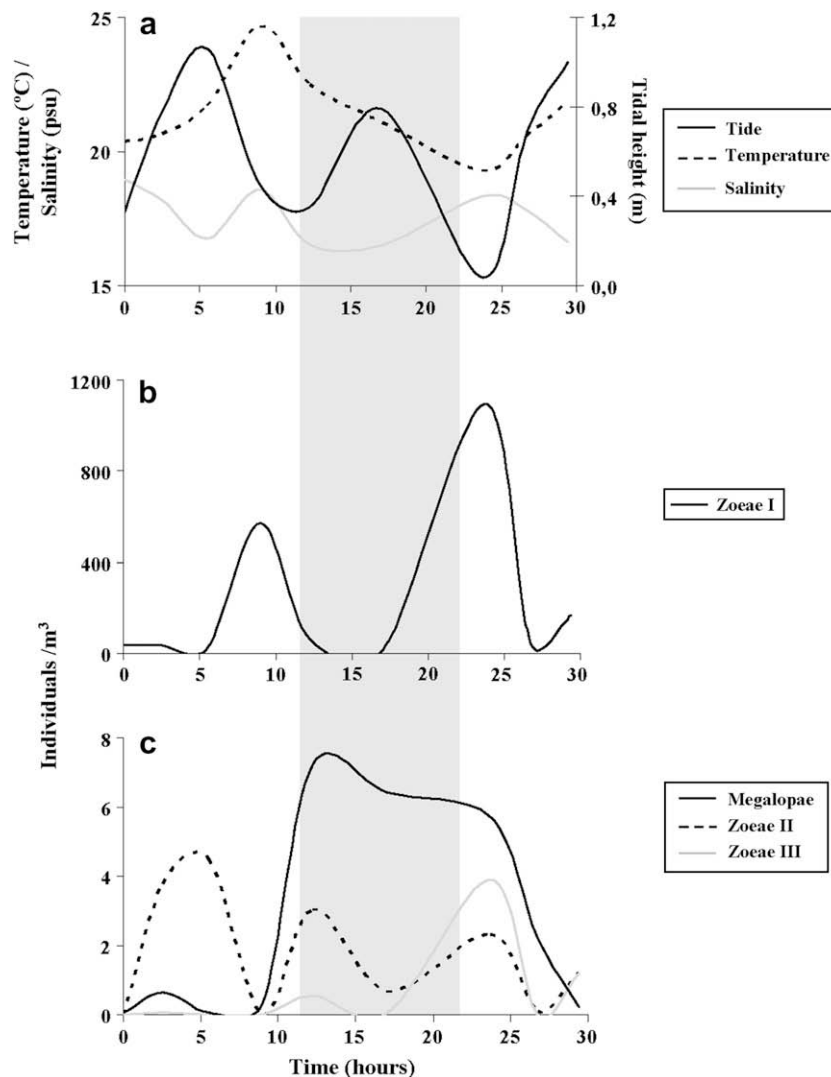


Fig. 2. 30-hour sampling at San Clemente creek: a) tidal, temperature and salinity fluctuations; b) density variations of *N. granulata* Zoeae I (larvae/m³); c) density variations of *N. granulata* Zoeae II and Zoeae III (larvae/m³). Grey zone: night.

larvae were captured in stations 3, 4 and 5 (Fig. 1a). In stations 3 and 4 densities were between 1 and 3 larvae/100 m³, about 1% of the total density of decapod larvae. All larvae in Station 3 were ZII; ZII and ZIII appeared in station 4. In station 5 densities were slightly higher (between 3 and 17 larvae/100 m³) and represented about 10% of total larvae. ZII, ZIII and ZIV stages were present. Larval presence did not correlate with depth, salinity or temperature. In the other section (Punta Médanos), larvae were found in stations 7 and 10 (Fig. 1a). In station 7, only ZII appeared, at the surface, while in station 10, ZIII and ZIV were captured, at the bottom. Densities were 0.8 and 36 larvae/100 m³ and corresponded to 1% and 3.6% of total of larvae in stations 7 and 10, respectively. Salinity values in this section showed slightly diluted water (salinity ranged 26.2–32.6), and some stratification.

In December, larvae were registered in Punta Rasa, Punta Médanos and Mar Chiquita (Fig. 1a). Sampling in Punta Rasa section was performed two days after San Clemente creek sampling. In this occasion, larvae appeared only in station 6, the nearest to coast, and even when densities were still low (1.8 and 2.8 larvae/100 m³) they represented 60 and 70% of the total decapod larvae collected (surface and bottom, respectively). In the bottom sample all larvae were ZIV, while at the surface, they were ZIII and ZIV. In Punta Médanos, larvae were found in the same two stations as in November. Only one larva was found in station 7 (ZIV) and a higher record appeared in the nearest to coast site (station 10): in the bottom, all larvae were ZIV (39 larvae/100 m³, 1.8% of total decapod larvae), and at the surface ZIII and ZIV (rate 3:1) appeared (39 larvae/100 m³, 0.03% of total decapod larvae). Like in November, the water was moderately diluted (25.2–32.1). In Mar Chiquita, one ZIII larva (0.35% of total decapod larvae) was collected at the surface in station 18, 1.8 km from the coast (Fig. 1a).

In February, *Neohelice granulata* larvae were present only in station 5 of the Punta Rasa section. They were ZIII (0.5 larvae/100 m³, 5.6% of total decapod larvae), and were in the surface sample. Water salinity in this section was higher (22.3–33.3) than in previous samplings; larvae appeared with the lowest salinity.

3.3. Larval dispersion in Mar Chiquita

Only sandy bars, parallel to coast, and not higher than 1 or 2 m were detected as bottom relief. Depth was 2 m in stations 1–3 (nearest to the shore, see Fig. 1c), 5 m in stations 4–6 and 12 m in the external stations (7–10, 4 km offshore), with an abrupt slope (45°) in the first 250 m and a more gentle, near constant inclination, from 500 m to 4 km offshore.

In March, *Neohelice granulata* larvae appeared in all samples; in December, in 61.5% of samples; in February, in 86% of samples, and in April, only in 6.2% of samples (S2 at surface). Other than *N. granulata*, decapod larvae were present in all samples, and represented the bulk of the sample. The lowest densities of *N. granulata* larvae (5–50 larvae/100 m³) were similar to the highest densities recorded in coastal waters between the Río de la Plata estuary and Mar Chiquita. The highest values were on the other hand one or two orders of magnitude higher (300–3000 larvae/100 m³). ZI to ZIV but no megalopae of this species were registered. When bottom and surface samples were compared, densities were always much higher in surface waters (Fig. 3a).

Salinity of water was never below full marine conditions and variations among stations were no higher than 0.9. Sediment discharge from the lagoon was evidenced by turbidity, which was always higher near the mouth (the highest value always appeared in stations 2 and 4, and was always higher at bottom than at surface), decreasing sharply easterly and southerly. Maximal temperature differences among samples from the same period were between 0.6 and 1.4 °C. Temperature varied seasonally: it was

higher in December and February, and fell down in March and April. Maximal and minimal absolute values were 21.8 and 18.8 °C (February and April, respectively).

In March, only stations 1–6 were sampled. One peak of ZI larvae appeared at the mouth of the lagoon (S2) and decreased afterwards, especially in SE direction in accordance with the S–N coastal drift direction. A small proportion of ZII appeared only in S4 (Fig. 3a).

In December, S3 and S6 were not sampled. The highest density of larvae appeared in S7 at surface and was formed by 80% ZII, 10% ZI and 10% ZIII. ZII appeared again in S8 at the bottom, and larvae in the rest of samples were ZI (Fig. 3a).

In February, the southern line of the sampling area (S3, 6 and 9) was not sampled, and station 10 was added. The highest density was registered at S4 (surface and bottom), where ZIV was the most represented stage, with smaller proportions of ZIII and ZI. In S5 (surface) density was high too and ZI, II, III and IV were represented. ZIV were present at the surface of S7, and at the bottom of S1, S8 and S10, although in low densities (Fig. 3a).

In April, S3, S6 and S9 were not sampled but S10 and S11 were added. *Neohelice granulata* larvae were present only at the surface of S2 (33.6 ZI larvae/100 m³, not shown); other decapod larvae were also very scarce, two-fold below previous samplings, probably showing the end of the reproductive annual period of many of the species in the area.

The intensity and direction of winds varied permanently blowing from opposite quadrants in the same day. When grouped by quadrants, wind periods favorable to larval retention varied in the weeks previous to the different sampling dates (Fig. 3b) and seemed to relate with the density of advanced larval stages and their proximity to coast.

Since the number of data per sampling date was low, all sampling dates were grouped for the CCA analysis. Bottom samples were not considered because of their very low densities. The only two factors that showed correlation with larval stages distribution were the northerly position and the temperature. All the advanced larval stages of *Neohelice granulata* (ZII to ZIV) appeared grouped and were associated with northern location and low temperatures (sampling stations 1, 4, 5 and 7, depending on the sampling date). The distribution of ZI and decapod larvae other than *N. granulata* were not related to any of the factors considered (Fig. 4).

4. Discussion

Determining the degree to which marine populations are sustained by self-recruitment or dispersal of larvae from external sources, and evaluating their consequences is an important challenge to face (Sweater et al., 2002). Among crabs, *Callinectes sapidus* is a well known example of larval dispersal: many detailed studies on water circulation as well as larval behavior support the idea that, in the east coast of USA, there are “extended populations, whose larvae are shared over broad geographical scales” (Epifanio, 2007). However, Sponaugle et al. (2002) concluded that some physical factors common in the ocean together with active behavioral input by the larvae, from simple vertical orientation to complex sensory abilities and strong swimming (known to occur in larvae of decapod crustaceans and fishes) may also lead to self-recruitment of local populations. In addition, the pelagic larval duration and the time to behavioral competency, as well as spatial and temporal patterns of spawning and larval release, will influence the likelihood of retention.

The connectivity of marine or estuarine species from South-western Atlantic has not been studied. Although crabs seem to be good models for such a research, only indirect evidences exist related to larval dispersal. On one hand, a complete set of physiological studies leads Giménez (2003) to suggest the existence of

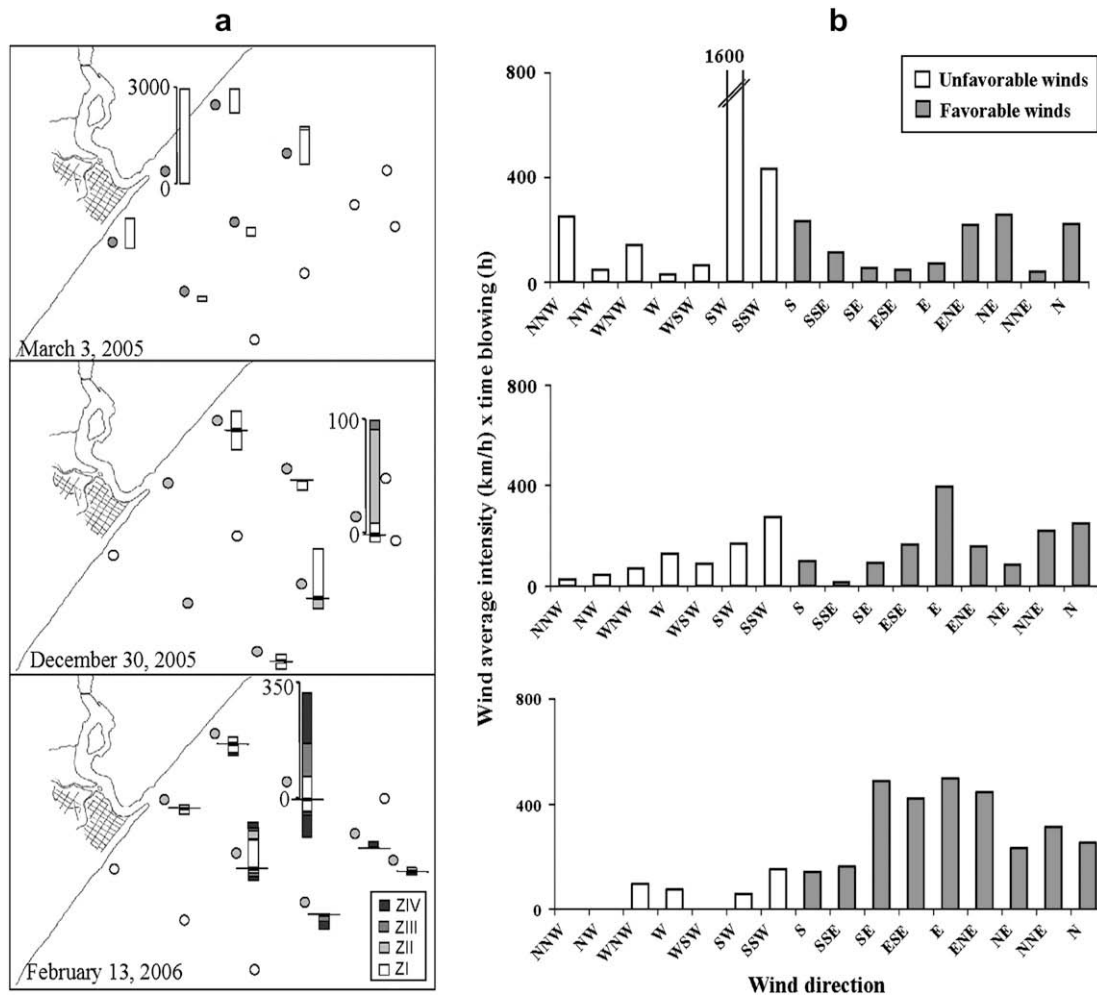


Fig. 3. a) Larval densities (larvae/100 m³) at Mar Chiquita lagoon in surface waters (bars above line) and bottom waters (bars below line) at each sampling date (except April 9, 2006). Grey circles: sampled stations. White circles: stations not sampled. ZI to ZIV: zoeal stages. b) Winds blowing during the week previous to larval samplings. Every wind record was multiplied by their intensity (km/hour) and added according to their direction. Favorable winds: with an onshore component and/or S component, opposite to coastal drift. Unfavorable winds: with an offshore component and/or N component which could favor advection by coastal drift.

larval pools offshore. On the other hand, a wind-driven limited dispersion was suggested in *Uca uruguayensis* on the basis of adult population distribution and characteristics, wind pattern and oceanographic conditions prevailing in the area (Bogazzi et al., 2001).

Considering the huge extension and density of the *Neohelice granulata* populations living in Samborombón Bay and in the coast of Uruguay, and the peaks (1000 ZI/m³) running out solely at San Clemente creek, a strikingly low density of larvae was registered in coastal waters of Buenos Aires province. Abundant decapod larvae (including several crab species) characterize most of the 132 extensive samples taken along the complete reproductive period of *N. granulata*, and covering two or three levels in the water column. The relative scarcity, and even lack, of *N. granulata* larvae in those samples suggest that they should be concentrated in other sites (e.g.: near the shore and/or near estuarine waters). This view is reinforced by the presence of advanced zoeae in (San Clemente Creek) and near (stations 4, 5 and 7 in Mar Chiquita) spawning sites.

The Río de la Plata estuary is well stratified, with a seasonal salinity distribution chiefly forced by dominant winds (Guerrero et al., 1997; Framiñan et al., 1999). The Punta Rasa section crosses the external part of the Río de la Plata saline front and covers the area to which waters are directed by winds from the east and northeast in spring and summer, during the reproductive season of

Neohelice granulata. We suggest that larvae exported from parental populations in Samborombón could be retained in this area by taking advantage of the different environmental clues present in this more or less predictable environment. For example they may select the high salinity/low temperature waters at the bottom of the Río de la Plata estuary, according to the physiological preferences of advanced larval stages. These waters are observed to penetrate more deeply in the estuary as a salt wedge (Guerrero et al., 1997). It is necessary to state however, that conditions prevailing during the sampling period (November 1999–February 2000) were unfortunately far from those typical of spring and summer, since the Río de la Plata discharge was about 10,000 m³/s below the average runoff (it was the lowest in 10 years). Also, an abnormal wind pattern was registered with southern winds intensively blowing at least during the previous week of the November sampling (Jaureguizar et al., 2007). In this way, we cannot discard a wider dispersion of *N. granulata* larvae from Samborombón Bay during more typical years, when the influence of the Río de la Plata estuary could extend to Punta Médanos (37° S) in spring and summer (Guerrero et al., 1997; Framiñan et al., 1999). Also, a southern extent of the influence of these estuarine waters, reaching Mar Chiquita, was proposed under occasional favorable conditions (Bogazzi et al., 2001; Jaureguizar et al., 2007). The presence of *N. granulata* larvae (only advanced stages) mainly in the nearshore station of Punta Médanos section

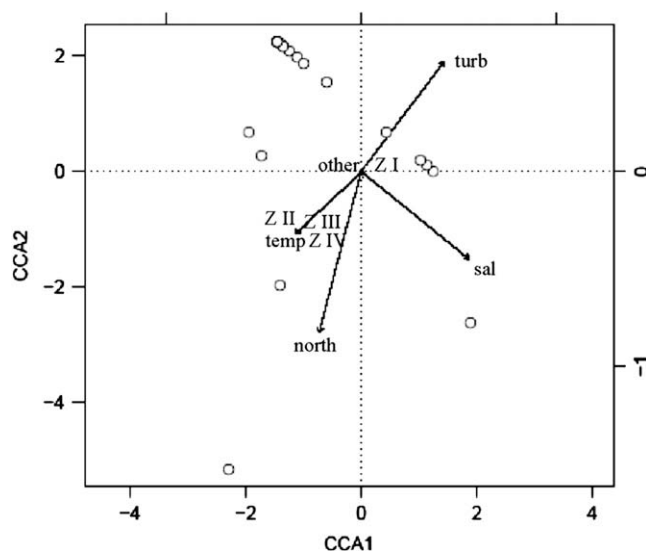


Fig. 4. Ordination diagram of the CCA analysis. Arrows represent environmental variables (turb: turbidity; sal: salinity; north: northerly position in the grid; temp: temperature), and points represent biological variables (Z I to Z IV: zoeal stages of *N. granulata*; other: decapod larvae other than *N. granulata*) and sampling stations (S1 to S10).

(Fig. 1a), together with their absence in the Faro Querandí and Mar Chiquita sections (Fig. 1a), reinforces the idea of a restricted larval dispersal.

Even though the coastal sampling in Mar Chiquita was not complete, our data are still important, considering the scarce info recorded about the largely neglected processes occurring very nearshore (Shanks et al., 2003). The retention of larvae near this lagoon, where oceanographic conditions are completely different from those in the Río de la Plata, is a surprising fact. The presence of different developmental stages in the same sample (Fig. 3a) indicates that the complete larval development takes place within the same area. In fact, as shown by CCA analysis, ZII to ZIV stages seem to have the same preferences. At the same time, the abrupt changes in density observed between adjacent stations may be related to the ability of larvae to detect small variations in physical conditions in a slightly heterogeneous environment. In spite of some variations in salinity or temperature recorded among stations, this is a well mixed shallow coastal area, without topographical features in the coast or in the bottom that could favor the formation of a more or less permanent front (Isla, 1980; this study). Although the collecting method is not the best to know the exact distribution of larvae in the water column, it is still clear that they are situated in the most superficial layer at least during ebb tides.

We do not know the process involved in keeping different larval stages together close to the parental population. Actively swimming larvae can substantially modify their horizontal transport even with simple vertical movements, by positioning in water column in a way that they take advantage of oceanographic processes and avoid excessive dispersion like in internal-wave mediated shoreward transport (Shanks and Wright, 1987), wind-driven transport (Natunewicz and Epifanio, 2001), and frontal transport (Wolansky and Hamner, 1988). Considering the superficial location of larvae, the correlation between the proximity to coast of the advanced stages (Fig. 3a) and the prevalence of favorable winds (Fig. 3b), the latter factor is probably involved. Larval swimming may contribute to this process, but the ability of *N. granulata* larvae to swim has been studied only in megalopae, capable of directed swimming oriented into a flow at moderate flow velocities (Valero et al., 1999). This wind-driven transport has

been proposed as the mechanism responsible for the distribution of the fiddler crab *Uca uruguayensis* in the Buenos Aires province coastal area (Bogazzi et al., 2001).

In summary, we have suggested two possible mechanisms, which are not mutually exclusive, to explain larval distribution of *Neohelice granulata* in the Río de la Plata and Mar Chiquita estuaries. Low salinity is probably avoided by larvae (but not by megalopae) anywhere it is present. So, larval behavior will be determined by the existence of salinity gradients, for example in the Río de la Plata estuary. Moreover, in situations where a salinity barrier does not exist, surface waters could be selected. In this way, ZI leaving the creeks adjacent to the estuary would rapidly descend to avoid low salinity, but if they were advected to marine waters, they could eventually return, being transported nearshore in surface waters by easterly winds until they find a salinity signal. In Mar Chiquita (and probably Bahía Blanca estuary), where low salinity waters leaving creeks are immediately mixed and low salinity signals do not remain, winds should be the main mechanism of retention.

Whatever the mechanism, if this hypothesis on a high self-recruitment is correct, and the wind is a major factor, we can speculate that populations of *Neohelice granulata* south of Mar Chiquita should have been established by larval transport during a different wind and/or coastal current patterns, or by adult migration in times of great development of the estuaries of Buenos Aires and north Patagonian rivers, as those recorded during the late Holocene sea level fluctuations, when transgressive and regressive processes originated a fringe of estuaries and coastal lagoons in many water courses. Those marshes disappeared with the descent of the relative sea level (Stutz et al., 1999; Vilanova et al., 2006).

5. Conclusion

In summary, even when zoeal stages of *Neohelice granulata* need fully marine to mixohaline salinities to develop and are rapidly exported to higher salinity waters if hatched at low salinities, the evidence available indicates that they are not dispersed far from their source population. This ability to avoid dispersion can be adapted to very different oceanographic conditions present in different coastal areas. Given the current pattern of water circulation, the connectivity, mediated by larvae, between San Clemente and Mar Chiquita populations will be possible only under exceptional conditions (higher Río de la Plata discharge) and the connectivity between Mar Chiquita and the southern populations will be unlikely. These findings do not support the model of estuarine population networks of *N. granulata* (Giménez, 2003).

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