

## Reproductive biology of the crab *Munida subrugosa* (Decapoda: Anomura: Galatheidae) in the Beagle Channel, Argentina

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*Munida subrugosa* was sampled monthly from November 1997 to November 1999 in the Beagle Channel by means of an epibenthic trawl. The reproductive cycle started in May, reflected by the occurrence of ovigerous females. Maximum size of oocytes, maximum value of gonadosomatic index in females (16.8 g mm carapace length [CL]<sup>-1</sup>) and males (1.6 g mm CL<sup>-1</sup>), and the proportion (~70%) of ovigerous females with full egg-clutches occurred in June. Since the proportion of ovigerous females in October was ~5% and the planktonic larvae reportedly hatch in September, the embryonic development lasted ~90–120 days. Females and males attained physiological maturity at 9.9 and 8.0 mm CL respectively, and males reached morphometric maturity at 24.4 mm CL. Fecundity was correlated with female size ( $r=0.85$ ) and was between 124 and 10,750 eggs per female. Average diameter of recently extruded eggs was 0.69 mm (SD  $\pm 0.06$  mm). At the beginning of the reproductive cycle, ovigerous females had partial broods of ~300 eggs, which represented <5% of complete clutch.

### INTRODUCTION

Galatheid crabs are particularly abundant at mid latitudes. They occur in the Eastern Pacific off the coast of Canada (48°N; Burd & Brinkhurst, 1984), Mexico (24°N; Auriolles-Gamboa & Balart, 1995) and Chile (36°S; Roa & Bahamonde, 1993) in the Western Pacific off New Zealand (40°S; Zeldis, 1985), in the north-east Atlantic (45°N; Garm & Hoeg, 2000), and in the Atlantic continental shelf off Argentina (40°S; Matthews, 1932). In the Atlantic waters surrounding the southern tip of South America, five galatheid species occur: *Munidopsis opalescens* Benedict, 1903, *Munida iris* Milne-Edwards, 1880, *Munida spinosa* Henderson, 1885, *Munida gregaria* (Fabricius, 1793), and *Munida subrugosa* (White, 1847) (Spivak, 1997; Arntz et al., 1999).

When species are of potential economic interest, knowledge on their reproduction is essential for designing fishery management rules. The commercial uses of galatheid species are multiple: as cocktail shrimp, as a source of astaxantins for pigmentation of chicken eggs and cultured salmon, as a source of lipids and proteins for balanced animal feeds, and as a source of digestive enzymes for cheese manufacturing (Auriolles-Gamboa & Balart, 1995). Galatheids are relatively small when compared to other anomuran crabs that are currently of commercial interest, as for example lithodids. However, their small size may be compensated by high abundance such that commercial yields could be important and profitable.

The crab *M. subrugosa* is an anomuran of ~7 cm total length and 15 g in weight. Off southern South America, *M. subrugosa* inhabits the continental shelf from Uruguay (35°S) to Cape Horn (55°S), including the Islas Malvinas (Falkland Islands, 51°S), and in the Pacific waters

*M. subrugosa* extends north to the Isla Chiloé (41°S; Boschi et al., 1992). The reported bathymetric distribution for *M. subrugosa* is from the sublittoral down to 1137 m depth (Arntz et al., 1999).

*Munida subrugosa* and *M. gregaria* were reported to co-occur in the Atlantic shelf off Argentina (Boschi et al., 1992). *Munida gregaria* has a juvenile pelagic phase, while adults are benthic and can perform vertical migrations into the water column (Zeldis, 1985). This species may occur in large pelagic swarms (Matthews, 1932; Rayner, 1935) with densities reaching up to 366 ind m<sup>-3</sup> (Zeldis, 1985). By contrast, *M. subrugosa* is seemingly benthic except at the larval stage. This species occurs at large benthic concentrations, at densities up to 27 ind m<sup>-2</sup> (Gorny & Retamal, in press). Particularly in the Beagle Channel, *M. subrugosa* and *M. gregaria* are sympatric (Vinueza, 1977; Tapella et al., 2002) and constitute an important fraction of the benthic communities. In terms of biomass, both species represent ~50% of the benthic community (Arntz & Gorny, 1996), and the density of *M. subrugosa* is eight-fold that of *M. gregaria* (Tapella et al., in press).

Although *M. subrugosa* may represent an economical potential resource, there is virtually no information about its reproductive biology. Hitherto, the only study dealing with reproduction ensues from a survey in the Strait of Magellan (Rodríguez & Bahamonde, 1986) an area neighbouring the Beagle Channel. Ovigerous female *M. subrugosa* were reported to occur in September, and from this single observation the authors speculated that the reproductive cycle begins in April, females carry eggs for 8–9 months, and larval hatching occurs between October and January (Rodríguez & Bahamonde, 1986). These speculations are coherent with previous information

on *M. subrugosa* larval hatching in the Beagle Channel (Lovrich, 1999). In plankton samples, the first zoeal stage appears in September, its density peaks in early November, and some individuals persist through January (Lovrich, 1999). Moreover, females reportedly attain their physiological maturity at 13.5 mm carapace length (CL) (Rodríguez & Bahamonde, 1986).

In this work, aspects of the reproductive biology of *M. subrugosa* in the Beagle Channel, at the southern limit of its distribution range are documented. Data on the reproductive cycle, size at maturity and fecundity were examined to acquire basic information on the biology of this species of potential economic importance.

## MATERIALS AND METHODS

### *Study site and sampling*

The study was carried out in the sector of the Beagle Channel (55°S 68°W) between Bahía Lapataia (54°52'S 68°32'W) and Punta Segunda (54°52'S 68°02'W). The Beagle Channel is situated at the southernmost tip of South America and is considered to be a subantarctic coastal environment. The surface seawater temperature averages 6.7°C over the year, and ranges from 4.2 to 4.3°C in August to 8.9–9.8°C in January. Salinity ranges from 26.7 psu in November–December to 31.3 psu during July (Balestrini et al., 1998).

Sampling was performed on a monthly basis from November 1997 to November 1999. Samples were obtained with an epibenthic trawl of 1.7 m mouth width and a net with 10-mm mesh size, specially designed to be operated from a small inflatable dinghy. Trawls were pulled at a speed of 0.65–0.80 m s<sup>-1</sup> during 5–25 min (mostly 5 min). The range of fishing depths extended from 10 to 150 m. After sampling all crabs were immediately fixed in 4% buffered formalin seawater.

In the laboratory, *Munida subrugosa* and *M. gregaria* were sorted by species, sex and ovigerous condition. Species were determined using the following characters: the basis of the rostral spine is wider in *M. gregaria*, ocular peduncles are longer in *M. gregaria*, *M. subrugosa* has a kidney-shaped cornea, and *M. subrugosa* bears a distal spine on the meropodite of the third maxilliped (Retamal, 1981).

Sex determination was based on the presence or absence of pleopods on female and male abdomens, respectively. The standard measure of body size, CL, was determined to the nearest 0.1 mm by means of a digital calliper. Carapace length was measured from the posterior edge of the orbital arch to the mid-dorsal posterior margin of the carapace. In order to determine if both chelae are symmetric, the length and height of the chelae were also measured. Chela length was the distance from the tip of the propodite to the lateral articulation on the carpus of the chela. Chela height was measured immediately posterior to the insertion of the dactylus. Since crabs easily lost their appendages during trawling and fixation procedures, a random sub-sample of entire animals was used to study chela symmetry. Length and height of both the left and right chelae of 169 males and 323 females were measured. The null hypothesis that chelae were symmetric in both sexes was tested using a paired *t*-test (Sokal & Rohlf, 1995).

### *Size at maturity*

Since the 'size at maturity' may be based on different criteria, in this study Comeau & Conan's (1992) approach was followed and their specific terminology to define different phases of maturity were used. Physiological maturity refers to the CL at which animals have mature gonads, and morphometric maturity is the CL of change in the growth allometry of the chela. Physiological maturity was determined by analysing the primary reproductive characters. A logistic function to the proportion of mature animals for each 1 mm CL size-class was adjusted with the method of least squares. The CL-value corresponding to 50% maturity from the logistic equation provided the size at physiological maturity (Wenner et al., 1974). Females were mature if they had eggs attached to the pleopods and males were mature if spermatophores occurred in their vas deferens. The presence of eggs was assessed in random sub-samples of ~50% of all females collected in July 1998 and July 1999, when most part of females were berried. Since the accumulation of spermatophores may be seasonal, in June 1998 and June 1999 sub-samples of males >5 mm CL were taken, so that each size-class of 1 mm CL contained ~10 individuals. To assess the presence of spermatophores we examined vas deferens smears between a slide and a coverslip under a microscope at a magnification of 100×. Morphometric maturity is based on the relative change in chela growth that represents the acquisition of secondary sexual characters (Hartnoll, 1978). The routine MATURE1 was used as described by Somerton (1980) to determine the proportion of morphometrically mature male individuals. Morphometric maturity was assessed from a random sub-sample representing ~10% captured males in June 1998 and June 1999. Values of 'juvenile' and 'adult' bound required by the routine were chosen by judging the scatterplot of chela size vs carapace length and were established at 18.0 and 26.5 mm CL, respectively.

### *Reproductive cycle*

Three standard methods for determination of the reproductive cycle in crustacean decapods were used: the temporal variation (1) of gonadosomatic index (GSI) for females and males; (2) of oocyte diameter; and (3) of proportion of ovigerous females. At each month sub-samples of 15–25 females (21–24 mm CL) and males (22–27 mm CL) were randomly selected. Crabs were measured and dissected. Their gonads were removed and dried to constant weight at 55°C. Gonad dry weight was recorded to the nearest 0.1 mg. The GSI was calculated as the ratio between the gonad dry weight and size (CL), multiplied by 1000. To calculate the oocyte diameter, another monthly subsample of 8–12 females >10 mm CL was randomly selected and dissected. In each female, the ovary was removed and oocytes were separated with needles on a slide. Eighty to 100 oocytes were randomly chosen and their diameter measured to the nearest 0.02 mm using an eyepiece micrometer mounted on a stereoscopic microscope. The proportion of ovigerous females was calculated as the ratio between ovigerous and non-ovigerous females >10 mm CL.

### Fecundity and egg diameter

The term fecundity is here considered as the number of eggs per clutch. Pleopods with attached eggs were removed from each female by cutting from the pleopodal base, and afterwards were preserved in 4% buffered formalin in seawater. If the quantity of eggs in a clutch was relatively small (<300), eggs were directly enumerated. In larger clutches, eggs were detached from the pleopods, the whole clutch was blotted and weighed to the nearest 0.1 mg. Three subsamples were then weighed to the nearest 0.1 mg, and eggs in each subsample were counted. For each subsample the total number of eggs was calculated proportionally. For each female, fecundity was the average of the three calculated clutch sizes.

In order to determine egg diameter, a subsample of 15 ovigerous females with complete broods was selected. Because egg diameter may change during the embryonic development, ovigerous females were selected to have clutches at the same stage of development (eggs recently extruded, uniform yolk, and no ocular pigment visible). From each female, 12–20 eggs were randomly chosen, preserved in 4% formalin in seawater, and their diameter measured to the nearest 0.02 mm using an eyepiece microscope on a compound microscope.

## RESULTS

### Chela symmetry and sizes at maturity

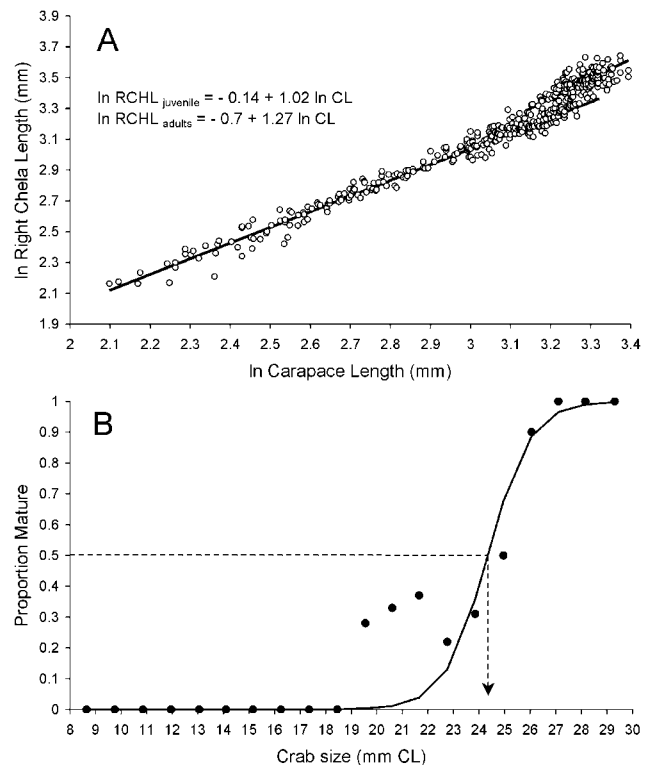
In *Munida subrugosa* dimensions of both chelae were similar. In 169 males chela length (paired *t*-test  $t_s=1.26$ ;  $P=0.21$ ) and chela height ( $t_s=0.33$ ;  $P=0.74$ ) for both chelae were similar. Equally, in 323 females chela length ( $t_s=0.25$ ;  $P=0.80$ ) and chela height ( $t_s=1.38$ ;  $P=0.74$ ) of the right and left chelae were similar. Therefore, in *M. subrugosa* chelae are symmetric. Hence, to determine the size at morphometric maturity we decided to use only right chela length as the measure of the chela size.

Size at morphometric maturity was calculated for 428 males (8.2–29.8 mm CL). The slope of the regression of the right chela length on the CL for morphometrically immature males (<18 mm CL) was significantly less ( $F=309.1$ ;  $P<0.001$ ) than that for morphometrically mature males (>26.5 mm CL). The estimated size of 50% morphometric maturity was 24.4 mm CL (95% confidence limits: 18.2–26.5 mm CL) (Figure 1A,B).

Fifty per cent of physiological maturity occurred at 9.9 mm CL in female and at 8.0 mm CL in male (Figure 2). The smallest female carrying eggs and the smallest male with spermatophores were 8.9 mm CL and 6.5 mm CL, respectively.

### Reproductive cycle

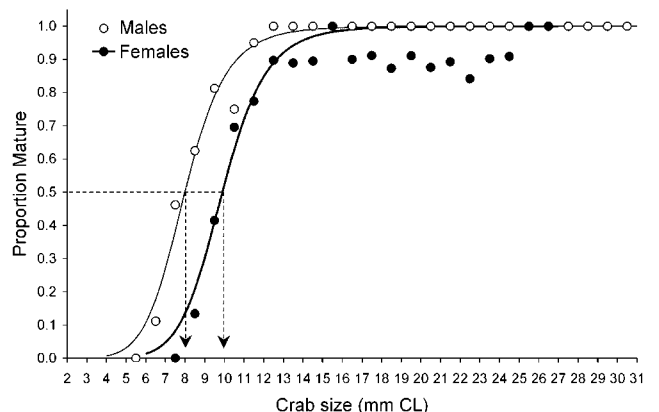
In female *M. subrugosa*, GSI values peaked in May–June, followed by decreasing values (Figure 3), suggesting the occurrence of oocyte extrusion. Moreover, this process might be drawn out because some large values of GSI still occurred until July–August. From September to March, GSI values were practically constant and very small. Hence, we propose that the accumulation of yolk, i.e. secondary vitellogenesis, began in March and extended through May. In males, maximum values of GSI occurred



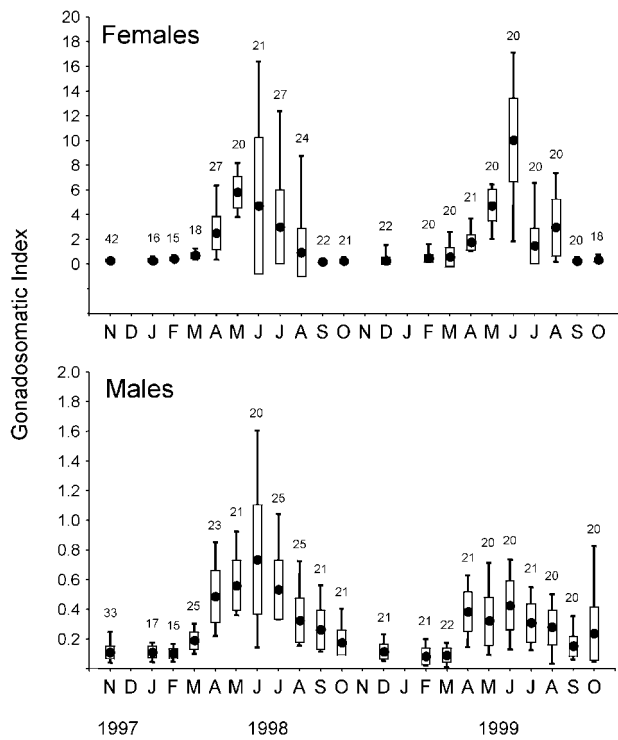
**Figure 1.** Morphometric maturity in male *Munida subrugosa* calculated for 428 crabs. (A) Relationship between the right chela length and the carapace length; (B) proportion of mature males on the basis of the allometric growth of chelae. Dotted arrow shows the size of 50% morphometric maturity: 24.4 mm CL. Log-linear functions for exclusive 'juvenile' and 'adults' are the fitted lines shown. RCHL, right chela length; CL, carapace length.

in June, and thereafter GSI values decreased gradually (Figure 3). From November to March the GSI values were relatively constant. Hence, mating might be extended from June to August and the accumulation of sperm material in the vas deferens probably occurred between April and June.

Two different types of oocytes occurred in the ovaries of *M. subrugosa*. In live animals, oocytes in previtellogenesis

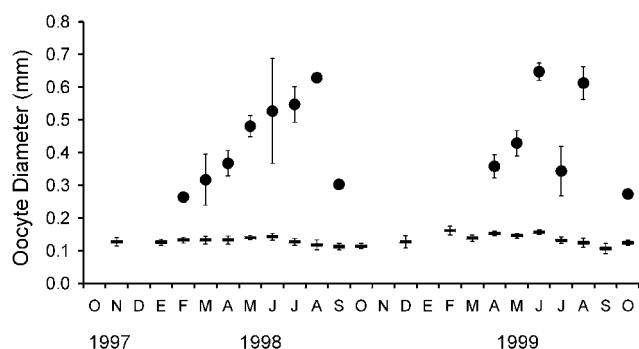


**Figure 2.** Physiological maturity for 283 male (5.4–30.5 mm CL) and 1133 female (7.4–26.9 mm CL) *Munida subrugosa*. Size-classes are represented by their midpoint, i.e. 5.5 mm CL corresponds to the size-class of 5.1 to 6.0 mm CL and so on. Size at 50% maturity is the intersection between the calculated logistic function and the ordinate at the proportion of 0.5: 8.0 and 9.9 mm CL in males and females, respectively.

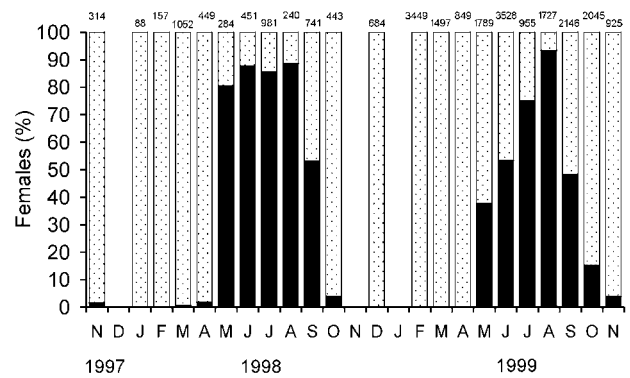


**Figure 3.** Monthly values of gonadosomatic index (dry gonadal weight/carapace length  $\times 1000$ ) for female and male *Munida subrugosa* from November 1997 to October 1999. Circles, empty rectangles and vertical lines are averages, standard deviations and range values of gonadosomatic index, respectively. Numbers above vertical lines are sample sizes. Months without sampling are bare.

or primary vitellogenesis were white or translucent and their diameter varied between 0.04 and 0.34 mm. Oocytes in previtellogenesis were always present in the ovaries, and were the sole type represented between October and January (Figure 4). Oocytes in secondary vitellogenesis occurred between February and September and were green or yellow, in live or fixed animals, respectively. Diameter varied from 0.36 to 0.90 mm. The average



**Figure 4.** Monthly average of the diameter of oocytes in secondary vitellogenesis (circles), or in pre-vitellogenesis and primary vitellogenesis (rectangles) for female *Munida subrugosa* from November 1997 to October 1999. Values of average and standard deviation were calculated from individual averages obtained from 8–12 (mostly 10) females. To obtain the averages, a total of 80–100 oocytes per female were measured. Vertical lines are standard deviation. Only months with samples are shown.



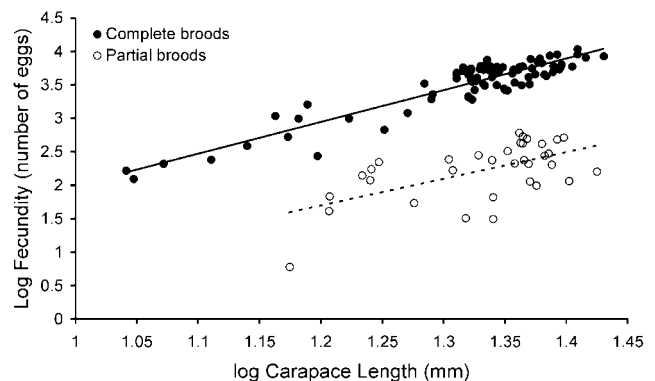
**Figure 5.** Percentage of ovigerous females (black bars) of *Munida subrugosa*  $> 10$  mm CL, from November 1997 to October 1999. Samples sizes are indicated above bars. Months with no samples are bare.

size of oocytes in secondary vitellogenesis was clearly seasonal, peaking between June and August, and gently decreasing thereafter until October (Figure 4). Therefore, oocyte extrusion occurred between June and August.

Ovigerous females of *M. subrugosa* mainly occurred between May and September (Figure 5). The monthly proportion of ovigerous females changed in the two sampling years: ovigerous females varied around 55–85% and between 40 and 95%, in 1998 and 1999, respectively. In October and November proportions of ovigerous females decreased and were minimal. Hence, oocyte extrusion occurred in May. However, at the beginning of the reproductive cycle of each year, ovigerous females had partial broods of  $\sim 300$  eggs, which represented  $< 5\%$  complete clutch (see below). In May and June 1998, 98.1% and 6.2% of ovigerous females had partial broods respectively. Similarly, in June and July 1999, 82% and 14.7% of ovigerous females had partial broods respectively. Hence, a partial extrusion of oocytes occurred at the beginning of the reproductive cycle, small enough not to affect average values of gonadosomatic index and oocyte diameter.

*Fecundity and egg diameter*

In females with complete broods, the number of eggs varied from 124 to 10,750 per female of 11.2 and



**Figure 6.** Scatterplot between the log-fecundity (eggs carried by female) vs log-female size of *Munida subrugosa* from the Beagle Channel, Tierra del Fuego, Argentina. Continuous and dotted lines represent the fitted linear function for complete and partial broods, respectively.

**Table 1.** Regressions of the logarithm of fecundity ( $F$ ) of complete and partial broods on the logarithm of female size (carapace length,  $CL$ ) of *Munida subrugosa* in the Beagle Channel, Argentina. All broods had eggs at the beginning of the embryogenesis, i.e. without eye pigment.

Brood type	Equation of regression	N	$r^2$	$F$
Complete	$\text{Log } F = -2.7 + 4.7 \text{ Log } CL$	85	0.85	474.5*
Partial	$\text{Log } F = -3.1 + 4.0 \text{ Log } CL$	34	0.34	17.6*
Slopes $H_0: b_1 = b_2$				1.15
Ordinates $H_0: a_1 = a_2$				815.8*

$r^2$ , coefficient of determination;  $F$ ,  $F$ -statistic of the linear regression; \*,  $P < 0.001$ .

25.7 mm CL, respectively. On average, females with complete broods carried 4332 eggs. By contrast, in animals with partial broods the number of eggs varied from six to 605 eggs per female of 15.0 and 23.0 mm CL, respectively. Fecundity of *M. subrugosa* increased with female size (Figure 6). Regressions of egg number of complete and partial broods on CL were significant, and both slopes were similar but ordinates were significantly different (Table 1). Females with partial broods have significantly fewer eggs attached in their pleopods than females with complete broods (Figure 6; Table 1). Partial broods had only 3.6% of eggs from complete broods. The adjusted value of the egg number of complete broods was significantly higher than that of partial broods (Table 1).

The average diameter for 245 eggs at early stages of development was of 0.69 mm (SD  $\pm 0.06$  mm). Egg diameter ranged in size between 0.56 and 1 mm.

## DISCUSSION

Results presented in this article constitute the first information on the reproductive aspects of *Munida subrugosa* at the southern limit of its distribution. In the Beagle Channel ovigerous females with partial broods appear in May. Hence, we suggest that the reproductive cycle starts in May with mating, egg extrusion and fertilization. We suspect that this process may extend further, until August, since GSI decreased and the proportion of ovigerous females increased gently after June (Figures 3 & 5). Males  $> 8$  mm CL and females 9.9 mm CL have their gonads mature, respectively. Females hold their eggs over a period of about three to four months, from about June to September, when larval hatching begins (Lovrich, 1999). Ovigerous females occur until November but at lower proportions, consistent with the occurrence of first zoeae in the plankton until December (Lovrich, 1999). In contrast to our interpretation, based on a few samples from the Strait of Magellan ( $\sim 54^\circ\text{S}$   $71^\circ\text{W}$ ) and scarce evidences, Rodríguez & Bahamonde (1986) speculated that the reproductive cycle of *M. subrugosa* starts in April, embryogenesis lasts 8–9 months, and larval hatching occurs between October and January. Physical conditions in the Strait of Magellan and the Beagle Channel are similar (Antezana, 1999) and therefore there would seem to be no reason justifying such a large difference in the duration of embryogenesis.

In the Beagle Channel, *M. subrugosa* showed an annual and seasonal reproductive cycle centered on winter. This reproductive pattern is associated with a marked seasonality in the Beagle Channel ecosystem where the primary

production peaks during spring–summer (M. Hernando, personal communication) and is followed by an increase in both solar radiation and temperature (Balestrini et al., 1998). High primary production followed by increased zooplankton production offers an abundant food source for meroplanktonic larvae in general (Gómez-Gutiérrez & Sánchez-Ortiz, 1997), and favours larval survival (Pearse et al., 1991). Synchronization of the reproductive cycle to the food availability along with egg morphology and larval development has been attributed as adaptations to planktotrophy (Thorson, 1950). For the Galatheaidea, Van Dover & Williams (1991) proposed that planktotrophic larvae hatch from eggs smaller than  $0.2 \text{ mm}^3$ , and most species pass through four or five zoeal stages and instars e.g. *Pleuroncodes planipes* Stimpson, 1860, *Galathea rostrata* Milne-Edwards, 1880 and undersigned *Munida* sp. Our results that *M. subrugosa* produces a large number of small eggs ( $0.10 \text{ mm}^3$ ), with a larval development of at least five zoeal stages (Roberts, 1973) suggest that larvae are probably planktotrophic.

The annual and seasonal reproductive pattern has been observed in several species of the genus *Munida*. Examples are *Munida longipes* Milne-Edwards, 1880, *Munida microphthalma* Milne-Edwards, 1880, *Munida sarsi* Huss, 1935, *Munida tenuimana* Sars, 1872, *Munida rugosa* Fabricius, 1775 and *Munida iris rutilanti* Zariquiey-Álvarez, 1952 (Brinkmann, 1936; Wenner, 1982; Atrill, 1988; Hartnoll et al., 1992; Sanz-Brau et al., 1998) from the north Atlantic Ocean and in *M. gregaria* from the south-west Pacific Ocean (Zeldis, 1985). Females of these species carry their eggs during winter and larval hatching occurs from spring to summer coincident with the first plankton bloom. Similarly, Gómez-Gutiérrez & Sánchez-Ortiz (1997) observed that the galatheid *Pleuroncodes planipes* has a seasonal reproduction as well, and that hatching of larvae coincides with the highest zooplanktonic biomass in upwelling regions.

The size at physiological maturity of female *M. subrugosa* is similar to those reported for other *Munida* spp. In this study, the size for 50% physiological maturity of 9.9 mm CL in *M. subrugosa* represents approximately one third of the maximum size reached by females. Similarly, Brinkmann (1936) reported 11.5 mm CL as the size at gonadal maturity in *M. sarsi*. The smallest ovigerous females of *M. sarsi*, *M. longipes* and *M. iris rutilanti* were of 9.6, 11.0 and 12.5 mm CL respectively (Wenner, 1982; Hartnoll et al., 1992; Sanz-Brau et al., 1998). Finally, Rodríguez & Bahamonde (1986) reported that female *M. subrugosa* physiological maturity is attained at 13.5 mm CL in the Strait of Magellan.

Sizes at physiological and morphometric maturity are very different in male *M. subrugosa*. Our results indicate that sizes at physiological (Figure 2) and morphometric (Figure 1) maturity are reached at 8.0 and 24.4 mm CL, respectively. Male physiological maturity occurs at a similar size to that of females. Similarly, in the northern Atlantic, male *M. longipes* and *M. valida* Smith, 1883 attain physiological maturity at 9–14 and 11.3 mm CL, respectively (Wenner, 1982). We suggest that in *M. subrugosa* functional or behavioural maturity (participating in mating couples) could be attained at an intermediate size between physiological and morphometric maturity sizes. For other male crab species, as for example *Chionoecetes opilio* (Fabricius, 1788) or *Paralithodes camtschaticus* (Tilesius, 1815), attaining the size of morphometric maturity is not a requisite to mate successfully (Paul, 1992; Sainte-Marie et al., 1999 and references therein). Maximum male size of *M. subrugosa* is ~31 mm CL and in 1999 males >24.4 mm CL constitute the 3% of the male fraction of the population (F. Tapella, unpublished results). Hence, it is not adaptive for the species to rely only on morphometric mature males to ensure mating and offspring production.

Fecundity of *M. subrugosa* was positively correlated with female size and the average number of eggs per complete brood was ~4300. In *M. sarsi* and in several species of the genus *Munidopsis* a positive correlation between clutch and body sizes has been reported (Van Dover & Williams, 1991; Hartnoll et al., 1992). *Munida subrugosa* is similarly fecund to other *Munida* spp.: *M. longipes* (9300 eggs maximum), *M. microphthalma* (3000 eggs maximum; Wenner, 1982) and *M. sarsi* (2000 eggs average; Hartnoll et al., 1992). In contrast, Wenner (1982) observed *M. valida* broods with up to 32,000 eggs and Hartnoll et al. (1992) found in *M. tenuimana* an average number of eggs per clutch of 630, but this was determined from seven females only. Moreover, the egg size of *M. subrugosa* is similar to that observed by Wenner (1982), Zainal (1990), Van Dover & Williams (1991), and Hartnoll et al. (1992) for thirteen species belonging to *Munida*.

The occurrence of partial or incomplete broods at the beginning of the reproductive cycle, i.e. in May–June, is puzzling. On the one hand, the proportion of complete broods increases after the first occurrence of ovigerous females, suggesting a replacement of partial broods by complete broods, or a gradual extrusion process extending over several days or weeks. The significant linear relationship between log fecundity of partial broods and log female size (Figure 6) suggests that the egg-extrusion, if gradual, is dependent on crab size since the beginning of the extrusion. However, we cannot from our monthly sampling frequency resolve whether the partial broods were lost and replaced or if there was a gradual increase in the number of eggs per clutch, which may imply multiple mating and therefore the intermittent fertilization of eggs. This hypothesis is possible since polyandry, i.e. mating of one female by several males, has been observed in other anomuran crabs of the family Hippidae (*Emerita talpoida* (Say, 1817), *E. analoga* (Stimpson, 1857) and *E. emerita* (Linnaeus, 1767) (cited as *E. asiatica* by Subramoniam, 1977)) (Sastry, 1983). On the other hand, we speculate that partial broods may also constitute a chemical signal for male attraction for mating, and therefore may be

replaced by a complete new clutch at the time of mating and fertilization. There is experimental evidence that eggs stripped from *Chionoecetes opilio* females may elicit some reaction from males (Bouchard et al., 1996).

The question of eco-physiological and ecological barriers for the distribution of reptant decapods towards the high Antarctic is still controversial. The genus *Munida* represents an important part of the biomass and abundance of the subantarctic decapod fauna (Arntz & Gorny, 1996; Tapella et al., 2002) and is assumed to be of commensurate ecological importance in the food web, due to its occurrence in large benthic and pelagic aggregations, as are krill *Euphausia* spp. in Antarctic waters (e.g. Miller, 1985; Shirakihara et al., 1986). An abbreviated larval development and a reduction in egg numbers with an increase in both larvae and egg-size with increasing latitude was shown for several taxonomic groups, such as decapods, echinoderms and prosobranchs, and was proposed as an ecological rule for adaptation at low temperatures and to a short, seasonally pulsed food input at higher latitudes (Thorson, 1950; Clarke, 1987; Pearse et al., 1991). Regarding reproduction, this adaptation was specifically exemplified in Caridean shrimps, the exclusive species of *Natantia* that occur in the Antarctic (e.g. Clarke, 1993; Wehrmann & Lardies, 1999; Thatje & Bacardit, 2000). It is likely that in *M. subrugosa*, numerous and small eggs that probably hatch planktotrophic larvae are adaptive constraints to colonize the waters south of the Antarctic convergence, and therefore *M. subrugosa* cannot compete with species more adapted to polar waters.

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