

Life History of the Galatheid Crab *Munida subrugosa* in Subantarctic Waters of the Beagle Channel, Argentina

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Abstract

Galatheid crabs of the genus *Munida* are the most abundant decapods in coastal waters off Tierra del Fuego, including the Beagle Channel (55°S, 68°W). Other galatheids off New Zealand, the North Pacific, and Central America, have proved to be of potential commercial interest, but the only fishery currently exploited is that for *Pleuroncodes monodon*, off central Chile (ca. 35°S).

Monthly benthic samples were taken in the Beagle Channel starting in November 1997 in order to investigate distribution, reproduction, and feeding habits of *Munida subrugosa*. Two galatheid species were found, *M. subrugosa* being significantly more abundant than *M. gregaria*. The reproductive cycle of *Munida subrugosa* started in June, and was reflected by the maximum size of oocytes, the maximum value of gonadosomatic index in both females and males, and by the proportion of ovigerous females. The embryonic development lasted 90-120 days. Fecundity (~100-11,000 eggs) correlated with female size. Females attained their gonadal maturity size at ~11 mm carapace length (CL). Males reached morphometric maturity at ~24 mm CL, although males ~10 mm CL presented spermatophores. *Munida subrugosa* has two different feeding habits, as a predator (feeding on crustaceans and macroalgae) and/or as a deposit feeder (ingesting sediment, foraminiferans, diatoms, and particulate organic matter). The proportion of inorganic matter was higher at depths >40 m, suggesting that the condition of deposit feeder increases with depth.

Introduction

The galatheid crabs *Munida subrugosa* and *M. gregaria* (Fig. 1) are anomurans, 5-7 cm total length, that are very abundant in waters of the southwestern Atlantic. *Munida subrugosa* is morphologically similar to *M. gregaria*, and since they are sympatric in the southwestern Atlantic, the two species have been confused and misidentified. Moreover, Williams (1980) suggests that they are morphological variants of the same species, but this topic is still a matter of controversy.

In the Southern Hemisphere, *M. subrugosa* and *M. gregaria* occur in large benthic concentrations, mainly off New Zealand and South America (Rayner 1935, Williams 1980). Around the southern tip of South America, in Atlantic waters, *M. subrugosa* and *M. gregaria* occur on the continental shelf from Uruguay (35°S) to Cape Horn (55°S), including the Islas Malvinas (Falkland Islands). Off the Chilean Pacific coast of South America, their southern distribution reaches the island of Chiloé (41°S; Retamal 1973). The bathymetric distribution of *M. subrugosa* is from the sublittoral down to 1,137 m depth (Gorny 1999).

The economic significance of *Munida* spp. was recognized by Rayner (1935) as early as 1935, but the interest in *M. subrugosa* has occurred only recently due to ecological concerns and the development of several commercial uses. For human consumption, decorticated tails are accepted as cocktail shrimp (Aurióles-Gamboa and Balart 1995, Lovrich et al. 1998; but see Kashkina and Kashkin 1993). Moreover, *P. monodon* proved to be a source of digestive proteases which serves in the manufacture of cheeses (García-Carreño and Fernández-Cortés 1995). Due to high levels of carotenoids, galatheids could be used as a source of pigments for tissue coloring in cultured salmon and trout, and for skin and egg coloring in chickens (Burd and Jamieson 1988, Kashkina and Kashkin 1993, Aurióles-Gamboa and Balart 1995, Carrillo-Domínguez et al. 1995). Finally, due to the amino and fatty acid balance of galatheids, either whole animals or waste portions provide a high quality source for the manufacture of balanced food (Burd and Jamieson 1988, Kashkina and Kashkin 1993, Zeldis 1989).

The only fishery for galatheids has developed off the Chilean Pacific coast (36°S), and in the 1980s produced profits between \$6.2 and \$11.8 million per year (US) (Aurióles-Gamboa and Balart 1995). In 1977, the annual landing for this fishery peaked at ca. 50,000 t of *Pleuroncodes monodon* and *Cervimunida johni*. Thereafter, landings dramatically decreased to ca. 8,000 t (Aurióles-Gamboa and Balart 1995) and the fishery was closed for 3 years due to overfishing (Roa and Bahamonde 1993). Other scientific initiatives were conceived for the development of new fisheries for galatheids, off the Mexican Pacific coast (25°N) for *P. planipes* (Aurióles-Gamboa and Balart 1995), off the North American Pacific coast at 48°N for *Munida quadrispina* (Burd and Jamieson 1988), and off the New Zealand Pacific coast at 45°S (Zeldis 1989). Nevertheless, none of these potential fisheries has developed yet. Currently, off the Atlantic coast of southern

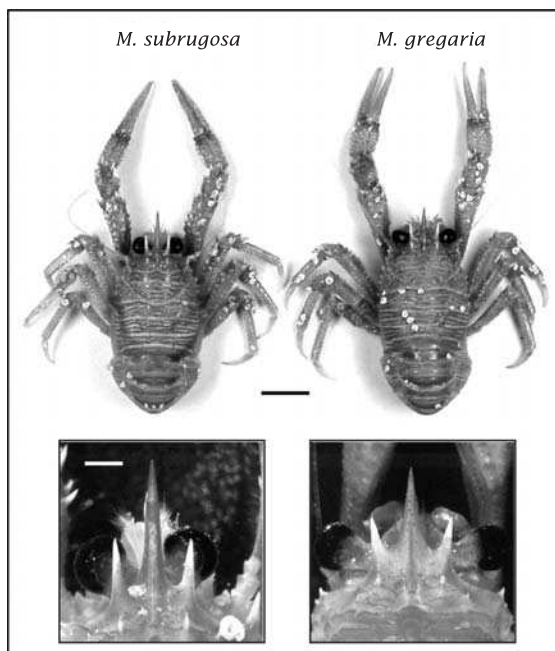


Figure 1. General aspect and morphology of the rostral spine, ocular peduncles, and cornea of *Munida subrugosa* and *Munida gregaria* collected in the Beagle Channel, Argentina. The black and white scale bars represent 1 cm (above) and 3 mm (below), respectively.

South America (ca. 40°S) *M. subrugosa* is the main species in the bycatch of the trawling fisheries for the shrimp *Pleoticus muelleri* and for the king crab *Lithodes santolla* (J.H. Vinuesa, CADIC, and A. Pettovello, Univ. Patagonia Austral, Puerto Deseado, Argentina, pers. comm.).

Munida spp. are suspected to be key species in the coastal subantarctic ecosystem of the southern tip of South America. First, *Munida* spp. are the dominant decapod species in the area, and in terms of biomass they constitute 50% of the benthic community (Arntz and Gorny 1996). Both species are very abundant and video-recorded concentrations are as high as 3-27 individuals per m² (Gutt et al. 1999; M. Gorny and M.A. Retamal pers. comm.). Second, the relatively small size, the highly valuable chemical composition, and high densities of occurrence make *Munida* spp. the favorite prey of numerous top predators (e.g., octopuses, crustaceans, fishes, birds, whales, sea lions, seals, and otters) (partially reviewed by Rodríguez and Bahamonde 1986). Third, like their Pacific relative *P.*

monodon, *Munida* spp. are believed to prey on small herbivores and graze on algae. Hence, these species are suspected to constitute a direct intermediate between the lower and the higher levels of the trophic web. Therefore, fishing for *Munida* spp. could have a negative effect on the abundance of the top predators, unless they are carefully managed.

Due to the collapse of other crustacean fisheries such as *Lithodes santolla* (Lovrich 1997), *Munida subrugosa* of southern South America could reach commercial interest in the near future. However, the background knowledge about its biology is currently limited. In this study we document basic biological parameters such as the abundance, reproduction, and feeding habits of *M. subrugosa* to provide some basic commercial exploitation guidelines, in order to ensure the lowest possible impact on the ecosystem.

Material and Methods

Study Site and Sampling

The Beagle Channel is situated at the southern tip of South America (55°S, 68°W) and is delimited by the Isla Grande de Tierra del Fuego to the north, and Isla Hoste and Isla Navarino to the south. The channel has an irregular sea bottom, consisting of muddy or mud-sandy sediments (Brambatti 1991).

Sampling was conducted on a monthly basis in a sector of 45 km of the Beagle Channel Argentina, from Punta Segunda to Bahía Lapataia, between November 1997 and December 1999. Samples were obtained with an epibenthic trawl net of 10 mm mesh size and 1.7 m mouth width, specially designed to operate with a small boat. For each sampling period one sample was obtained at each of six randomly selected positions at each of three sampling locations (Punta Segunda, Ushuaia, and Lapataia) in each of two depth strata namely <40 m and >40 m. The 40 m depth is known for the lower bathimetric distribution of benthic macroalgae, e.g., *Macrocystis pyrifera* (Küneman 1970). Tows were performed at 0.65-0.80 m per second during 5-25 min. The initial and final positions of the tows were recorded with a geostationary satellite positioning system. The maximum depth of each haul was also recorded. All but 30 captured crabs were immediately fixed in 4% formalin in seawater. The other 30 crabs were frozen at -18°C.

In the laboratory, both species (*Munida subrugosa* and *M. gregaria*) were determined to specific levels based on the following characters: (1) basis of rostral spine wider in *M. gregaria*, (2) ocular peduncles longer in *M. gregaria*, (3) cornea of *M. subrugosa* kidney-shaped (Fig. 1) and (4) meropodite of the third maxilliped in *M. subrugosa* bearing distal spine (Retamal 1981). Crabs were further sorted by species, sex, and ovigerous condition. The standard measure of body size, carapace length (CL), was determined to the nearest 0.1 mm on all collected crabs with a dial calliper. The carapace length was the midline distance between the posterior orbital margin, excluding rostral spine, to the posterior median margin.

Density and Biomass

Crab densities of *M. subrugosa* and *M. gregaria* and biomass of *M. subrugosa* were calculated using the tow distance and the trawl width, and are presented as number of crabs or wet weight of crabs per 100 m², respectively. Tow distance over the bottom was estimated as the difference between boat positions at the beginning and at the end of each tow. Wet weight used for biomass calculations was evaluated from a subsample of 369 *M. subrugosa*, which were measured and weighed to the nearest 0.01 g. A predictive regression (Sokal and Rohlf 1995) between CL and wet weight (ww) was used, as follows: $\log ww = 3.03 \times \log CL - 3.17$ (Tapella, unpubl. results). Each 0.1 mm CL size class of size frequency distributions was transformed to its corresponding wet weight. Biomass of each size class >10 mm CL was calculated by multiplying the wet weight by the number of animals present in the size class interval. Biomass per tow was then computed as the sum of the biomasses per size class.

Maturity Size

We used two methods to determine the size at which 50% of individuals were mature: (1) Analysis of the reproductive features. This method adjusts a logistic function to the proportion of mature animals for each size class to provide 50% maturity. Both females and males were considered mature if they had eggs attached to the pleopods or spermatophores in their vas deferens, respectively. The proportion of mature females was calculated for each 1 mm CL size class interval. (2) Allometric growth of the right chela (males only). This method is based on the relative change in chela growth at sexual maturity (Hartnoll 1978). We used the routine MATURE1 (Somerton 1980) to determine the proportion of morphometrically mature individuals. Values of "juvenile" and "adult" required by the routine were chosen by judging the scatterplot of chela size versus carapace length and 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 of (1) the gonadosomatic index (GSI) for females and males, (2) the oocyte diameter, and (3) the proportion of ovigerous females. Each month a subsample of 15-25 *M. subrugosa* crabs of both sexes >10.9 mm CL (gonadal maturity size) was randomly selected. Crabs were measured and dissected. Their gonads were removed and dried at 55°C to constant weight. Gonad dry weight was recorded to the nearest 0.1 mg. A gonadosomatic index was calculated as the ratio between the ovary dry weight and size (CL), multiplied by 1,000. Each month, a subsample of 8-11 females >10.9 mm CL was randomly selected and dissected. The ovary was removed and preserved in 4% formalin seawater. In each female, 80-100 oocytes were randomly chosen, and their diameter measured to the nearest 0.02 mm using

an eyepiece micrometer on a compound microscope. The proportion of ovigerous females was calculated as the ratio between ovigerous and non-ovigerous females >10.9 mm CL.

Fecundity was defined as the number of eggs per clutch, and was estimated only in females with broods recently extruded (eggs with uniform yolk and no ocular pigment visible). Pleopods with eggs attached were removed from each female by cutting from their base, and preserved in buffered 4% formalin seawater. Later, eggs were detached from the pleopods and the clutch was blotted and weighed to the nearest 0.1 mg (*WC*). Three subsamples were then weighed to the nearest 0.1 mg (*ws*) and eggs in each subsample were counted (*ns*). Fecundity (*F*) was calculated as:

$$F = \sum_{i=1}^3 (WC \times ns / ws) / 3$$

Natural Diet

For analysis of stomach contents, samples of *M. subrugosa* were collected once every 3 months. Immediately after trawling, one subsample of 10-30 individuals per stratum was randomly selected. To identify food items and quantify their relative abundances in the stomach contents, animals of one of the subsamples were injected with and submerged in 4% formalin seawater. Crabs were dissected, their stomachs excised, and the contents rinsed into a dish with 1 ml of 4% formalin seawater. Relatively large food items were identified to the lowest taxonomic level possible under a binocular microscope at 20× magnification. Two 0.4-ml subsamples of the stomach content were mounted on slides and examined under a binocular microscope at 100×. We recorded the occurrence of each item with an ocular grid marked with 25 intersection points. From each slide we examined 3 fields giving a total number of 150 intersection points for each animal. The relative abundance (*RA*) and the frequency of occurrence (*FO*) of each item were calculated as follows:

$$RA = (i_a / \sum i) \times 100$$

$$FO = (N_i / N_t) \times 100$$

where i_a is the number of intersection points for item *a*; $\sum i$ is the number of intersection points for all items, N_i is the number of stomachs with item *i* and N_t is the total number of stomachs.

To quantify the organic matter present in the stomach contents, the other subsample was preserved frozen at -20°C until the time of processing. Crabs were defrosted, dissected, the stomach incised, and contents rinsed into a ceramic dish with 1-3 ml of filtered water. The stomach contents were dried to constant weight at 56°C, weighed, burned for 24 h at

450°C, and the ashes were weighed. The quantity of organic matter of the stomach contents was the difference between the dry and ash weights.

Results

Density of Munida subrugosa and Munida gregaria and Biomass of M. subrugosa

In the study area, *Munida subrugosa* and *M. gregaria* simultaneously occurred in our trawl samples. In 1999, the overall average density of both species combined was 47.5 (\pm 1S.D. = 92.8) individuals per 100 m² ($n = 64$). However, *Munida subrugosa* was the more abundant species, and had a density at most 8 times greater than *M. gregaria*. The density of both species was on average 2.5 times higher at <40 m depth (Fig. 2), and was only higher at >40 m depth in March and September 1999 (Fig. 2). Densities of both species differed among the three studied locations and between both depth strata (Table 1). At <40 m depth, *M. subrugosa* was always more abundant than *M. gregaria*, with both species occurring at similar densities only in Lapataia. At >40 m depth, *M. gregaria* was virtually absent and occurred at an average density of 0.02 (\pm 0.05) individuals per 100 m². During 1999, the mean biomass of *M. subrugosa* was 3.4 g per m² (\pm 6.2; $n = 58$). As expected, the biomass of *M. subrugosa* was significantly higher at <40 m (4.9 g per m²; $n = 35$) than at >40 m of depth (1.3 g per m²; $n = 27$) (Mann Whitney test, $U = 685$; $P = 0.003$). For the studied sector of the Beagle Channel, the estimated biomass of the stock of *M. subrugosa* was 558.9 t at <40 m and 121.3 t at >40 m depth.

Gonadal and Morphometric Maturity

In females 50% of gonadal maturity occurred at 10.9 mm CL (Fig. 3). The smallest female carrying eggs was 8.9 mm CL. A total of 54 males of 8.8-30.5 mm CL were examined and all had spermatophores in their vas deferens. Size at morphometric maturity was calculated for 428 males (8.2-29.8 mm CL). The slope of the regression of right chela length on the carapace length 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; Fig. 4).

Reproductive Cycle

In female *M. subrugosa*, GSI values peaked in May-June, followed by decreasing values (Fig. 5), suggesting the occurrence of oocyte extrusion. This process might extend until July-August, because GSI values were still widely distributed. From September to March, GSI values were practically constant. Hence, we propose that the accumulation of yolk, i.e., secondary vitellogenesis, began in March and extended through August. In males,

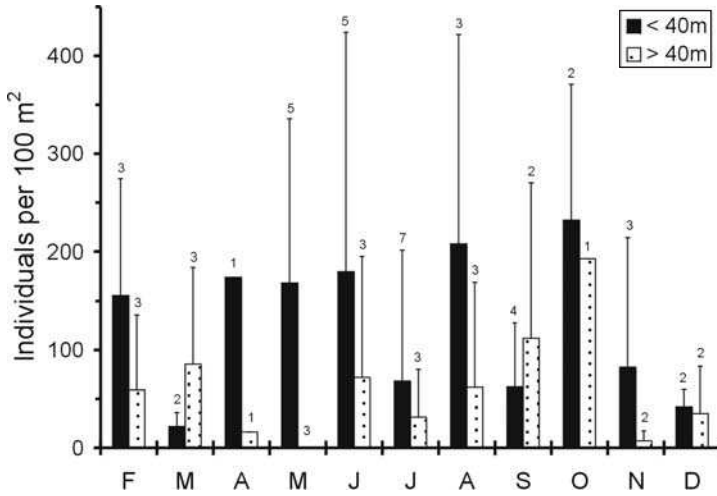


Figure 2. Average abundance of *Munida subrugosa* and *Munida gregaria* during 1999 at two depth strata in the Beagle Channel, Argentina. Lines above bars represent the standard deviations. Numbers above bars are sample sizes.

Table 1. Abundance of *Munida subrugosa* and *Munida gregaria* during 1999, at two depth strata, in three different locations in a sector of 45 km of the Beagle Channel, Argentina.

Beagle Channel locations		<i>M. subrugosa</i>		<i>M. gregaria</i>	
		<40 m	>40 m	<40 m	>40 m
Lapataia	Density	56.75	0.03	38.77	0
	S.D.	78.18	0.05	55.57	0
	<i>n</i>	13	6	13	6
Ushuaia	Density	143.21	91.66	10.53	0.03
	S.D.	168.4	90.89	15.32	0.06
	<i>n</i>	16	14	16	14
Punta Segunda	Density	108.75	31.89	0	0.03
	S.D.	121.72	60.19	0	0.07
	<i>n</i>	8	7	8	7

Abundances are given as densities: individuals per 100 m². S.D. = standard deviation; *n* = number of trawls.

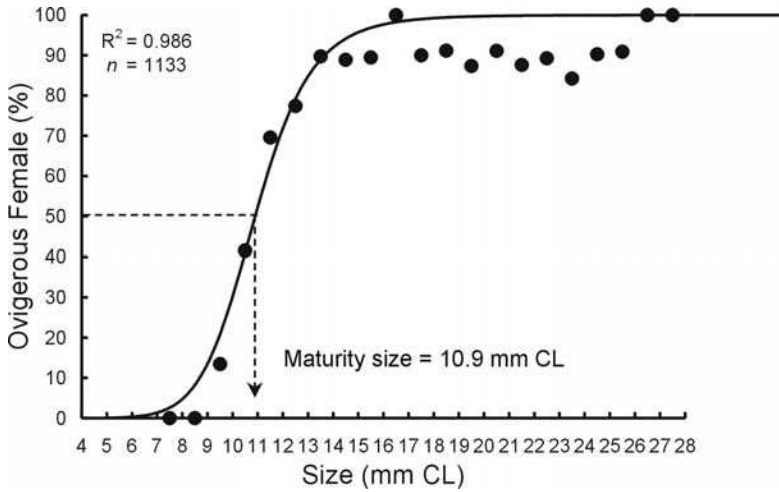


Figure 3. Gonadal maturity in female *Munida subrugosa*. Size at 50% maturity is given by the intersection between the calculated logistic function and the ordinate at 50%. R^2 is the determination coefficient of the logistic function; n is the sample size.

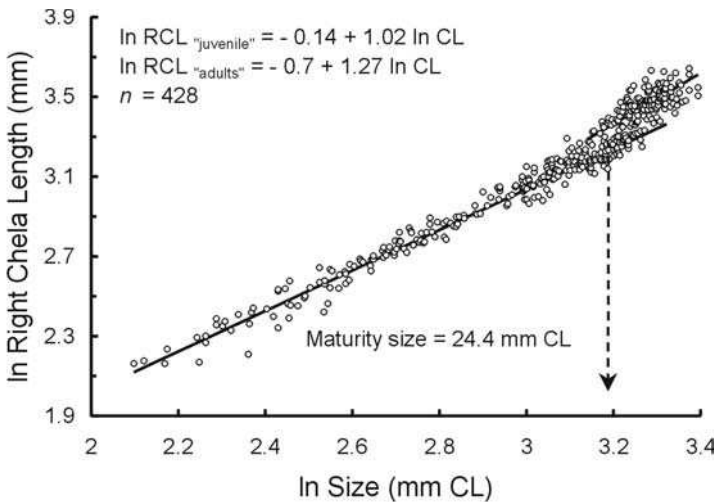


Figure 4. Relationship between right chela and carapace lengths in male *Munida subrugosa*. Dotted arrow shows the proportion of 50% of morphometric maturity. Loglinear functions for exclusive “juvenile” and “adults” are shown. RCL is the right chela length; CL is the carapace length; n is the sample size.

maximum values of GSI occurred in June, and thereafter GSI values decreased gradually (Fig. 5). From November to March the GSI values were relatively constant. Hence, mating might have extended from May to August and the accumulation of sperm material in the vas deferens likely occurred between April and June.

Two different types of oocytes occurred in the ovaries of *M. subrugosa*. In live animals, oocytes in pre-vitellogenesis or primary vitellogenesis were white or translucent and their size varied between 0.04 and 0.34 mm diameter. Oocytes in pre-vitellogenesis occurred permanently in ovaries, and were exclusively present between September and February. Oocytes in secondary vitellogenesis were green or yellow, in live or fixed animals, respectively. Sizes varied from 0.36 to 0.9 mm in diameter and occurred between March and August. Average oocyte size was clearly seasonal, peaked in June, gently decreased thereafter until September, and remained approximately constant between October and February (Fig. 6). Between June and August standard deviations of the average oocyte size were larger than in other months. Therefore, oocyte extrusion occurred between June and August.

Ovigerous females of *M. subrugosa* mainly occurred between May and October (Fig. 7). The monthly proportion of ovigerous females changed in the two sampling years: ovigerous females varied around 80% in 1998 and between 40% and 90% in 1999. In October and November proportions of ovigerous females decreased and were minimal. Hence, oocyte extrusion occurred in May.

Fecundity

Fecundity of *M. subrugosa* correlated positively with female size. The log of the number of eggs per female increased significantly with the log of female CL ($\log F = -2.6 + 4.6 \log CL$; $F = 495.5$; $P < 0.01$; $r^2 = 0.82$). The number of eggs per female varied from 124 eggs for a female of 11.15 mm CL to 10,750 eggs for a female of 25.65 mm CL.

Feeding Habits

A total of 582 stomachs of *M. subrugosa* were analyzed, of which only 3% were empty. Food items were identified in 260 stomachs (158 at <40 m and 102 at >40 m depth), and another 322 stomachs were used to quantify the organic matter of the stomach content (158 at <40 m and 164 at >40 m depth). Macroscopically, the stomach content was an amorphous mass, frequently green, in which no definite material could be recognized.

In the Beagle Channel, two food categories constituted the diet of *M. subrugosa*: benthic material and food items. Sediment and undetermined material were present in nearly all stomachs of analyzed individuals (Table 2), and accounted for 20-30% in relative abundance of food items in the stomach contents (Table 2). The undetermined material was particulate organic matter (POM). However, a fraction of POM could be food in a high degree of digestion. The diet of *M. subrugosa* was also composed of at

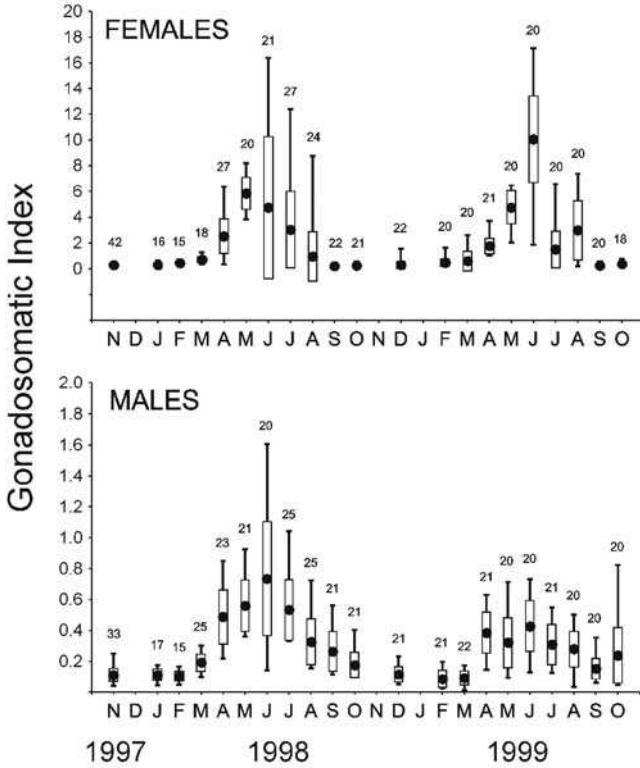


Figure 5. Monthly values of gonadosomatic index (dry gonadal weight/carapace length \times 1,000) for female and male of *Munida subrugosa* from November 1997 to October 1999. Circles, empty rectangles, and vertical lines are averages, standard deviations, and range values of gonadosomatic index, respectively. Numbers above vertical lines are sample sizes.

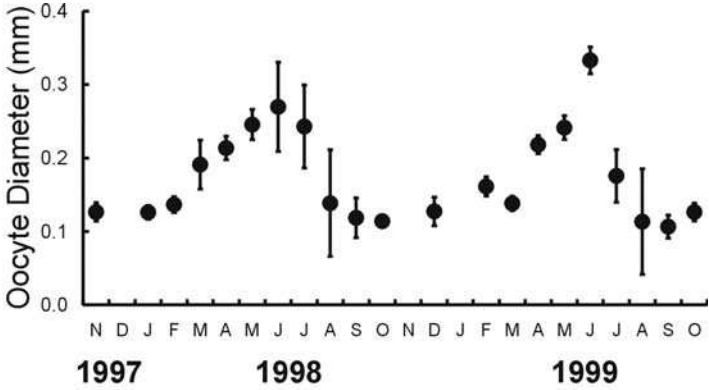


Figure 6. Monthly average oocyte diameters for female *Munida subrugosa* from November 1997 to October 1999. Values of average and standard deviation were calculated from individual averages obtained from 8-12 (mostly 10) females. To obtain the individual averages, 80-90 oocytes of each female were measured.

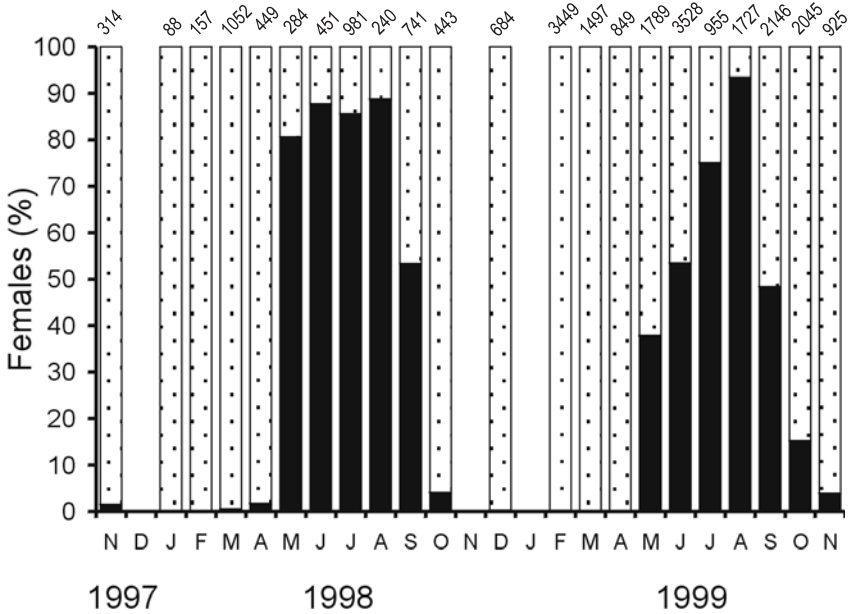


Figure 7. Percentage of ovigerous females (black bars) of *Munida subrugosa* >10.9 mm CL, between November 1997 and October 1999. Sample sizes are indicated above bars. Months with no samples are bare.

Table 2. Frequency of occurrence and relative abundance of food items of *Munida subrugosa* at two depth strata of the Beagle Channel.

Food items		Frequency of occurrence (%)		Relative abundance (%)	
		<40 m	>40 m	<40 m	>40 m
Algae	Algae undetermined	34.2	33.3	6.2	5.5
	<i>Ballia</i> spp.	17.7	18.6	1.4	1.1
	<i>Rhizoclonium</i> spp.	5.7	0	0.4	0
	<i>Cladophora</i> spp.	10.8	8.8	0.8	0.7
	<i>Monostroma</i> spp.	0	3.9	0	2.0
	<i>Hincksia</i> spp.	0	8.8	0	0.8
	<i>Desmarestia</i> spp.	4.4	3.9	1.9	0
	<i>Trailiella</i> spp.	36.1	18.6	2.3	0.8
	Other algae	12.7	7.9	1.6	1.8
	Diatoms	42.4	22.5	1.6	0
Worms	Oligochaeta	20.2	14.7	1.8	1.0
	Nematoda	14.6	32.3	0.8	1.6
	Polychaeta	0	10.8	0	1.8
	Polychaete tubes	19.6	0	4.7	0
Crustacea	Crustacea undetermined	46.8	55.9	11.4	14.7
	Ostracoda	1.9	6.9	0.1	1.2
	<i>Munida</i> spp.	8.9	2.9	5.7	1.9
	Other Crustacea	5.7	7.8	0.3	0
Others	Plant leaves	7.0	0	1.4	0
	Parazoa	5.1	2.0	0.1	0.1
	Foraminifera	55.7	31.4	1.9	0
	Other protozoans	1.3	19.6	0.1	2.0
	Hydrozoa	7.0	2.9	0.1	0.1
	Bryozoa	0.6	0	0.1	0
	Mollusca	7.0	0	0.6	0
	Echinoidea	4.4	0	0.1	0
Sediment	95.6	100	21.8	30.8	
Particulate organic matter	94.9	100	32.9	32.1	

Other protozoans are rotiferans and undetermined cysts. Other algae include the following genera: *Sphacelaria*, *Hymenena*, *Ceramium*, *Griffithsia*, *Ulva*, *Chaetomorpha*, *Ectocarpus*. Other crustaceans include amphipods and copepods (mostly Harpacticoida).

least 28 food items (Table 2). In terms of percentage of occurrence, Foraminifera, diatoms, crustaceans, nematodes, some small macroalgae such as *Ballia* spp. and *Trailliella* spp., and polychaete tubes appeared as the main food items in the diet of *M. subrugosa* (Table 2). However, in terms of relative abundance only crustaceans, algae, and polychaete tubes were dominant food items (Table 2). The occurrence of conspecific or congeneric preys was also recorded.

The proportion of inorganic matter in the stomach contents was higher at >40 m depth. Between April 1998 and December 1999, the proportion of organic matter in stomach contents was constant at 46.8 (± 13.5)% and 36.1 (± 9.0)% at <40 m and >40 m depth, respectively. Moreover, the proportion of organic matter at <40 m depth was significantly higher than at >40 m depth (Student's $t = 3.53$; $P < 0.001$).

Discussion

Results presented in this article constitute the first information on the biology of *M. subrugosa* in the Beagle Channel. Although we found that *M. subrugosa* and *M. gregaria* are more abundant at depths <40 m, they occur differentially in the Beagle Channel. We speculate that *M. gregaria* is likely excluded from soft bottoms with 3-dimensional structures (e.g., with algae or polychaete tubes of *Chaetopterus* spp., at sites Ushuaia and Punta Segunda). These types of bottoms could provide an adequate benthic habitat for the juvenile phase of *M. subrugosa* (unpubl. data), whereas the juvenile *M. gregaria* are pelagic and occur in the water column (Zeldis 1985). Therefore, juvenile *M. gregaria* are likely exported offshore from the Beagle Channel, explaining their lesser abundance inside the channel. Adults probably occupy marginal habitats with apparently higher quantities of inorganic material and terrigenous debris such as occurs at Lapataia site.

The results of abundance derived from our benthic trawls are useful for comparison with other quantitative methods. In the Strait of Magellan and the channels of Tierra del Fuego, visual methods, such as photographs or video recordings, provide average and maximum densities of *Munida* spp. between 3-12 and 7-27 individuals per m², respectively (Gutt et al. 1999; M. Gorny and M.A. Retamal, pers. comm.). These visual methods surveyed areas of 1,578 and 257 m² of seafloor (Gutt et al. 1999; M. Gorny and M.A. Retamal, pers. comm.) that are much smaller than the 57,454 m² trawled in our study during 1999. Methods of direct observations could be biased if, at the scale of the sampling units, the spatial distribution of crabs is patchy (Conan and Maynard 1987), as occurs with both *M. subrugosa* (M. Gorny and M.A. Retamal, pers. comm.) and *M. gregaria* (Zeldis 1985). We also realized that our trawl may underestimate abundances of *Munida* spp. A video recording of our trawl mouth let us determine that only 15% of crabs occurring in the trawl path were lost by escaping behavior (Tapella, unpubl. results). These two types of biases could explain the

differences between our average density of *Munida* spp. of 0.5 and the 8-28 individuals per m² in previous visual studies.

Our estimations of biomass are the first for galatheids in the Beagle Channel, and serve to evaluate the economical potential of the *Munida* fishery. The average biomass of 3.5 t per km² estimated for *M. subrugosa* >5 mm CL is relatively low compared with the reported biomass of other economically valuable species. Aurióles-Gamboa and Balart (1995) estimated the biomass of the benthic phases of *Pleuroncodes planipes* off Mexico to be between 4 and 176 t per km². After the fishery collapse and 3 years of closure, the biomass of *P. monodon* off central Chile varied between 20 and 47 t per km² (Roa and Bahamonde 1993). Our estimations of biomass could increase by about 10% if the potential abundance of *M. gregaria* is considered for biomass calculations.

In the Beagle Channel the reproductive cycle of *M. subrugosa* is annual and begins with mating, which mainly occurs in June (Figs. 5-7). However, mating may extend further, until August, since gonadosomatic indexes and oocyte diameter decreased slowly after June (Figs. 5 and 6). Females >10.9 mm CL are mature and keep their eggs in their abdomens over a period of 3 months, mainly between June and September, when larval hatching occurs (Lovrich 1999). Ovigerous females occur until November but at lower proportions (Fig. 7), a fact which agrees with the occurrence and abundance of recently hatched zoeae in the plankton until December (Lovrich 1999). This contrast with a limited number of samples from the Strait of Magellan, from which Rodríguez and Bahamonde (1986) speculated that the reproductive cycle of *M. subrugosa* begins in April, the embryogenesis lasts 8-9 months, larval hatching occurs between October and January, and females attain gonadal maturity at 13.5 mm CL.

In male *M. subrugosa*, size at morphometric maturity does not serve as a good indicator of the size at which the crabs reproduce as may occur in other anomuran crabs such as lithodids. Our results indicate morphometric maturity at 24.4 mm CL (Fig. 4) and we speculate that gonadal maturity (spermatophores in the vas deferens) is attained at about 10 mm CL. For males, attaining the size of morphometric maturity is not a requisite to mate successfully (Paul 1992, Sainte-Marie et al. 1999, and references therein). Moreover, extremely divergent sizes of males and females at coupling, e.g., a 25 mm CL male and a 10 mm CL female, may constrain the adequate fertilization of extruding eggs. Therefore, we hypothesize that male *M. subrugosa* attain functional or behavioral maturity (participating in mating couples) at an intermediate size between gonadal and morphometric maturity sizes. Moreover, we suggest that functional maturity could be attained immediately after gonadal maturity.

Munida subrugosa of the Beagle Channel has two different and complementary feeding habits. As a predator *M. subrugosa* grazes on small macroalgae or feeds on crustaceans. As a deposit feeder *M. subrugosa* uses POM as a source of energy. Such a bipartite feeding habit was also observed in other galatheid species (Nicol 1932, Cartés 1993, Kashkina

and Kashkin 1993, Aurióles-Gamboa and Pérez-Flores 1997). Moreover, POM could provide additional food not considered in this study, such as bacterial flora adhered to organic and inorganic particles (Petchen-Finenko 1987). Channels around Tierra del Fuego and particularly the Beagle Channel could serve as an environment for the accumulation of organic matter of terrigenous origin, which could serve as a direct or indirect food source for *Munida* spp. (see "plant leaves" in Table 2). This is supported by the fact that channels are oceanographically isolated because there is limited water exchange through the shallow connecting passages and the open ocean (Antezana 1999). Hence, the organic matter such as leaves of the deciduous forest of the southern beech *Nothofagus* spp. may be retained in the channels. This is supported by the fact that leaves occur in our trawl throughout all the year (M.C. Romero, unpubl. results). Our observations also suggest that feeding habits are likely related to crab distribution depth, since animals at >40 m depth showed greater quantities of sediment (Table 2) and inorganic matter in their stomachs, thus probably the condition of deposit feeder increases with depth. The condition of deposit feeders is also supported by high abundance of *Munida* spp. found associated with soft bottoms containing high concentration of phytodetritus and biogenic debris (Gutt et al. 1999; M. Gorny and M.A. Retamal, pers. comm.). Moreover, as deposit feeders, *M. subrugosa* crabs are probably responsible for bypassing the organic matter recycling by bacteria, and thus could make this organic matter available to top predators.

We hypothesize that *Munida subrugosa* plays a key role in the marine benthic ecosystem of the Beagle Channel for several reasons. First, this species is highly abundant (0.5 to 70 individuals per m², this study and Gutt et al. 1999). In terms of wet weight, *M. subrugosa* is one of the most dominant species, accounting for 50% to benthic captures (Arntz and Gorny 1996), and in terms of numbers, represents more than 90% of decapod fauna (Arntz et al. 1999, Pérez-Barros 2001). Second, larvae and adults of *M. subrugosa* are prey of several marine organisms, most of which are top predators and also of economic interest (partially reviewed by Rodríguez and Bahamonde 1986). Third, because of its feeding habits, *M. subrugosa* may constitute short trophic chains. As a deposit feeder *M. subrugosa* is able to incorporate rotting organic matter into the trophic web, otherwise only available to decomposers or to detritivores not frequently preyed upon. As a herbivore, *M. subrugosa* is the direct link between primary producers and terminal predators (Longhurst et al. 1967). Therefore, trophic chains in which *M. subrugosa* participate could be more efficient in the energetic transfer, because fewer trophic levels in a trophic chain imply less energetic losses.

High abundances of *Munida* spp. in southern South America suggest the potential that a fishery could be developed in the near future. The results of this study can serve as the initial basis for developing this fishery, until more biological information is available. Given the condition of

M. subrugosa as a key species in the ecosystem of the Beagle Channel, any fishery should be extremely conservative. The exploitation of intermediate trophic links at a large scale could undermine the food base of those species occupying higher trophic levels. Thus, the overall commercial marine stocks would decrease and the stability of the ecosystem would be threatened (Kashkina and Kashkin 1993). Furthermore, in contrast to open ocean areas in which other galatheid fisheries have been developed (c.f. Roa and Bahamonde 1993, Auriolles-Gamboa and Balart 1995), the relatively small area of the Beagle Channel constrains the development of the fishery to a small scale. Hence, we suggest that the management of the fishery for *Munida* spp. should consider:

1. Fishing should be banned during the period of egg-carrying, i.e., May-October. This could also be advantageous for the development of the fishery for *Munida* spp. as a complement to the king crab fishery, during its closed season, e.g., November-December (Lovrich 1997).
2. Landings should be limited by means of quotas as occurs in the Chilean fishery for *P. monodon*. Until population parameters that allow the forecast of the stock dynamics (e.g., growth and natural mortality rates, and generational time) can be calculated we recommend that quotas should be conservative and based on annual stock assessments.
3. A size limit could be imposed taking into consideration our calculations of female gonadal maturity and fecundity. Since larger animals yield more meat (Lovrich et al. 1998), a minimum legal size of 20 mm CL will maximize meat yields of landed animals, but still allow for reproductive opportunities for the sublegal crabs not retained. A size limit along with limited landings should ensure that the reproductive potential will not be significantly reduced.
4. Gear limitations should consider features like mesh size and gear design. The mesh size is used in the *P. monodon* fishery and will allow the control of legal size limits. The design of the gear should minimize sea-bottom disturbance, as is known to occur with standard beam trawls with tickler chains (c.f. Kaiser et al. 1994), and should maximize captures of the target species. Moreover, if authorized gear is small and operated by small-scale fishers, the fishery effort could be kept relatively controlled and the impact on the *Munida* spp. populations probably minimized.

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