

Seasonality of larvae of Brachyura and Anomura (Crustacea Decapoda) in the Beagle Channel, Argentina*

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SUMMARY: This is the first study in the Beagle Channel that reports the larval seasonal distribution, abundance and duration of the larval stages of Anomura and Brachyura, on the basis of a fortnightly sampling programme. An identification key to the specific level of zoeal stages is included. Between September 1987 and March 1989, 304 plankton samples were taken by means of oblique hauls from the bottom to the sea-surface. Eighty-five percent of the samples were taken shallower than 60 m depth. Decapod larvae occurred only in spring and summer. All but two taxa showed a single cohort of larvae which emerge at the beginning of the spring. A second cohort of *Munida* spp. and *Halicarcinus planatus* also occurred during summer. The most abundant taxa were *Munida* spp. (312 larvae · 10 m⁻³), *Peltarion spinosulum* (288 larvae · 10 m⁻³), *H. planatus* (143 larvae · 10 m⁻³) and *Pagurus* spp. (79 larvae · 10 m⁻³), which represented 97% of the total larvae collected. Larvae of Pinnotheridae, *Eurypodius latreillii*, *Libidoclaea granaria*, and *Paralomis granulosa* were about an order of magnitude less abundant. Relative abundances of larvae correspond to relative abundances of the respective benthic stages. The absence of certain larval stages or of certain species (*Acanthocyclus albatrossis* and *Lithodes santolla*) probably indicates their differential distribution within the Beagle Channel. Particularly, lithodid larvae may have benthic or epibenthic habits.

Key words: Crab, southwestern Atlantic, southeastern Pacific, Subantarctic, development, antiboreal.

RESUMEN: ESTACIONALIDAD DE LARVAS DE BRACHYURA Y ANOMURA (CRUSTACEA DECAPODA) EN EL CANAL DEL BEAGLE, ARGENTINA. – En este artículo se presenta la distribución estacional, abundancia y duración de los estadios larvales de los Anomura y Brachyura presentes en el plancton del Canal del Beagle, Argentina, sobre la base de muestreos quincenales. Se incluye además una clave para la identificación de los estadios zoea al nivel taxonómico de especie. Entre septiembre de 1987 y marzo de 1989, se tomaron 304 muestras de plancton, la mayoría provenientes de lances oblicuos desde el fondo hasta la superficie del mar. El 85% de las muestras se tomaron a <60 m de profundidad. Las larvas estuvieron presentes sólo en primavera y en verano. Todos los taxa excepto dos presentaron una cohorte que provino de la eclosión de los huevos que ocurrió a comienzos de la primavera. *Munida* spp. y *Halicarcinus planatus* presentaron también una segunda cohorte durante el verano. Los taxa más abundantes fueron *Munida* spp. (312 larvas · 10 m⁻³), *Peltarion spinosulum* (288 larvas · 10 m⁻³), *H. planatus* (143 larvas · 10 m⁻³) y *Pagurus* spp. (79 larvas · 10 m⁻³), y representaron el 97% de las larvas recolectadas. Las larvas de Pinnotheridae, *Eurypodius latreillii*, *Libidoclaea granaria*, y *Paralomis granulosa* fueron aproximadamente un orden de magnitud menos abundantes que las anteriores. La abundancia relativa de las larvas se corresponde aproximadamente con la abundancia relativa de los estadios bentónicos de los respectivos taxones. La ausencia de ciertos estadios larvales o de ciertas especies (*Acanthocyclus albatrossis* y *Lithodes santolla*) podría ser debida a una distribución diferencial de las larvas de anomuros y braquiuros dentro del Canal del Beagle. En particular, debido a la ausencia de las larvas de Lithodidae en el plancton se plantea la hipótesis de que sean bentónicas o epibentónicas.

Palabras clave: Cangrejo, Atlántico sudoccidental, Pacífico sudoriental, Subantártida, desarrollo, antiboreal.

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INTRODUCTION

In the southwestern Atlantic, studies on larvae of Crustacea Decapoda have only addressed taxonomical and/or biogeographical aspects, and were conducted in the Argentinean continental shelf and slope, between 36°S and 55°S latitude (e.g., Boschi, 1981; Bacardit, 1986). The available information comes from oceanographic surveys, carried out primarily to evaluate commercial fishery resources (e.g. Angelescu, 1981).

From the zoogeographic perspective, the Fuegian district is unique because of two facts. First, this is the only area where Atlantic and Pacific species mingle. However, this connection is relatively recent, since the current paths of interchange, i.e., the Magellan Strait and the Beagle Channel were covered by glaciers and became marine environments only 9,000 years ago (Rabassa *et al.*, 1986). Second, despite increasing isolation leading to an independent evolution of South American and Antarctic faunas, exchange of marine species between these two areas remains more intense than between other southern continents. Furthermore, Anomura and Brachyura decapods are virtually absent from the Antarctic benthos (Arntz *et al.*,

1994). Notwithstanding the potential ability of the planktonic larvae to spread out from the Magellanic province to Antarctica, the reasons for their absence constitute a scientific challenge.

This article represents the first contribution on the seasonal distribution, abundance and duration of the Anomuran and Brachyuran larval stages in the plankton of the Beagle Channel, Argentina, on the basis of a fortnightly sampling programme. Furthermore, I provide a key for the identification of zoeal stages of brachyuran and anomuran crabs.

MATERIAL AND METHODS

Studied area

The studied area of the Beagle Channel is located south of the city of Ushuaia and includes Bahía Ushuaia, the surrounding waters of the Bridges Islands, and Bahía Golondrina (Fig. 1). The Channel has an irregular sea-bottom carved by glaciers (Rabassa *et al.*, 1986), which probably provides abundant microhabitats and shelters for the benthic organisms. The temperature at 25 m depth varies seasonally between 5.4°C in August and 9.8°C in

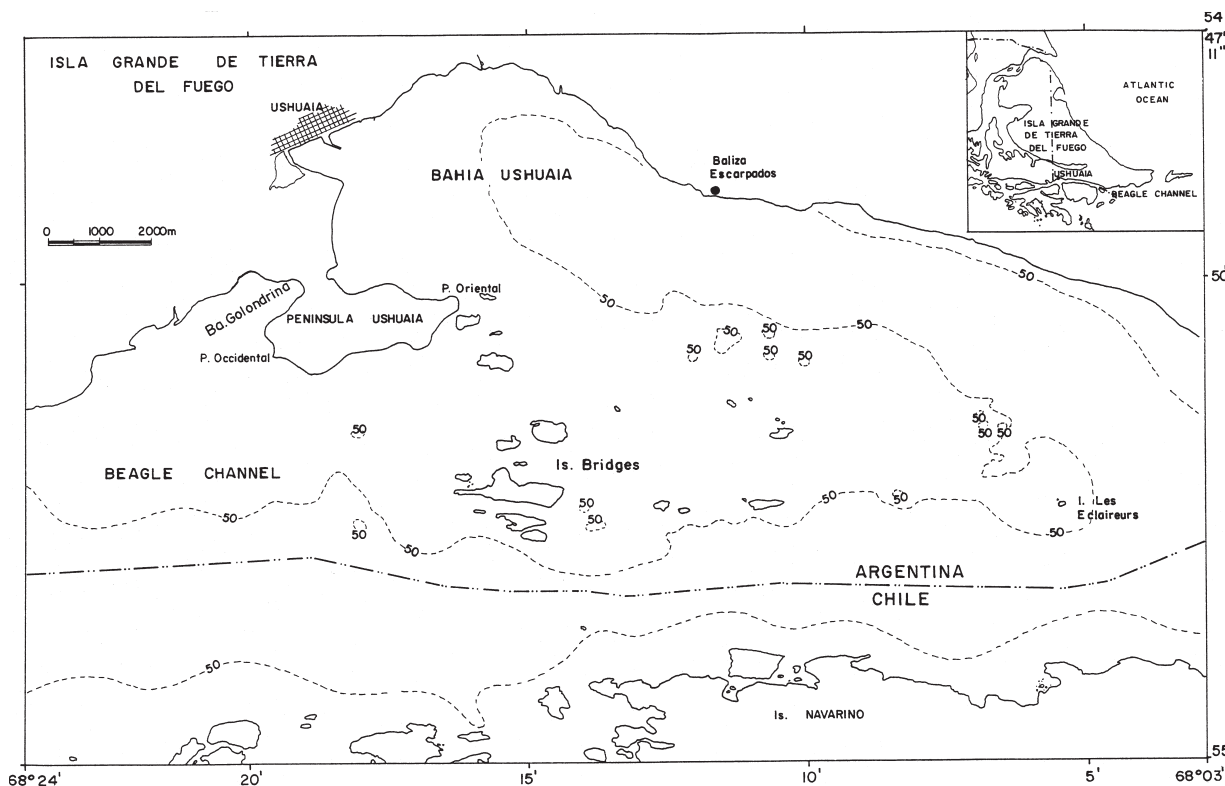


FIG. 1. – Location of sampling. The dashed line indicates the 50 m isobath.

March, while the salinity at 25 m depth varies between and 27.0 g l⁻¹ in December and 31.2 g l⁻¹ in November (annual average salinity \pm 1 SD at 25 m = 29.4 \pm 1.1 g l⁻¹, own unpublished data). In the area of Bahía Golondrina and Bridges Islands, permanent currents are mainly from the southwest at a maximum of 2.6 and 15.6 cm s⁻¹ respectively (Balestrini *et al.*, 1990). In Bahía Ushuaia, a permanent current gyre moves westwards along the northern coast of the bay at 2.0 cm s⁻¹, and then progresses to the southeast along the southern coast at 16.3 cm s⁻¹.

Sampling procedures

Between September 1987 and March 1989 a total of 304 samples were taken roughly every two weeks at randomly selected sites, with a Hensen planktonic net of 0.4 m mouth-diameter with a mouth-reducing cone and a mesh of 200 μ m. Between September 1987 and May 1988, vertical or oblique hauls were performed from the bottom to the sea-surface, so that the entire water column was sampled. Between June 1988 and March 1989, only oblique hauls of 10, 15 or 20 minutes of trawling (mainly 10 minutes) were performed at 3.7 km h⁻¹ from the sea-bottom to the surface. Later, tow time was converted into volume of filtered water by means of a calibration curve calculated from TSK-currentmeter data. On average, the volume of filtered water was 4.7 m³ haul⁻¹ (range: 1.1–6.7 m³ haul⁻¹). I am confident that estimations of densities were comparable since the filtration efficiency was very similar among all samples, e.g., trawling speed was precisely controlled and net clogging never occurred. Only hauls done after June 1988 were considered as quantitative, and only for these, density of larvae is presented.

Each sample was immediately fixed and preserved in 4% buffered formalin in sea-water. For each sample, all Anomura and Brachyura larvae were determined to the lowest taxonomic level and larval stage, and enumerated.

Larval identification

Three taxa could not be identified to the species level for lack of published descriptions. However, larvae were judged to be *Pagurus* spp. based on Scelzo (1976). Based on the absence/presence of uropods, *Pagurus* spp. zoeae were sorted into two stages of development: early (without uropods) and late (with uropods). The “early zoea” category probably includes the first two zoeal stages (*c.f.* Scelzo

and Boschi, 1969). Pinnotherid larvae were morphologically similar among themselves and were supposed to belong to a single taxon herein named Pinnotheridae. However, they did not concur with the available descriptions for *Pinnaxodes chilensis* (H. Milne Edwards, 1837) (see Schwabe, 1936; Gutierrez Martinez, 1971), which may be present in the Beagle Channel (Boschi, *et al.*, 1992). The taxonomy of *Munida subrugosa* Henderson, 1847 and *M. gregaria* (Fabricius, 1793) is a subject of controversy. The morphological features that distinguish adults of both species may depend on the habitat where individuals are found, i.e., pelagic vs. benthic (Williams, 1973; 1980). Adults of both species are present in the area (Vinuesa, 1977; Rodriguez and Bahamonde, 1986; Boschi *et al.*, 1992; pers. obs.; but see Arntz *et al.*, 1996). Larvae of both species may be present simultaneously in the Beagle Channel (Bacardit, 1986), and they may be morphologically similar (Rayner, 1935). Hence, in the present study I decided to name the larvae *Munida* spp., although their characters coincided with those of *M. subrugosa* (Roberts, 1973).

RESULTS

A total of 304 plankton samples were obtained over the 18 months of sampling. Samples from depths shallower than 60 m represented 85% of the total number. Twenty-two samples were taken in Bahía Golondrina, 98 in Bahía Ushuaia (between Punta Oriental and Baliza Escarpados), and 184 at the Bridges Islands (Fig. 1). Of the 14 species of Anomura and Brachyura recorded for the Beagle Channel (*c.f.* Arntz *et al.*, 1996), at least 8 occurred in my samples. The following is a key for the identification of larvae expected to be found in the plankton samples of the Beagle Channel. This key is provided with the bibliographical references, in which the reader may find the original descriptions of larvae.

Key for identification of Anomura and Brachyura zoeae of the Beagle Channel

1. Dorsal spine on carapace..... 2
 - No dorsal spines on carapace 6
2. No lateral spines on carapace 3
 - One pair of lateral spines on carapace 4
3. One spine external to telson furca, rostral spine shorter than dorsal spine.

- *Libidoclaea granaria* Milne Edwards and Lucas, 1842 (see Fagetti, 1969)
- No spines external to telson furca, rostral spine as long as dorsal spine
..... *Acanthocyclus albatrossis* Rathbun, 1898 (see Campodonico and Guzmán, 1973)
 - 4. Lateral spines on the posterior margin of the carapace, directed postero-ventrally, as long as the rostral spine; last segment of pleon with lateral expansions; telson wide at base
..... Pinnotheridae
 - Lateral spines at the mid-carapace, directed laterally, extending slightly past the margin of the carapace; telson narrow at base. 5
 - 5. Three spines external to telson furca
..... *Eurypodius latreillii* Guérin, 1828 (see Bacardit, 1986)
 - No spines external to telson furca
..... *Peltarion spinosulum* (White, 1843) (see Iorio, 1983)
 - 6. Carapace globose with posterior projection covering one or two pleon somites, frontal spine directed ventrally, telson as typical furca.
..... *Halicarcinus planatus* (Fabricius, 1775) (see Boschi *et al.*, 1969)
 - Carapace oblong, frontal spine directed anteriorly, two posterior-lateral processes or spines; telson flat or concave 7
 - 7. Rostrum wider at base, with serrations at tips; telson notably concave. *Munida* spp. (see Roberts, 1973)
 - Rostrum bare; telson flat or slightly concave . 8
 - 8. Posterior carapace spines small. Telson slightly flat; 6 to 8 pairs of spinulose processes.

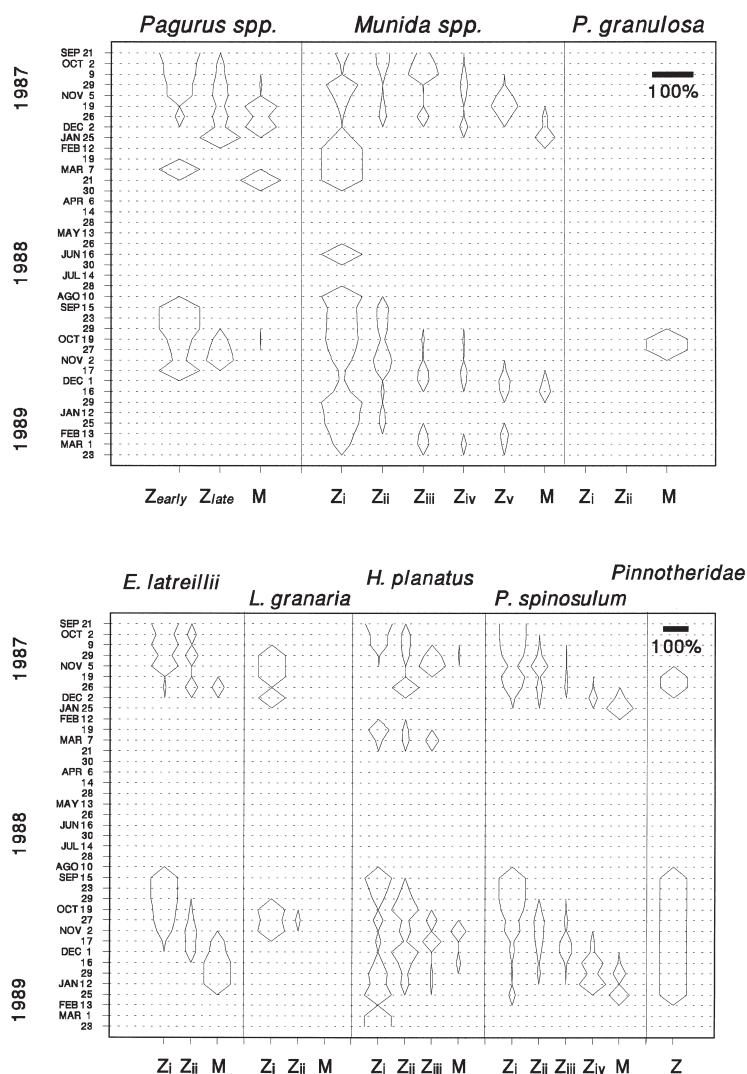


FIG. 2. – Percentage occurrence of larval stages of the anomuran (above) and brachyuran (below) larvae in the Beagle Channel, Argentina. The total of larvae of a given species on a given date of sampling represents 100%. References: Z: zoea; M: megalopa.

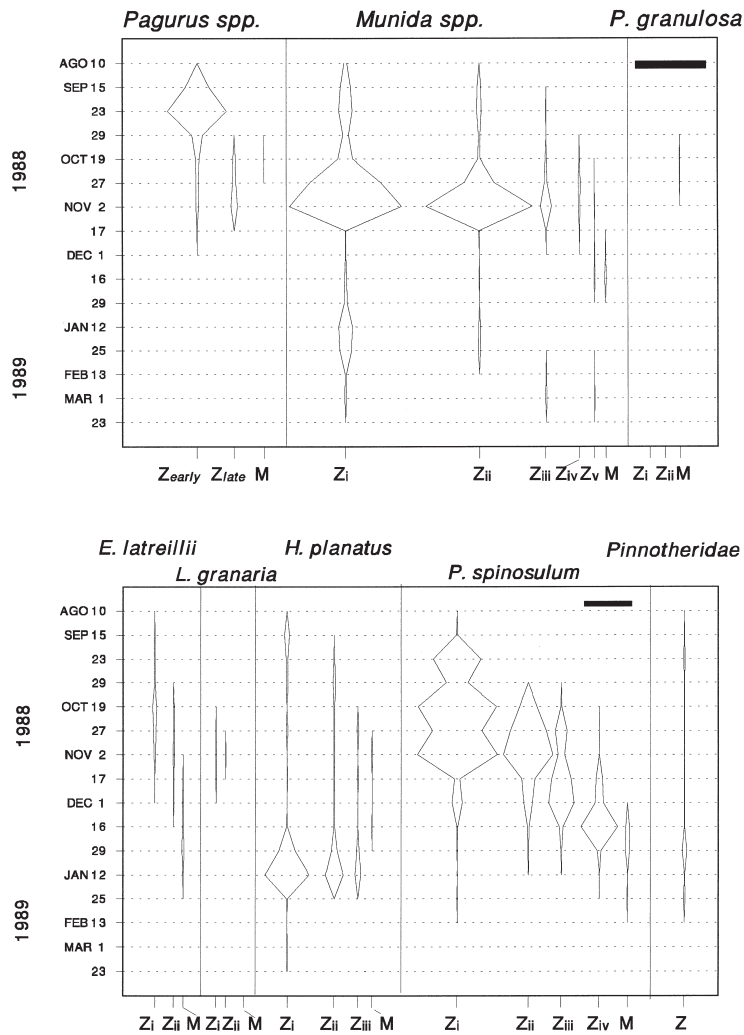


FIG. 3. – Average density of larval stages of the anomuran (above) and brachyuran (below) larvae in the Beagle Channel, Argentina. References: Z: zoea; M: megalopa. The scale bar represents 100 individuals · 10 m⁻³.

- *Pagurus* spp. (see Scelzo, 1976)
- Posterior carapace spines prominent. Telson concave with 9 to 11 pairs of spinulose processes. Small spines on abdominal somites 9
- 9. Posterior carapace spines wider and robust; dorsal spines on abdominal somites more developed; uropods in zoeae II and III
..... *Lithodes santolla* (Molina, 1782)
(see Campodonico, 1971)
- Posterior carapace spines and dorsal spines on abdominal somites less developed; no uropods.
..... *Paralomis granulosa* (Jacquinot, 1847)
(see Campodonico and Guzmán, 1981)

Seasonal Distribution

In the Beagle Channel, Anomura and Brachyura larvae exhibited a marked seasonal pattern of abun-

dance, and occur mainly in the spring and summer (Fig. 2). In 1987, eggs of the most common species had already hatched, when sampling was initiated in September 21. By the end of March 1988, no larvae were found in the Beagle Channel. In 1988, some zoeae I of *Munida* spp. appeared in June at a density of 0.2 individuals · 10 m⁻³, but larvae of other species were captured only starting in mid-September.

In terms of larval density, 4 of the 8 Anomura and Brachyura taxa together represented 97% of the total number of larvae collected in the 1988-1989 spring-summer (Fig. 3; Table 1). The average density for all species and stages combined was 5.4 larvae · 10 m⁻³ (range: 0.1-24.5 larvae · 10 m⁻³). The maximum density for all species combined was 625 larvae · 10 m⁻³ and occurred at the beginning of November 1988 (Fig. 3). Maximum densities for the

TABLE 1. – Total of larvae collected in 304 hauls between September 1987 and March 1989. The 100% of percentage frequency refers to the total of larval individuals caught per 1 m^3 . “Channel” refers to sampling done in the Channel system and West of Beagle and “S Beagle” to sampling done South of Beagle Channel in 1994 (see Gorny *et al.*, 1996). * refers to *L. smithii*.

Taxa	Total of larvae collected	Percentage frequency ($N \cdot 10 \text{ m}^{-3}$)	Percentage frequency of adults (Gorny <i>et al.</i> 1996)	
			Channel	S Beagle
<i>Peltarion spinosulum</i>	4946	52	62	8
<i>Munida</i> spp.	3112	27	2	84
<i>Halicarcinus planatus</i>	764	11	-	<1
<i>Pagurus</i> spp.	1131	7	17	5
<i>Eurypodius latreillii</i>	191	2	16	5
Pinnotheridae	78	1	-	<1
<i>Libidoclaea granaria</i>	17	0.1	5*	-
Lithodidae	5	<0.1	-	<1
Total	10,244			

sampling period for larvae of all stages of *Munida* spp., *Peltarion spinosulum*, *Halicarcinus planatus*, and *Pagurus* spp. were 312, 288, 143, and 79 individuals $\cdot 10 \text{ m}^{-3}$ respectively. Larvae of all stages of Pinnotheridae, *Eurypodius latreillii*, *Libidoclaea granaria* and *Paralomis granulosa* were about an order of magnitude less abundant, with maximum densities of 9.9, 9.5, 1.8 and 0.7 individuals $\cdot 10 \text{ m}^{-3}$ respectively.

All but two taxa of Brachyura and Anomura hatch once a year in early spring, since complete larval cohorts were detected (Figs. 2 and 3). In summer 1987, only zoeae I of *Munida* spp. were caught, while in summer 1989 all zoeal stages were found. The spring 1988 cohort of *Munida* spp. was about an order of magnitude more abundant than the summer 1989 cohort (Fig. 3). Two cohorts of *Halicarcinus planatus* were detected: the first in spring and the other in summer (Fig. 2), and the summer cohort was at least one order of magnitude more abundant than the spring cohort (Fig. 3). The occurrence of *Pagurus* spp. larvae in the summer 1988 was occasional, since only one larva was caught in each of two hauls (Fig. 2).

DISCUSSION

In the Beagle Channel the time of larval hatching of Brachyura and Anomura taxa is clearly seasonal. Larvae occur at the beginning of the spring and the hatching frequency is annual, as occurs in the Argentinean continental slope south of 40°S (Bac-

ardit, 1986; Boschi, 1989). The exceptions to the annual hatching pattern are *Halicarcinus planatus* and *Munida* spp., which clearly exhibited two cohorts. Similarly, in the Kerguelen Islands (70°E ; 50°S) larvae of *H. planatus* occur during November–March, but the seasonality of larval stages was not reported (Richer de Forges, 1977). By contrast, in the Argentinean continental shelf, *H. planatus* larvae occur only during spring (Bacardit, 1986). My results suggest that in the Beagle Channel larval development of *Munida* spp. is variable: the spring cohort is more abundant, develops normally and reaches the megalopal stage, while the summer cohort may fail to fully develop, as in the case near the Islas Malvinas (Falklands) (Rayner, 1935; Bacardit, 1986). Similarly, in the southwestern Pacific, *M. gregaria* zoeae I that emerge late in the season may not develop further (Zeldis, 1985). In the Beagle Channel, it is essential to resolve the differential pattern of distribution and reproductive cycles of *Munida subrugosa* and *M. gregaria* before positing any hypothesis about larval seasonality.

The percentage occurrence of the Anomura and Brachyura larvae showed in this study coincides roughly with the percentage occurrence of adults. *Peltarion spinosulum* is the dominant species since frequencies of occurrence of both larvae and adults are high (Table 1). Larvae of *Munida* spp. and *Halicarcinus planatus* represented together 38% of total larvae collected, although benthic stages of these species were not well represented in the 1994 samples from the Channel system and Beagle Channel (Gorny *et al.*, 1996). This was probably because *H. planatus* is more abundant in the inter- and subtidal environments, which were not sampled in 1994. Although *Munida subrugosa* was very scarce in the Channel System during the 1994 sampling (Gorny *et al.*, 1996), we have recently recorded that in spring and summer and in terms of numbers, *M. subrugosa* is the most important species in shallow waters (<50 m depth) of the Beagle Channel near Ushuaia (unpubl. results). Its seasonal abundance is also reflected in the diet of the omnivorous fish *Eleginops maclovinus* (Valenciennes, 1830) (see Isla and San Román, 1995). Therefore, the relative abundance of larvae of this species agrees with the relative abundance of benthic stages.

On average, decapod larvae were less abundant in the Beagle Channel than in the Antarctic. Average density in the Beagle Channel was about one order of magnitude lower than the average density of 41 individuals $\cdot 10 \text{ m}^{-3}$ reported for the 4 Antarctic

Caridea (Piatkowski, 1987). However, maximum densities of $600 \text{ larvae} \cdot 10 \text{ m}^{-3}$ of the Antarctic shrimp *Notocrangon antarcticus* (Pfeffer, 1887) are comparable with maximum average densities found in November 1988 in the Beagle Channel. Since Caridea larvae were not considered in the present study, no further comparison is feasible.

Certain larvae were difficult to identify to the specific level because larval development of some species is not known and/or the presence of certain species was only recently reported (c.f. Arntz and Gorny, 1996). Three species of *Pagurus* may occur in the Beagle Channel, and larvae caught during this study probably belong to any or all of them. *Pagurus comptus* White, 1847 is the most abundant species, while *P. gaudichaudii* H. Milne Edwards, 1836 is a scarce one (Gorny *et al.*, 1996; pers. obs.). *Pagurus forceps* may also occur in the Beagle Channel, since it was reported off the Staten Island and south of the Navarino Island (Yaldwin, 1958). Larvae classified as *Libidoclaea granaria* agreed with the description presented by Fagetti (1969). However, *L. smithii* (Miers, 1886) also occurs in the Channel system and Beagle Channel (Gorny *et al.*, 1996). Its larval development is unknown, and morphological differences between larvae of the two species may be subtle. Therefore, a certain degree of uncertainty may be associated with the classification of *Libidoclaea* spp. larvae. Pinnotheridae species probably present in the Beagle Channel are *Pinnixa valdiviensis* Rathbun, 1907, *Pinnaxodes chilensis*, and *Pinnotherelia laevigata* Milne Edwards and Lucas, 1843 (see Boschi *et al.*, 1992; Gorny *et al.*, 1996). Larvae collected during the present study did not agree with the description of *P. chilensis* larvae (c.f. Gutierrez-Martinez, 1971), and the presence in the Beagle Channel of *P. laevigata* has not yet been confirmed. Hence, pinnotherid larvae collected during the present study probably belonged to *Pinnixa valdiviensis*. Moreover, despite their absence in an extensive sampling (Fenucci, 1975), the presence of *P. valdiviensis* south of the Beagle Channel was confirmed by Gorny *et al.* (1996), and my results support their occurrence in the Beagle Channel.

The absence of certain larval stages or larvae of certain species from the plankton probably indicates their differential distribution within the Beagle Channel. During this study, *Libidoclaea granaria* megalopae were not caught and zoeae II were caught only once during spring 1988 (Fig. 3). In the Beagle Channel, benthic stages of *Libidoclaea* spp. occur in waters >200 m deep (pers. obs.; Gorny *et*

al., 1996). As in other majid species, the bathymetric distribution of larvae may change with larval development, i.e., late stages close to settlement may have a depth-distribution similar to the benthic stages (e.g. Kon, 1980). Therefore, the occurrence of *Libidoclaea* spp. larvae may have been misjudged, since my sampling was conducted mainly in waters shallower than 60 m depth. Larvae of *Acanthocyclus albatrossis* were absent from my samples, although benthic stages occur at high densities ($\sim 50 \text{ individuals} \cdot \text{m}^{-2}$) in some mussel beds in the eastern Beagle Channel (67°18' W; 54°53' S; pers. obs.). Hence, I suggest that their absence near Ushuaia may be due to the dominant eastwards currents (Balestrini *et al.*, 1998), which prevent larvae from entering the western sector of the Beagle Channel through the Paso MacInlay.

Some *P. granulosa* larvae were found in October 1988 and none of *L. santolla* were caught. Larval absence markedly contrasts with the abundance of benthic stages in shallow waters <50 m deep, which have supported fishery since the 1960s. However, the 7% of ovigerous females of *L. santolla* reported for 1988 (Lovrich, 1997) may partially explain the absence of larvae from plankton samples. Lithodid larvae also were missing from plankton samplings conducted previously in the Beagle Channel and in the Argentinean continental shelf and slope (Boschi *et al.*, 1984; Bacardit, 1986), where about 90% of females were ovigerous (Vinuesa and Lovrich, unpubl. results). Similarly, in the eastern Bering Sea, *L. aequispinus* Benedict, 1894 larvae were absent from plankton samples since they are more benthic than planktonic in habit (Jewett *et al.*, 1985), while larvae of its sympatric *Paralithodes camtschaticus* (Tilesius, 1815) and *P. platypus* (Brandt, 1850) were present (Somerton and Otto, 1986). In laboratory cultures, larvae of *P. granulosa*, *L. santolla*, *L. aequispinus* and *L. maja* Linnaeus, 1758 have a marked demersal behavior (Vinuesa *et al.*, 1985; 1989; Shirley and Zhou, 1997, K. Anger, pers. comm.). Hence, I hypothesize that in the Beagle Channel lithodid larvae have benthic or epibenthic habits which make these larvae difficult to obtain by means of conventional methods of plankton sampling.

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