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### Seasonal abundance and vertical distribution of crab larvae from northern Patagonia (Argentina): implications for their transport in a biogeographic boundary region

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ORIGINAL ARTICLE

## Seasonal abundance and vertical distribution of crab larvae from northern Patagonia (Argentina): implications for their transport in a biogeographic boundary region

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### Abstract

In species with meroplanktonic larval phases, some reproductive traits (i.e. seasonality and larval behaviour) interact with hydrographic features to determine larval transport. This work reports the seasonal, diel and ontogenetic changes in vertical distribution of crab larvae in the boundary region between the Argentine and the Magellanic biogeographic provinces of the Atlantic coast off northern Patagonia (Golfo Nuevo; 42.75°S, 65.00°W). Larval seasonality was studied from 47 plankton hauls taken from August 2004 to July 2005. Vertical distribution was studied from 45 stratified plankton hauls carried out in August 2005, December 2005 and April 2006. Crab larval stages were detected throughout the year, but abundance was higher from midwinter to midsummer. Species from southern regions – *Munida gregaria*, *Peltarion spinosulum* and *Halicarcinus planatus* – were abundant during winter and aggregated mainly near the surface, regardless of the hour of the day. In contrast, species from northern regions – *Platyxanthus patagonicus*, *Ovalipes trimaculatus*, *Leucippa pentagona*, *Leurocyclus tuberculatus*, *Cyrtograpsus* spp. and *Pachycheles chubutensis* – were abundant during spring and summer and were usually aggregated near the surface during the night and dispersed in subsurface layers during the day. Ontogenetic changes in vertical distribution were not observed. Residual currents reported in the area (3–6 km·day<sup>-1</sup>) and duration of larval life (approximately 15–70 days) suggests a minimum potential transport on a 100-km scale. Biological information reported in this work could be explicitly incorporated in a circulation model to accurately predict larval transport and connectivity.

**Key words:** *Decapod, larvae, vertical migrations, dispersal, Southwestern Atlantic*

### Introduction

Meroplanktonic larvae of crabs and other decapod crustaceans develop in the water column from hatching to settlement during periods varying from a few days to several months. During this time they feed on phytoplankton, smaller zooplankters or their own food reserves (Anger 2001). Larval life has profound effects on the population dynamics of most crab species because of high mortality rates (Welch & Epifanio 1995; Garvine et al. 1997) and spatial uncoupling from parental distribution because of passive transport (Caley et al. 1996). As a consequence, in mid-latitudes, where cyclic fluctuation of environmental

variables (e.g. temperature and photoperiod) modulate primary and secondary production (Colebrook 1984; Olive 1995; Gove & Paula 2000) and endogenous rhythms of organisms (Naylor 2010), seasonal timing of reproductive events, particularly hatching, is synchronized to maximize larval survival (Clarke 1992; Olive 1995). Biogeographic boundaries, where species are often at their latitudinal limits, can provide additional information on the adaptive value of these reproductive traits.

With few exceptions (Kingsford et al. 2002; Jeffs et al. 2003), dispersal attained by self-propulsion of swimming crab larvae is negligible in comparison with that imposed by horizontal currents typical in

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coastal and estuarine systems (Young 1995). Nevertheless, crab larvae can perform significant vertical migrations (Mileikovsky 1973; Schmalenbach & Buchholz 2009). When stratified flow conditions exist in the water column, larvae can perform ‘partial navigations’ (Kingsford et al. 2002) by adjusting their vertical position and concentrating at specific layers of the water column by active swimming behaviour (Young 1995). Horizontal transport is then modulated by the interaction between seawater dynamics and behavioural traits of larvae (Queiroga & Blanton 2004). For example, in specific environments such as estuaries, rhythmic larval migrations synchronized with tidal or daily variations in circulation often produce ‘selective tidal stream transport’ (Forward et al. 2003) resulting in transport patterns different from those predicted based on average water circulation. Moreover, because larvae’s vertical swimming behaviour may change throughout ontogenesis, different larval stages may display dissimilar dispersal patterns depending on the horizontal speed and direction of distinct seawater layers (Tankersley & Forward 2007).

Direct measurement of larval transport is a difficult task, particularly on broad geographical scales, mainly because of the difficulty of tracking individual larvae. New techniques have been developed to determine the geographical origin of recruits (DiBacco & Levin 2000; DiBacco & Chadwick 2001; Carson et al. 2008), but they only allow partial testing of a transport hypothesis. Alternatively, hydrodynamic models have been developed to project tracks of particles. These models allow the exploration of transport and connectivity between population subunits from different geographic regions. If planktonic larvae are considered as passive particles homogeneously distributed in the water column, it can be assumed that transport is mainly determined by physical processes (Epifanio & Garvine 2001; Marinone et al. 2008). However, as not only marine circulation but also selection of seawater strata by means of vertical swimming are recognized as the main modulators of larval transport, numerical simulations should combine spatio-temporal circulation with seasonality of abundance and the distribution of larvae resulting from vertical migrations (Metaxas & Saunders 2009).

The southeastern part of the South American continental shelf includes two biogeographic regions: the Argentinean (23–42°S) and Magellanic (42–56°S) provinces, each with its own characteristic decapod assemblage (Spivak 1997). Coastal and shelf waters off northeastern Patagonia between about 40° and 44°S represent a transition zone between both regions where species of crabs and other taxa present contrasting life-cycle schedules (Dellatorre & Barón 2008; Leal et al. 2008; Dellatorre & González-Pisani 2011; Gonzalez-Pisani 2011). Although early studies

on decapod larvae of both provinces have addressed taxonomic issues (Boschi 1964; Boschi et al. 1967, 1969; Boschi & Scelzo 1968; Bacardit 1985a,b; Vera & Bacardit 1986) and biogeographical problems (Boschi 1981; Bacardit & Vera 1986; Lovrich 1999), no study has been conducted on the seasonality and the presence and abundance of crab larvae in this transition zone. In this zone, it should be expected that seasonal patterns of larval abundance typical of both assemblages are found, allowing the distinction between their different evolutionary adaptations to temperate and cold waters in the Argentinean and Magellanic provinces to be seen.

Based on field sampling of crabs (larvae and adult specimens) along with *in situ* recording of environmental variables (light and depth conditions, wind direction), some hypotheses concerning the spatial distribution and transport of crab larvae have been considered for species typical of the Argentinean province (Anger et al. 1994; Bogazzi et al. 2001; Bas et al. 2009). Two of these studies (Anger et al. 1994; Bas et al. 2009) propose an export strategy for the larvae of two intertidal species: *Neohelice granulata* (Dana, 1851) and *Cyrtograpsus angulatus* (Dana, 1851). Furthermore, Bogazzi et al. (2001) suggested that the southern limit of the *Uca uruguayensis* (Nobili, 1901) population is explained by the wind patterns affecting the transport of larvae concentrated in surface layers. For species typical from the Magellanic province, field studies on crab larvae have focused on the seasonality of abundance (Lovrich 1999), the vertical distribution and some adaptive developmental traits (Thatje et al. 2003), but no particular hypothesis has been proposed regarding their transport mechanisms. In this study, we describe the general patterns of temporal abundance and vertical distribution of brachyuran and anomuran larvae, comparing them to species typically occurring in the Argentinean and Magellanic biogeographic provinces, and briefly discussing the potential implications for larval transport.

## Methods

### *Study area*

This study was conducted in Golfo Nuevo (GN), northern Patagonia (42.75°S, 65.00°W, Chubut, Argentina; Figure 1), an elliptical basin 2440 km<sup>2</sup> in surface area (Rivas & Ripa 1989), communicating with the Southwestern Atlantic through a southeast-facing 17-km wide strait (Mouzo et al. 1978). The gulf is deeper than the adjacent continental shelf. Its maximum depth is 184 m, whereas the depth of the adjacent shelf is 50–60 m. Surface seawater temperature (SST) monthly averages range from a

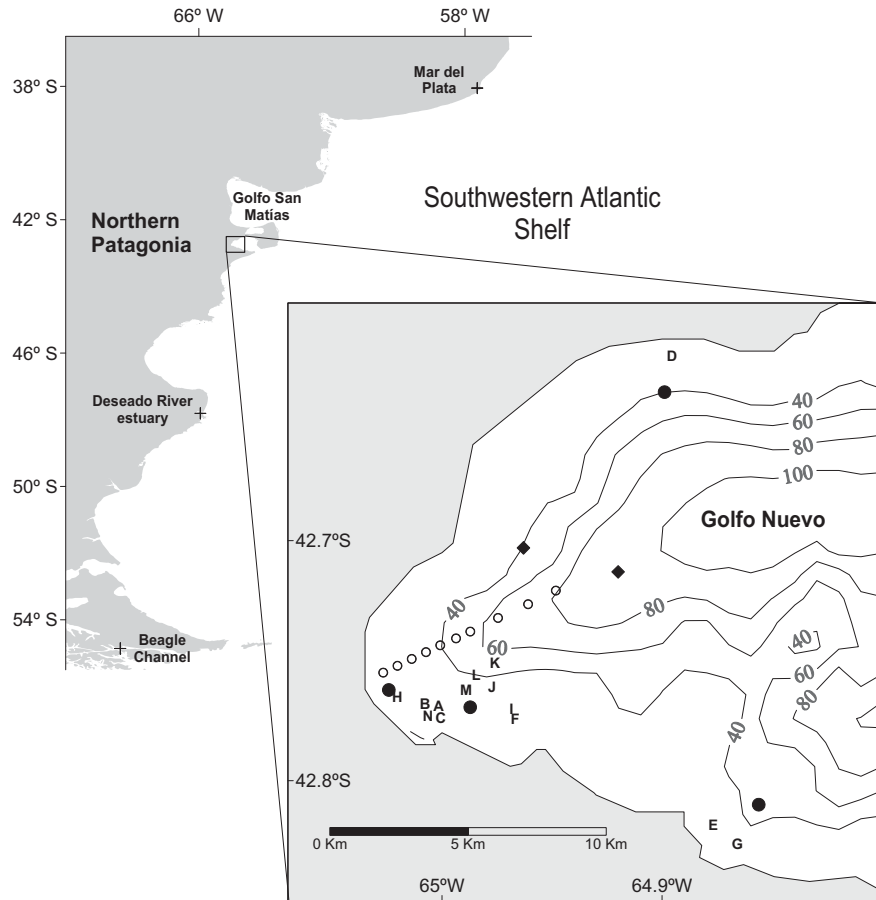


Figure 1. Bathymetry of the west coast of Golfo Nuevo. Black circles and diamonds indicate plankton sampling stations for seasonal and stratified samples, respectively. Capital letters indicate CTD stations from October 2004 to February 2005; empty circles indicate CTD stations during January 2008. Patagonian coastal locations quoted in the discussion are indicated in the left panel.

minimum of  $9.6^{\circ}\text{C}$  in September to a maximum of  $17.2^{\circ}\text{C}$  in February (SST data obtained from satellite estimations for the period 1987–1998, AVHRR Oceans Pathfinder NOAA–NASA), and salinity varies seasonally from 33.5 to 33.9‰ (Rivas & Ripa 1989). Tides are semidiurnal with a period of 12.42 h and amplitude ranging between 1.96 and 5.99 m on neap and spring tides, respectively (Dragani et al. 1994). The vertical thermo-haline structure of GN is strongly influenced by the thermal structure (salinity variations are negligible; Rivas & Ripa 1989). A thermocline ( $\sim$  pycnocline) forms during the warm season (from October to April) at depths of approximately 25–30 m and disappears during the cold season (from May to September; Rivas & Ripa 1989). Water circulation in GN has been studied by means of numerical simulations (Rivas 1989; Tonini 2010) that revealed the presence of a main cyclonic gyre (homogeneous throughout the water column) throughout the year and the generation of a smaller anticyclonic gyre off the west coast during the cold season (autumn and winter). Current velocities are often slower than

$5\text{ cm}\cdot\text{s}^{-1}$ , except for the area near the mouth, where tidally forced currents are stronger (Tonini 2010). Connectivity with the adjacent shelf has not been studied; however, based on its temperature and salinity fields, GN has been considered a semi-enclosed basin (Rivas 1990) with a moderate rate of water exchange with the adjacent shelf.

The circulation in the inner shelf, near the mouth of GN is forced by large tides, intense offshore winds and the barotropic pressure gradients generated by the Malvinas Current (Palma et al. 2008). The depth-averaged circulation consists of a broad northeastward flow with average velocities of  $\sim 3.5\text{ cm}\cdot\text{s}^{-1}$  and peaks of more than  $7\text{ cm}\cdot\text{s}^{-1}$  (Piola & Rivas 1997; Palma et al. 2008). The vertical structure of the circulation is roughly equivalent to a two-layer flow where the upper layer is directed toward the east and the bottom layer in the opposite direction (Palma et al. 2008)

#### Plankton sampling

*Seasonality.* From August 2004 to June 2005, 47 zooplankton hauls were taken in the western



region of GN at bottom depths between 6 and 40 m (black circles, Figure 1). Samples were taken with a 295- $\mu\text{m}$  mesh size Hensen plankton net with a flowmeter (Ogawa Seiki) attached to its mouth. The net was towed at approximately  $3.6 \text{ km}\cdot\text{h}^{-1}$  for 15 min. Twenty-three hauls were subsurface horizontal tows (at 1–3 m depth on sites with 6–10 m bottom depth), the other 24 were oblique tows with the net consecutively remaining at depths of approximately 30, 15 and 2 m for 5 min in sites with 35–50 m bottom depths.

*Vertical distribution.* Forty-five stratified zooplankton samples were taken in August and December 2005 and in April 2006, with the same sampling device used for the study of seasonality, equipped with a mouth closure mechanism activated by a messenger. Samples were taken near the northwest coast of GN at two fixed stations with 35 m (shallow) and 80 m (deep) bottom depths, located 2.7 and 6.4 km from the shore, respectively (black diamonds, Figure 1). On each sampling date, samples were taken in different water column strata with nominal depths of 3, 10, 30 and 70 m (the last, only at the deep site), at least once during daylight and once during night hours on consecutive days. For each sampling, the zooplankton net was deployed open with the mouth facing up until reaching the desired depth, towed for 10 min at approximately  $3.6 \text{ km}\cdot\text{h}^{-1}$ , then closed by a messenger and raised back to the surface.

In this study, sampling depth strata were selected based on the vertical thermo-haline structure of GN described by Rivas & Ripa (1989) and the vertical stratification of the northern Patagonian shelf characterized by Rivas & Piola (2002), aiming to include the surface stratum, the subsurface mixed layer, the thermocline region and the bottom layer. However, because the vertical structure of the water column is considered to be highly variable in the nearshore region (Rivas & Piola 2002; Dellatorre et al. 2012), it was specifically evaluated by means of conductivity, temperature and depth (CTD) profiles at different locations in the study area. Fourteen CTD profiles were taken from October 2004 to February 2005 in the western portion of GN at sites with depths between 8 and 46 m (Figure 1). To evaluate depth-related variations in vertical structure, 20 additional CTD profiles were completed on 14 and 16 January 2008 along a 10-station transect perpendicular to the west coast of GN with a bottom depth range of 8–85 m (Figure 1). Interannual variations in the vertical thermo-haline structure of the water column are not expected to be of relevance when compared with short-term variations (in temporal scales from minutes to seasons; Rivas & Ripa 1989; Rivas &

Piola 2002; Dellatorre et al. 2012). Therefore we assumed that these data, taken approximately two years later than the plankton samples, would be of relevance for this study.

#### *Larval identification*

Each plankton sample was fixed on board immediately after sampling with 5% formalin in seawater solution. In the laboratory, all brachyuran and anomuran decapod larvae were sorted using a binocular microscope and identified to the lowest taxonomic level, following larval descriptions available in the literature. In two winter samples, in which the first larval stages of *Munida gregaria* (Fabricius, 1793) and *Peltarion spinosulum* (White, 1843) were extremely abundant, three subsamples (33 ml each of a sample volume of 1000 ml) were used to estimate the first zoeal stage density of both species. Subsequently, the entire sample was inspected to identify and count the remaining species/stages. A key was composed for the identification of anomuran and brachyuran first zoeae from GN, which is available upon request from the corresponding author. Because of the lack of morphological descriptions of larvae belonging to the family Pinnotheridae and the superfamily Paguroidea reported to live in the study area (Spivak 1997), the identifications were done following the keys from Lovrich (1999) and Pohle et al. (1999), and species/stages were grouped in the categories Pinnotheridae spp. and Paguroidea spp. Early zoeal stages of species from the genus *Cyrtograpsus* are virtually identical (Spivak & Cuesta 2000) and were only identified to the generic level.

#### *Data analysis*

Larval density was estimated on the basis of total larval abundance of each sample, divided by the estimation of filtered water. Samples were grouped bimonthly from August 2004 to July 2005 because of the unbalanced sampling effort and to perform robust statistical analysis to detect significant peaks of larval abundance. Seasonality of occurrence and abundance of different species and stages was described based on the average density of each larval species/stage in all samples of each bimonthly period.

Zoeal stages were grouped as early and late stages, taking the total number of stages for each species into consideration. For *Leucippa pentagona* (Milne Edwards, 1833), *Leurocyclus tuberculatus* (Milne Edwards & Lucas, 1843) and *Pachycheles chubutensis* (Boschi, 1963), early and late zoeal stages coincide with the only two zoeal stages in those species. For *Peltarion spinosulum*, *Platyxanthus patagonicus* (Milne Edwards, 1879), *Munida gregaria*, *Halilcarcinus*

*planatus* (Fabricius, 1775) and *Cyrtograpsus* spp., zoeae I and II (ZI and ZII) were grouped as early stages and the rest as late stages. For *Ovalipes trimaculatus* (de Haan, 1833), the first four zoeal stages (ZI–ZIV) were grouped as early stages and the fifth to eighth zoeal stages (ZV–ZIIIV) as late stages. Independent ANOVA analyses and post-hoc tests (Fisher’s Least Significant Difference) were performed to compare densities between bi-monthly samples of early zoeal stages of each species. This comparison allows for the detection of significant peaks of larval abundance, which could indicate hatching seasonality. Late zoeal stages were not compared statistically because of the low densities recorded. In all cases, larval densities ( $D$ ) were transformed into  $\text{Log}_{10}(1 + D)$  in order to normalize distributions and homogenize variances.

To assess whether individual species/stages were aggregated in any specific depth stratum during daylight or night hours, a quotient ( $Q$ ) analysis was performed following Yannicelli et al. (2006). The frequency of occurrence of each species/stage at each depth stratum ( $pf_D$ ) was calculated by dividing the total number of specimens caught in each stratum by the total number of specimens caught in all sampled strata. After that, the frequency of each depth stratum sampled ( $ps_D$ ) was calculated by dividing the volume filtered from each stratum by the total volume filtered for all strata sampled. Estimates of  $Q$

were done dividing those two quantities ( $pf_D / ps_D^{-1}$ ) and values of  $Q$  over 1 were used to indicate environmental preference (van der Lingen et al. 2001; Yannicelli et al. 2006).

## Results

### Hydrography

CTD profiles showed that the thermal structure of the west coast of GN is spatially and temporally variable (Figures 2 and 3). A thermocline was observed in all of the temperature profiles at variable depths between near-surface and approximately 30 m (Figures 2 and 3). Cross-shore temperature sections based on CTD profiles taken in January 2008 (Figure 3) allowed for the recognition of the differential effects of wind turbulent mixing on the vertical thermal structure of the water column at different depths. On 14 January a vertical structure characterized by a 20-m deep thermocline, homogeneous on the horizontal scale, was observed along the cross-shelf section. On 16 January, after a period of intense southerly wind (duration: 13 h; average intensity:  $41.1 \text{ km}\cdot\text{h}^{-1}$ ; range of direction:  $167\text{--}217^\circ$ ), the vertical structure at sites with bottom depths less than 80 m was homogeneous, whereas the thermocline was still observed slightly deeper at 30 m depth at the deeper sites (Figure 3).

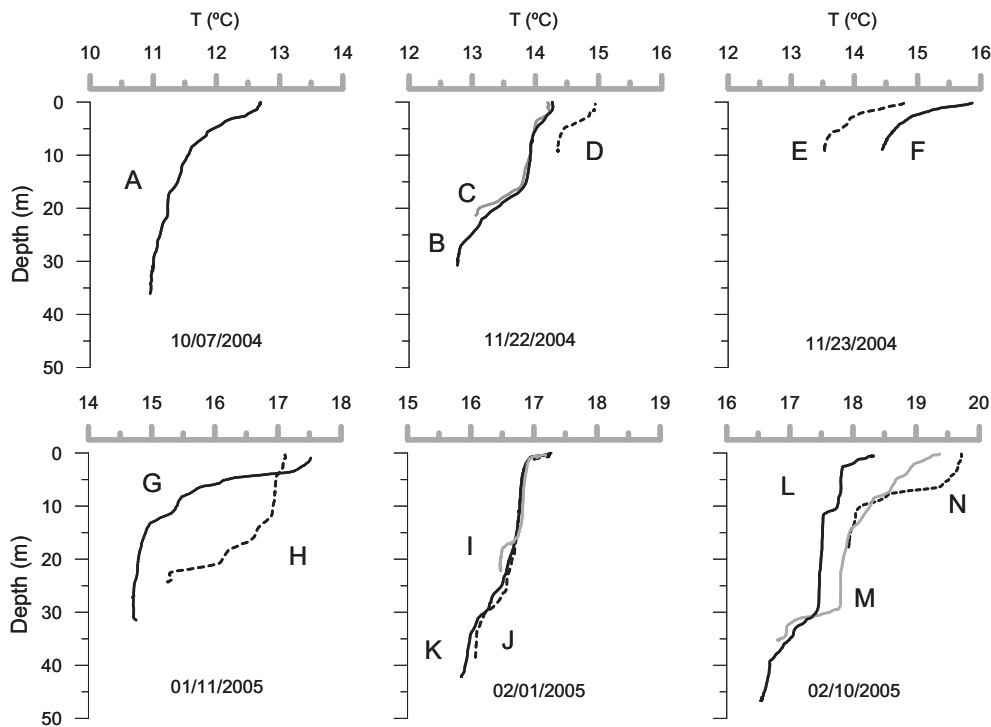


Figure 2. Depth–temperature (CTD) profiles (from surface to bottom) for nearshore stations of Golfo Nuevo from October 2004 to February 2005. Letters indicate the geographic position of the sampling station as shown in Figure 1. Date format: MM/DD/YYYY.

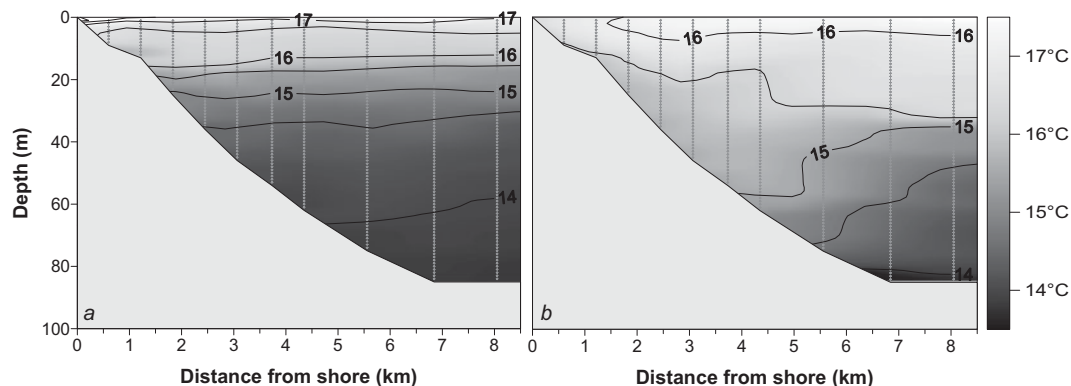


Figure 3. Cross-shore temperature section on the west coast of Golfo Nuevo calculated from 10 CTD profiles (grey dotted lines) on a transect. Plots *a* and *b* represent the vertical thermal structure at 14 and 16 January 2008, respectively, after an event of intense south wind.

### Seasonality

Larval stages of nine decapod species were identified in 47 plankton hauls (7370 m<sup>3</sup> of total filtered volume) collected from August 2004 to July 2005 (Table I). Also, larvae of the genus *Cyrtograpsus*, the family Pinnotheridae and the superfamily Paguroidea occurred in the samples. A clear seasonal pattern of abundance was observed for all taxa identified. Total larval abundance was high during the 6 months

from August to January and decreased from February to July (Table I). Early zoeal stages of *Munida gregaria* and *Peltarion spinosulum* were abundant during the winter (from June to September) (Figure 4A,B). *Peltarion spinosulum* larvae virtually disappeared from the water column towards late spring (after November), whereas those of *M. gregaria* were found in lower abundance during the rest of the year. *Halicarcinus planatus* (Figure 4E) larvae were also recorded at high densities during winter (August–

Table I. Average density (number of specimens per 1000 m<sup>3</sup>) of each species/stage (zoeal stages indicated with numbers, m: megalopa; n/i: stages not identified) analysed during the complete sampling programme. Seasonal and stratified samples were taken from August 2004 to July 2005, and from August 2005 to April 2006, respectively. Total filtered volume in m<sup>3</sup>. B<sub>1</sub> and B<sub>2</sub> represent two unidentified larval forms.

Identified species	Larval stages	Seasonal samples						Stratified samples		
		Aug–Sept	Oct–Nov	Dec–Jan	Feb–Mar	Apr–May	Jun–Jul	Aug	Dec	Apr
<i>Munida gregaria</i>	1–2	2036	137	12	1	4	384	14902	1	0
	3–5	1	1	0	0	0	0	30	0	0
<i>Peltarion spinosulum</i>	1–2	359	12	0	0	0	26	3584	0	0
	3–4	0	0	0	0	0	0	22	0	0
<i>Halicarcinus planatus</i>	1–2	262	4959	97	6	5	5	14	0	0
	3	16	2266	6	0	0	0	0	0	0
<i>Leurocyclus tuberculatus</i>	1	2	3128	4	12	6	0	0	80	19
	2	0	555	4	8	7	0	0	71	14
	m	0	67	2	5	15	0	0	3	0
<i>Leucippa pentagona</i>	1	0	1556	15	8	74	0	0	54	93
	2	0	682	3	2	9	0	0	30	51
	m	0	56	0	2	17	0	0	2	16
<i>Cyrtograpsus</i> spp.	1–2	1	1043	293	174	22	0	0	71	4
	3–5	8	169	11	148	41	0	0	52	21
	m	0	0	0	1	12	0	0	0	2
<i>Ovalipes trimaculatus</i>	1–4	0	16	3	22	0	0	0	73	1
	5–8	0	0	0	0	0	0	0	0	0
<i>Platyxanthus patagonicus</i>	1–2	0	155	0	0	1	0	0	27	0
	3–4	0	0	0	0	0	0	0	22	0
<i>Pachycheles chubutensis</i>	1	0	5	7	19	8	0	0	5	0
	2	0	0	7	11	0	0	0	60	14
Paguroidea spp.	n/i	23	87	5	25	3	78	60	119	0
Pinnotheridae spp.	n/i	1	12	2337	142	713	0	0	16	4
B <sub>1</sub>	n/i	0	0	0	0	0	0	0	30	5
B <sub>2</sub>	n/i	0	0	0	0	0	0	0	16	14
Number of samples		7	12	9	7	8	4	18	15	13
Total filtered volume		1730	2298	1073	807	784	677	3016	2029	939

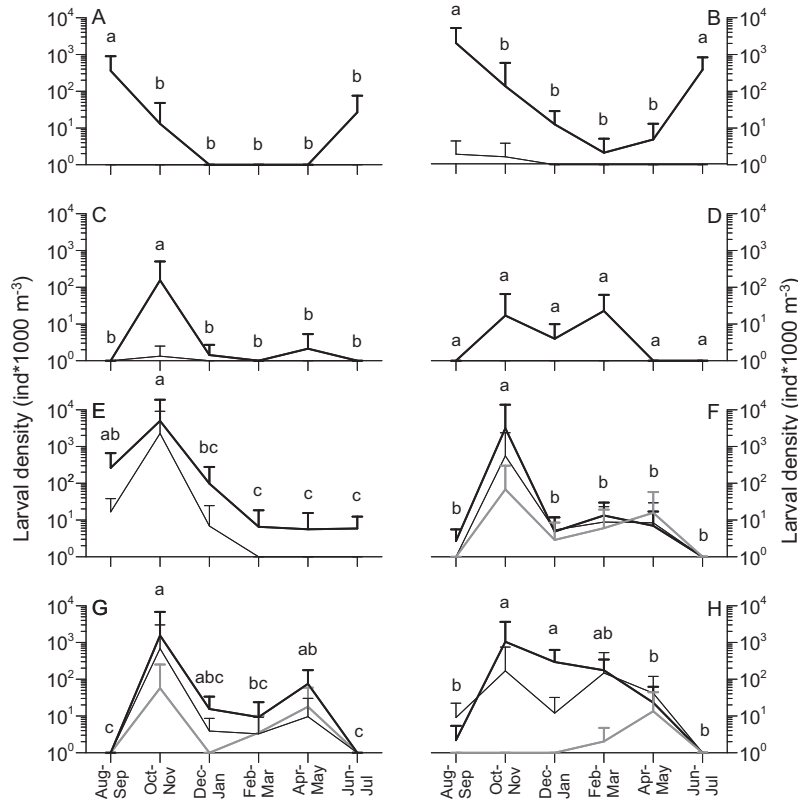


Figure 4. Seasonal larval abundance of *Peltarion spinosulum* (A), *Munida gregaria* (B), *Platyxanthus patagonicus* (C), *Ovalipes trimaculatus* (D), *Halicarcinus planatus* (E), *Leurocyclus tuberculatus* (F), *Leucippa pentagona* (G) and *Cyrtograpsus* spp. (H) from August 2004 to July 2005. Mean density plus one of early zoeae, late zoeae and megalopae are represented by thick black, thin black and grey lines, respectively. Vertical bars represent standard deviation. Lowercase letters indicate significant differences in Zoea I abundance.

September) and peaked in spring (October–November). Larvae of these three species were further considered ‘winter larvae’ because they were the only taxa recorded in high abundance during winter (from June to September; Figure 4, Table I). In contrast, the other abundant taxa identified, virtually absent from winter samples and peaking during spring (October–November), were considered ‘spring larvae’ (Figure 4). *Platyxanthus patagonicus* larvae were abundant during spring (October–November) and were almost undetectable during the rest of the year (Figure 4C). *Ovalipes trimaculatus* larval abundance also peaked in spring and had a second peak during late summer (February–March; Figure 4D). *Leurocyclus tuberculatus* (Figure 4F) larval abundance peaked in spring, and then its abundance decreased, remaining at lower levels during the rest of the year. *Cyrtograpsus* spp. (Figure 4H) and *Leucippa pentagona* (Figure 4G) were detected in high abundances from October to May. Larval stages of Pinnotheridae and *Pachycheles chubutensis* were detected mainly from December to May, while those of Paguroidea were found during most of the year (Table I). The seasonal variation of larval species/stage abundance in samples obtained from the stratified zooplankton hauls was similar to that

identified in samples obtained for the analysis of seasonality (Table I).

#### Vertical distribution

From a total of 46 plankton hauls (5984 m<sup>3</sup> of filtered volume) collected from August 2005 to April 2006, larval stages of the same taxa recorded in the previous section were identified, with the addition of two new unidentified brachyuran larval taxa (Table I). Identified taxa were approximately the same in samples taken in December 2005 and April 2006, differing from those taken in August 2005 (Table I). Vertical distributions were similar in December and April, but densities were low in samples taken in the latter month. Therefore, only data from August (*Munida gregaria*, *Peltarion spinosulum* and *Halicarcinus planatus*) and December 2005 (the remaining taxa) are reported to describe vertical distribution. The general patterns of vertical distribution of different larval species/stages identified were non homogeneous (Figures 5 and 6; Table II). Late-zoeal and megalopa stages of all identified species were scarce in the samples (Table I), and the vertical distribution patterns of different ontogenetic stages were similar in most cases (Table II).



Table II. Quotient ( $Q$ ) analysis.  $Q$  values of each species/stage at each depth stratum (3, 10, 30 and 70 m depth), in the shallow (35 m bottom depth) and at the deep (80 m bottom depth) site. Values  $\geq 1$  (bold numbers) indicate environmental preference. Zoecal stages grouped as early and late stages are indicated with numbers.

Species	Zoecal stage	Shallow						Deep							
		Day			Night			Day				Night			
		3	10	30	3	10	30	3	10	30	70	3	10	30	70
<i>Munida gregaria</i>	1–2	<b>2.9</b>	0	0	<b>1.8</b>	0	0.3	<b>2.9</b>	0.1	0.4	0.3	<b>1.5</b>	0.4	0	0.6
	3–5	<b>2.9</b>	0	0.1	0.4	0	<b>1.6</b>	<b>2.7</b>	0	0	0.6	<b>1.8</b>	0	0	0.8
<i>Peltarion spinosulum</i>	1–2	<b>2.0</b>	0	0	<b>1.9</b>	0	0.1	<b>3</b>	0.1	0.7	0.1	<b>1.7</b>	0.1	0	0.8
	3–4	<b>2.5</b>	0.2	0.3	<b>1.9</b>	0	0.2	<b>2.9</b>	0.4	0.2	0	<b>1.8</b>	0	0	0.6
<i>Cyrtograpsus</i> spp.	1–2	0.1	0.9	<b>1.7</b>	0.6	0.5	<b>1.8</b>	0	0	<b>3.5</b>	0.3	<b>4.8</b>	0	0	0
	3–5	0.1	0.9	<b>1.7</b>	<b>1</b>	0.7	<b>1.3</b>	0	0	<b>3.9</b>	0	<b>4.7</b>	0	0	0
<i>Pachycheles chubutensis</i>	1	0.5	<b>2.3</b>	0.4	0.2	0.6	<b>2.1</b>	0	<b>1.7</b>	<b>2.9</b>	0	0.6	0.2	<b>1.9</b>	<b>1.1</b>
	2	0.4	<b>2.1</b>	0.6	0.1	0.5	<b>2.3</b>	0	<b>2.9</b>	<b>2.1</b>	0	0.1	0.4	<b>2.9</b>	0.3
<i>Leurocyclus tuberculatus</i>	1	0.1	0.4	<b>2.1</b>	<b>2</b>	0.8	0.4	0	0	<b>2.3</b>	<b>1.1</b>	<b>1.4</b>	0	0	<b>2.7</b>
	2	0	0.2	<b>2.4</b>	<b>2</b>	0.7	0.4	0	0	<b>1.4</b>	<b>1.7</b>	<b>3.4</b>	0	0	<b>1.1</b>
<i>Leucippa pentagona</i>	1	0	<b>1.1</b>	<b>1.7</b>	<b>2</b>	0.8	0.3	0	0	<b>1.5</b>	<b>1.7</b>	<b>4.5</b>	0	0	0.2
	2	0	0.9	<b>1.8</b>	<b>2.3</b>	0.7	0.2	0	0	<b>1</b>	<b>2</b>	<b>4.4</b>	0	0	0.3
<i>Ovalipes trimaculatus</i>	1–4	<b>2.3</b>	0	0.9	<b>1.8</b>	0.2	<b>1.1</b>	0.7	0.3	<b>1.4</b>	<b>1.2</b>	<b>4.8</b>	0	0	0
<i>Platyxanthus patagonicus</i>	1–2	0.2	0.3	<b>2.2</b>	<b>1.8</b>	0.7	0.7	0	0	<b>1.3</b>	<b>1.8</b>	<b>2.4</b>	<b>1</b>	0	0.9
	3–4	0	<b>1.9</b>	<b>1</b>	<b>1.8</b>	0.8	0.5	0	0	<b>1.5</b>	<b>1.6</b>	<b>4.3</b>	0	0.2	0.2
<i>Halilcarinus planatus</i>	1–2	<b>2.6</b>	0.1	0.3	0.8	0	<b>1.2</b>	<b>3</b>	0.1	0.5	0.1	<b>1.3</b>	0.8	0	0.5

Larval stages of *M. gregaria* were markedly abundant in surface samples, exceeding 600 larvae  $\cdot m^{-3}$  in some cases. At the shallow (35 m bottom depth) and deep (80 m bottom depth) sampling sites, larvae of this species and *P. spinosulum* were more abundant close to the surface regardless of the hour of the day (Figures 5 and 6, plots A and B; Table II). Early zoecal stages of *H. planatus* were scarce in the winter, stratified samples (Table I). Approximately 75–95% of the specimens sampled during daylight hours were aggregated near the surface (independently of the bottom depth in the sampling site). During the night, approximately 50% of *H. planatus* larvae were found close to the surface, but at the shallow sampling site, a high proportion of larvae were also found near the bottom (Table II).

*Cyrtograpsus* spp. larvae were mainly aggregated in the 30 m depth stratum (approximately representing the thermocline stratum) during the day (Table II). During the night hours different patterns of vertical distribution were found at both sampling sites. At the shallow site *Cyrtograpsus* spp. larvae were found homogeneously distributed in the column. By contrast, in the deep sampling site *Cyrtograpsus* spp. larvae were only found near the surface (Figures 5 and 6, plots C; Table II). High densities of *Pachycheles chubutensis* larvae were mainly found in mid-depth strata (10 and 30 m; Figures 5D and 6D) during daylight hours. During the night they were found at 30 m or deeper (Figures 5 and 6, plots D; Table II). *Leurocyclus tuberculatus* and *Leucippa pentagona* larvae showed similar patterns of vertical distribution. Both species were mainly aggregated near the surface during the night and in deeper strata

during the day (Table II; Figures 5 and 6, plots E and F). Late larval stages of *Ovalipes trimaculatus* were absent in all of the samples taken in this study (Table I). At the shallow sampling site, early stages of this species were aggregated near the surface and near the bottom regardless of the hour of the day (Figure 5, plots G; Table II). Instead, at the deep sampling site larvae were clearly aggregated near the surface during the night (Table II) and dispersed through the entire water column during the day, with slightly higher densities in the 30 and 70 m strata (Figure 6, plots G; Table II). Larvae of *Platyxanthus patagonicus* were aggregated near the surface during the night, and were found in deeper waters during the day, regardless of the sampling site (Figures 5 and 6, plots H; Table II).

## Discussion

In northern Patagonia, crab larvae were present throughout the year in the meroplanktonic community and their densities peaked during spring. Most species reported in this study were abundant during spring and summer (spring larvae), but three of them (*Munida gregaria*, *Peltarion spinosulum* and *Halilcarinus planatus*) occurred at high densities during winter (winter larvae). The last, *H. planatus*, peaked in spring but was also recorded in high densities during late winter (August–September). Interestingly, the geographic range of species with ‘spring larvae’ includes most of the Argentine zoogeographic province, between 23 and 42°S, whereas species with ‘winter larvae’ are typical of the Magellanic province (between 42 and 55°S)

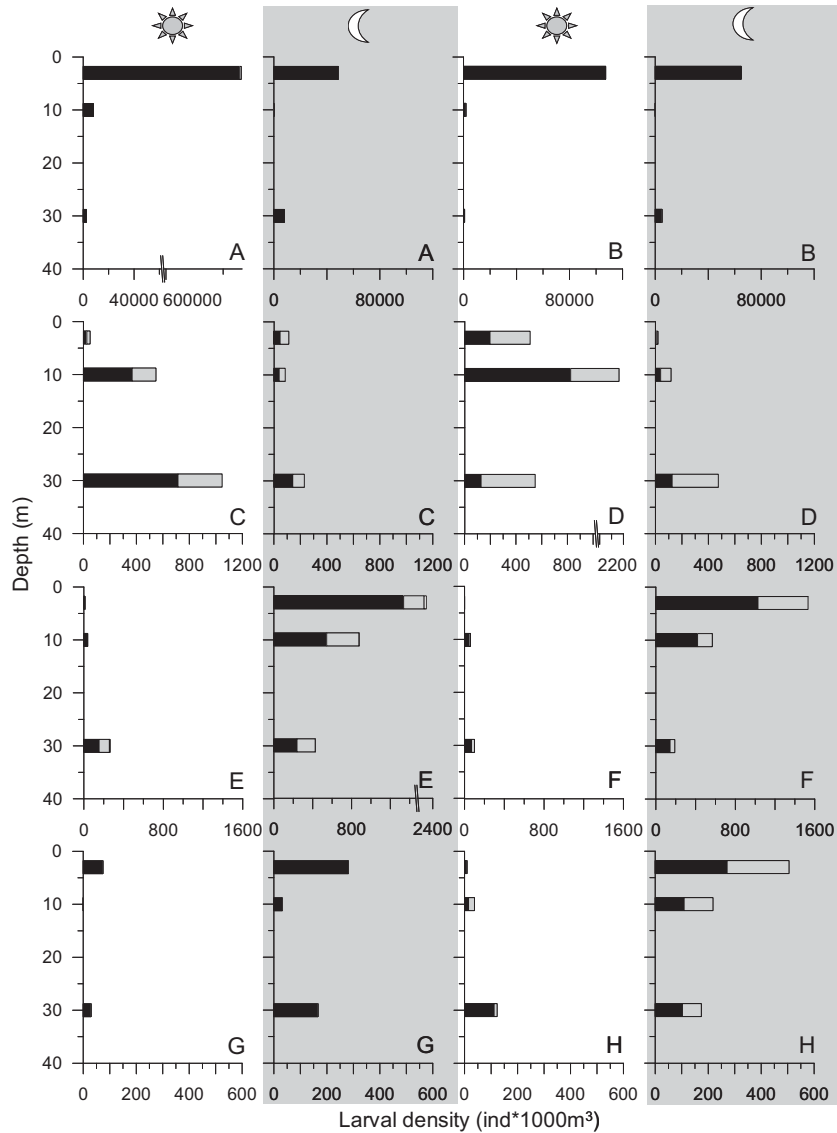


Figure 5. Larval density at each sampling stratum (3, 10 and 30 m depth) at the shallow site (35 m bottom depth) during daylight (clear charts) and night (shaded charts) hours. Dark, grey and white (only in E) bars correspond to early and late zoea, and megalopa stages, respectively, of *Munida gregaria* (A), *Peltarion spinosulum* (B), *Cyrtograpsus* spp. (C), *Pachycheles chubutensis* (D), *Leurocyclus tuberculatus* (E), *Leucippa pentagona* (F), *Ovalipes trimaculatus* (G) and *Platyxanthus patagonicus* (H). Plots A and B were drawn on the basis of stratified samples taken in August 2005; remaining plots were drawn from samples taken in December 2005. Note different scales on x-axis.

(Spivak 1997). Northern Patagonia represents the southern (coldest) part of the range of distribution of species with spring larvae; therefore, low temperatures in autumn and winter may represent a constraint for development of their early life-stages. In contrast, this region represents the northern (warmest) part of the geographic range of distribution of most of the Magellanic species, and the development of early life stages may be constrained by high temperatures during the warm season. Alternatively, all of the identified species have planktotrophic development (Boschi et al. 1969; Roberts 1973; Iorio 1983; Iorio & Boschi 1986; Schoeman & Cockcroft 1996; Spivak & Cuesta 2000; Pohle &

Marques 2003; González-Pisani et al. 2006; Santana & Marques 2009) and seasonal patterns of larval abundance could also be constrained by food availability. Phytoplankton abundance in coastal northern Patagonia varies seasonally, with high values ( $\sim 100 \text{ mg chl } a \text{ m}^{-3}$ ) during winter (from June to August) and relatively low ( $< 5 \text{ mg chl } a \text{ m}^{-3}$ ) during the rest of the year (Villafañe et al. 2004; Helbling et al. 2005). Zooplankton biomass peaks following phytoplankton blooms in southern Patagonia (Sabatini & Alvarez Colombo 2001) and the same trend is expected in northern waters. In this context, we can hypothesize that ‘winter species’ could be adapted to feed on microplankton cells

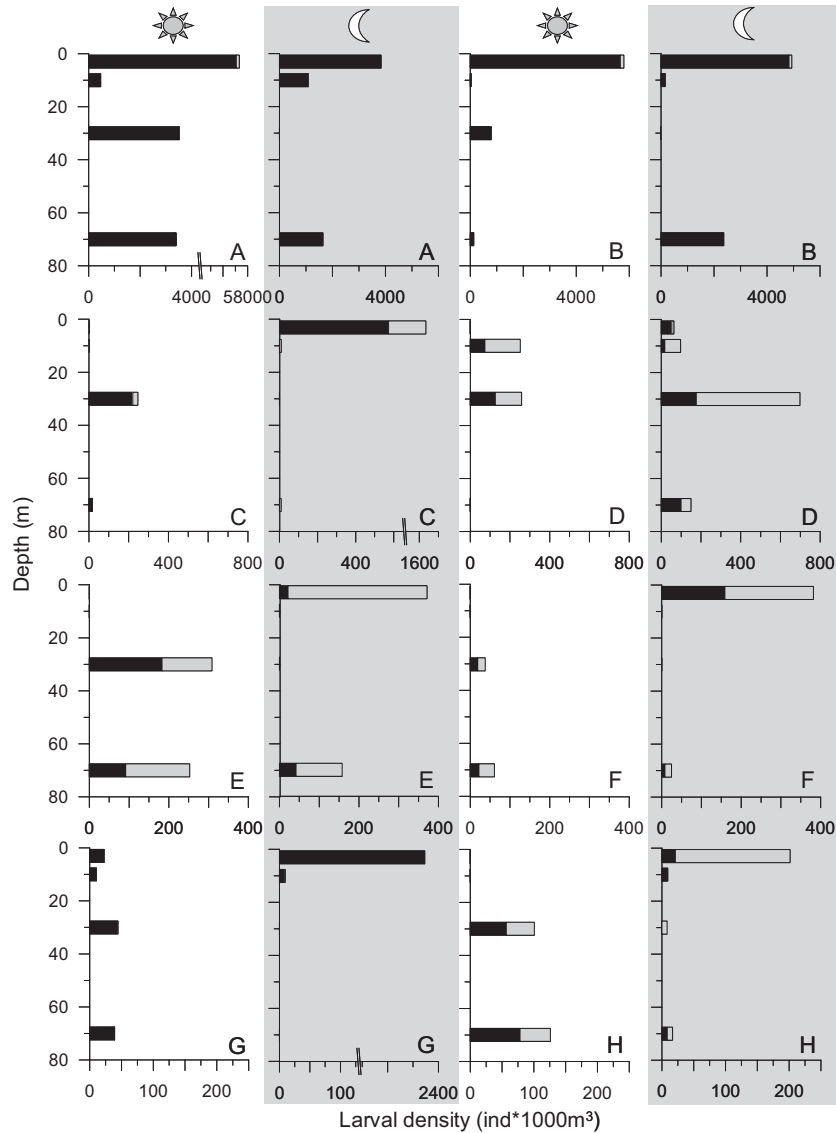


Figure 6. Larval density at each sampling stratum (3, 10, 30 and 70 m depth) at the deep site (80 m bottom depth) during daylight (clear charts) and night (shaded charts) hours. Dark and grey bars correspond to early and late zoeal stages, respectively, of *Mumida gregaria* (A), *Peltarion spinosulum* (B), *Cyrtograpsus* spp. (C), *Pachycheles chubutensis* (D), *Leurocyclus tuberculatus* (E), *Leucippa pentagona* (F), *Ovalipes trimaculatus* (G) and *Platyxanthus patagonicus* (H). Plots A and B were drawn on the basis of stratified samples taken in August 2005; remaining plots were drawn from samples taken in December 2005. Note different scales on x-axis.

(mainly diatoms  $> 20 \mu\text{m}$ ; Helbling et al. 2005), while ‘spring species’ would feed on larger zooplankton.

The reproductive seasonality of most species identified in this work has been studied previously. The peak of abundance of early larval stages of *M. gregaria* agreed with the hatching season (from July to December) reported for the species in coastal areas of GN (Delatorre & Barón 2008). However, the presence of a few ZI larvae of *M. gregaria* during summer and autumn was unexpected, considering the complete absence of breeding females reported during these seasons (Delatorre & Barón 2008). The reproductive cycle of *P. spinosulum* has not been

studied, but from its seasonal larval occurrence it could be inferred that hatching occurs during winter. At the southern extreme of its geographic distribution ( $55^\circ\text{S}$ ), *H. planatus* is the only species that produces two yearly larval cohorts (Diez & Lovrich 2010) that extend their occurrence in the plankton from September until January (Lovrich 1999). At the Deseado River estuary ( $48^\circ\text{S}$ ), *H. planatus* has multiple spawning and ovigerous females are present during most of the year (May–February) (Vinuesa & Ferrari 2008). Although the reproductive cycle has not been studied in coastal waters off northern Patagonia, the seasonality of larval abundance registered in this study (Figure 4E) suggests a year-round

reproductive activity of *H. planatus*, lower during summer and autumn, and peaking during winter. *Platyxanthus patagonicus* has a brief hatching season in northern Patagonia, peaking in September–October (Leal et al. 2008). The only peak of larval abundance registered during October–November in this study is consistent with the seasonal reproductive schedule previously reported, but might indicate a slight delay in the seasonal peak of hatching. On the other hand, the larval abundance of *Ovalipes trimaculatus* peaked in spring and in late summer, which is consistent with the reported hatching peaks in GN (Dellatorre 2009). The reproductive cycle of *Cyrtograpsus* spp. has not been studied in northern Patagonia. However, it is known that in Mar del Plata (38°S, Figure 1) high frequencies of breeding females of *Cyrtograpsus altimanus* (Rathbun, 1914) and *C. angulatus* (Dana, 1851) occur simultaneously from July to March (Silva 2009). Based on the records of *Cyrtograpsus* spp. larvae in this study (October–May), we hypothesize that the breeding season in the region is two or three months delayed when compared with that reported for Mar del Plata. Oviparous females of *Leurocyclus tuberculatus* were recorded throughout the year with the exception of May and June in GN (Gonzalez-Pisani 2011). Accordingly, larvae of this majid were present in the zooplankton samples in all months except for June–July. Notwithstanding the wide range of latitudinal distribution of *Leucippa pentagona* (Spivak 1997), no published information is yet available on its reproductive seasonality, but the seasonal variations of larval abundance shown in this study suggest a wide breeding season, similar to that of *L. tuberculatus*.

The thermo-haline structure of Golfo Nuevo was previously studied on the basis of seasonal CTD profiles at 24 oceanographic stations (Rivas & Ripa 1989). This study showed horizontal homogeneity of salinity and temperature fields and strong seasonal variations. The vertical structure evolved from a completely mixed state at the end of winter, to a strongly stratified state at the end of summer; the thermocline position was suggested to be between 30 and 40 m depth, and the nearshore region was poorly resolved (Rivas & Ripa 1989). Our data were collected mostly in the nearshore region and showed strong spatial and temporal variability of the vertical thermal structure (Figures 2 and 3). A previous study showed intense fluctuations of the vertical thermal structure at 20 m depth in the same region (Dellatorre et al. 2012) and was interpreted as short-term upwelling–downwelling events driven by wind and tidal forcing. Coastal dynamics (including vertical mixing and upwelling/downwelling processes) are highly variable at short spatial and

temporal scales within GN and could homogenize the vertical structure (and hence the planktonic community) to depths lower than 70 m (Figure 3). Therefore, we assumed that larval vertical distribution recorded at the deeper site (80 m bottom depth) could better represent larval behaviour, and consequently further discussion will focus on larval patterns of vertical distribution observed at this site.

During winter, larvae were mainly aggregated near the surface regardless of the hour of the day, whereas in spring and summer, they were usually aggregated near the surface during the night and dispersed into subsurface layers during the day. No differences in vertical distribution between larval ontogenetic stages were recorded. These results suggest the existence of diel vertical migrations of most species with ‘spring larvae’. The adaptive value of the vertical distribution and migration patterns has been mainly related to food availability and predation pressure (Morgan 1987; Morgan & Anastasia 2008). However, UV radiation (UVB in particular) could significantly affect survival (Hernández-Moresino & Helbling 2010) and may represent another selective pressure. The near-surface position of ‘winter larvae’ could be explained by high productivity (and probably higher food availability) and low UVB radiation during winter and early spring (Helbling et al. 2005). Alternatively, higher UVB radiation, together with higher concentrations of visual predators could explain the daily migration of ‘spring larvae’ to deeper waters during the day.

Diel vertical migrations of *H. planatus* larvae observed in this study were similar to those previously recorded on the west coast of South America (Yannicelli et al. 2006). On the other hand, larvae of *M. gregaria* were previously found to be homogeneously distributed in the water column on the west coast of South America (León et al. 2008) and aggregated in the lower part of the water column (between 30 and 100 m depth) at the southern tip of South America (Thatje et al. 2003). Near-surface aggregations of *M. gregaria* zoeae observed in this study differ markedly from the vertical distribution patterns of its conspecifics on the west and south coast off South America (Thatje et al. 2003; León et al. 2008), suggesting that the vertical migration behaviour, a trait with a clear adaptive value (Ringelberg 2010), could have geographic variations in relation to regional hydrographic dynamics (Thatje et al. 2003).

Numerical simulations of water circulation in GN (forced by tides and wind) predict the development of a permanent, vertically homogeneous cyclonic gyre and the seasonal formation of a smaller anticyclonic

gyre near the west coast during autumn and winter (Tonini 2010). Therefore, larvae may be transported in a clockwise direction, regardless of their vertical positions, at speeds up to  $5 \text{ cm}\cdot\text{s}^{-1}$  (nearly  $4 \text{ km}\cdot\text{day}^{-1}$ ). Alternatively, during winter larvae could also be transported in an anticlockwise direction near the west coast. Outside of GN, circulation on the continental shelf is dominated by a general northeastward flow, with mean velocities between  $3.5$  and  $7 \text{ cm}\cdot\text{s}^{-1}$  (Palma et al. 2004, 2008). However, the currents are not homogeneous in the vertical scale; near-surface flux is northeastward and more intense than the water column's average, while near-bottom flux is southwestwards (Palma et al. 2008). On the continental shelf, larvae aggregated near the bottom (i.e. *Pachycheles chubutensis*) would be retained near the coast. In contrast, near-surface aggregated larvae (i.e. *M. gregaria* and other 'winter larvae') would be transported offshore and towards the northeast. In southern Chile, the horizontal distribution of *M. gregaria* larvae suggested that early zoeae were transported offshore and that juveniles return to the coast carried by sub-surface onshore flow (León et al. 2008). Interestingly, this potential offshore transport would be similar to that proposed herein for northern Patagonia but achieved by means of a different migration behaviour (as discussed above) associated with different regional hydrodynamics.

Depending on the species, larval life-span lasts a few to several weeks at temperatures typical of northern Patagonia (Boschi et al. 1969; Iorio & Boschi 1986; Schoeman & Cockcroft 1996; Spivak & Cuesta 2000; Anger 2001; Pohle & Marques 2003; Santana & Marques 2009). Transport of crab larvae at speeds predicted for residual currents in the region ( $3$  to  $6 \text{ km}\cdot\text{day}^{-1}$ ) (Palma et al. 2008; Tonini 2010) during their typical life cycle suggest high levels of connectivity within GN, and potential transport on the scale of hundreds of kilometres on the continental shelf. Although the high temporal variability of circulation driving forces (tides and winds) are considered in the circulation models (Palma et al. 2008; Tonini 2010), temporal scales (monthly or annual average) used to summarize the results may not be adequate to predict larval transport patterns. In other words, larvae performing high-frequency vertical migrations could be transported in a strikingly different way than that predicted from average circulation. However, the larval seasonality and vertical distribution patterns reported in this study could be explicitly incorporated in a circulation model (i.e. Regional Ocean Model System; Shchepetkin & McWilliams 2005) to predict larval transport and connectivity more accurately.

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