REPRODUCTION OF *MUNIDA GREGARIA* (DECAPODA: GALATHEIDAE) IN SAN JORGE GULF, SOUTHWEST ATLANTIC OCEAN

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ABSTRACT

Munida gregaria is a galatheid very abundant in coastal waters of southern South America playing an important role in the trophic webs of the subantarctic coastal ecosystem. Different reproductive aspects of this species were studied from samples obtained by coastal trawlers between September 1997 and December 2000, which allowed the analysis of a total of 10,868 crabs. The reproductive period started in June, and females with small clutches composed of non-fecundated eggs were found in many cases. The size of clutches increased during the reproductive period, and the simultaneous presence of eggs at different stages of development was observed in the same female. In part of the population, larval hatching started in September, after which females mated again. These embryos hatched between late November and mid-December. Females reached physiological maturity between 9 and 12 mm CL and males between 6 and 8 mm CL. Fecundity was initially low (less than 500 eggs/female), and clutches were completed during the reproductive season, until a maximum of 7545 eggs. During the reproductive season males migrate to shallow waters where they gather for mating.

INTRODUCTION

Munida gregaria (Fabricius, 1793) is a small galatheid decapod (total length up to 75 mm) particularly abundant in coastal cold-temperate waters of the Argentine Sea up to 41°S (Vinuesa, 2005). In the present work, *Munida gregaria* was considered as synonym of *Munida subrugosa* (White, 1847) in agreement with Williams (1973 and 1980), who studied specimens from New Zealand, and with Pérez Barros et al. (in press), who conducted a recent genetic study in the Beagle Channel. It is worthy to mention, however, that adults of this species exhibit two different morphologies, and the type "subrugosa" is the only one found today in San Jorge Gulf.

In common with many other galatheids, the squat lobster, commonly named "langostilla" in Chile and Argentina, is found in numerous populations, with densities ranging between 0.5 and 7 crabs/m^2 in the Strait of Magellan (Gutt et al., 1999) and less than 0.5 crabs/m^2 in the Beagle Channel (Tapella et al., 2002a). To date, it represents the only species of *Munida* found in San Jorge Gulf, with densities between 0.1 and 2.1 crabs/m^2 in coastal waters (Vinuesa, unpublished).

Many authors have recognized the potential economic importance of *M. gregaria* (= *M. subrugosa*) (Rayner, 1935; Vinuesa, 1977; Rodríguez and Bahamonde, 1986; Lovrich et al., 1998). The squat lobster, like other commercially exploited galatheids, could be used as an ingredient of balanced feeds in salmonid culture (Kato, 1974; Zeldis, 1989; Villarreal, 1995) and in shrimp-cocktails (Lovrich et al., 1998). In addition, it could be used as a source of enzymes and pigments (Villarreal, 1995) and of proteases in cheese production (García-Carreño and Hernández-Cortés, 1995), as well as in aviculture (Carrillo-Domínguez et al., 1995).

Munida gregaria also plays an important role in trophic webs as the prey of fish, birds, and mammals (Rayner, 1935; Moreno and Jara, 1984; Rodríguez and Bahamonde, 1986; Romero et al., 2001). In San Jorge Gulf, juvenile and adult crabs are part of the diet of twenty-four fish, four mollusk, and four crustacean species (Vinuesa, 2003).

Knowledge of reproduction is essential for the proper management of any fishing resource, especially before the exploitation phase. The understanding of the reproductive biology of the squat lobster is particularly relevant because of its key role in San Jorge Gulf. The reproductive strategies of decapod crustaceans are mainly related to their environment. Decapods from deep waters with highly stable conditions show similar characteristics to those inhabiting permanent warm waters. Conversely, decapods living at high and mid-latitudes adopt different reproductive strategies in response to different seasonal environmental conditions (Sastry, 1983).

Literature concerning the reproduction of the species has provided information on various aspects of this process. Rayner (1935) and Rodríguez and Bahamonde (1986) have reported the seasonal reproductive pattern of *M. subrugosa* from Atlantic Patagonian waters and the Magellan Strait, respectively. Recently, Tapella et al. (2002a and 2002b) described the reproductive biology of this species in the Beagle Channel. So far, data on the reproduction of the squat lobster in San Jorge Gulf are fragmentary, and the only available information has been provided by Tapella et al. (2005), who compared the fecundity in populations from this site and the Beagle Channel. However, the need of a more detailed study of the reproductive characteristics of *M. gregaria* in San Jorge Gulf is justified by the long distance between this (45-47°S) and the Beagle Channel (ca 55°S) and by their different environmental conditions.

MATERIALS AND METHODS

The samples were obtained by coastal trawlers operating among Caleta Cordova, Comodoro Rivadavia and Caleta Paula Ports, all of which are located in San Jorge Gulf (Fig. 1). Squat lobsters were captured between October 1997 and December 2000 at depths from 27 to 86 m, and at a distance less than 20 miles from the coast. The geographical position,

Fig. 1. San Jorge Gulf, south-west Atlantic Ocean.

depth, type of bottom, time, direction, and speed were recorded for each tow. The openings of the bottom nets were about 50 to 70 mm. Two other samples were made in June and July 2002 to check for egg development, and ten females with reduced fecundity were collected each month, to identify proliferative cells. All samples were collected onboard during the selection of fish.

Sex was determined by the relative size of the body and chelipeds in animals larger than 22-23 mm CL, and by the presence of a modified second pleopod in males. The relative age of the exoskeleton was assessed by the hardness and colour of the carapace, and by the presence of epizoic organisms. Females were considered to be ovigerous if they carried at least a small but detectable number of eggs on their pleopods.

The morphometric measurements were performed with a digital caliper accurate to 0.1 mm. Total length (TL) was measured from the rostral end to the distal end of the telson, and carapace length (CL) from the orbital rear margin to the middle of the rear margin of the carapace, without including the rostral spine.

Sex Ratio

The analysis of male/female ratio was determined for each sample in which crabs were present. A replicated test of goodness of fit (G-test) was used (Sokhal and Rohlf, 1995), under the extrinsic hypothesis that the sex ratio was 1:1.

Gonad Development

The reproductive cycle was studied in females larger than 15 mm CL by examining texture, colour, and development of the ovary, and size of the oöcytes. The ovary was macroscopically classified into four stages: $0 =$ no visible ovary. $1 =$ ovary whitish, small and flaccid. $2 =$ ovary cream, yellow or light green (light orange in fixed samples), firm and poorly developed (in the initial vitellogenic stage). $3 =$ ovary green to dark green (strong orange in fixed samples) and well developed, in advanced vitellogenic stage, close to or fully mature.

The increase in oöcyte size and egg-laying characteristics were studied in subsamples of 10 females selected randomly from each sample. For each female, the diameter of 80 oöcytes was measured using a stereoscopic microscope with an ocular micrometer to the nearest 0.2 mm.

Sexual Maturity

In females, mean size at first sexual maturity (when 50% of females attain sexual maturity) was estimated by recording the CL of individuals with eggs and maturing ovaries. Ovaries of small females were also examined at the beginning of the reproductive season to identify immature crabs and those that presumably attained sexual maturity during the reproductive period.

Male gonad maturity was established on the basis of the presence of spermatophores in the deferent ducts. In regard to the size at first sexual

Table 1. Sampling dates, depth of capture, total number of males and females, sex ratio, and p values of G-test statistics.

Date	Depth(m)	N	♂/♀	p
10/13/97	86	285	5.48	0
10/15/97	64	51	7.50	<0.0001
10/16/97	54	251	0.76	0.0269
12/17/97	65	133	6.82	0
12/19/97	77	111	2.00	0.0004
12/19/97	60	185	4.44	0
05/12/98	73	382	1.26	0.0242
08/30/98	33	423	0.10	0
12/07/98	56	421	0.55	<0.0001
01/26/99	58	441	0.72	0.0007
02/28/99	44	467	0.34	0
04/02/99	70	342	1.30	0.0172
05/06/99	56	756	0.85	0.0241
06/19/99	53	380	1.57	<0.0001
06/27/99	38	298	0.69	0.0174
07/14/99	47	1067	1.76	0
08/31/99	46	340	0.53	<0.0001
09/26/99	63	310	1.38	0.0044
09/28/99	37	113	0.85	0.4519
10/26/99	55	70	0.89	0.6325
10/31/99	46	53	1.52	0
11/30/99	48	545	0.38	0
12/23/99	27	535	0.46	0
03/23/00	68	301	0.84	0.1194
04/19/00	58	182	1.36	0.0376
05/11/00	40	107	1.01	0.9230
06/20/00	62	278	0.94	0.6313
07/12/00	49	331	1.42	0.0014
08/07/00	62	324	0.95	0.6567
09/26/00	50	388	0.96	0.6846
10/23/00	66	455	1.08	0.4254
11/16/00	30	164	0.93	0.6394
12/14/00	27	368	0.35	0

maturity, a previous analysis performed on 323 males had shown that all individuals larger than 15 mm CL were mature. Therefore, the carapace length of smaller males was recorded from samples collected in July 1999 and March 2000 (N = 251).

Fecundity

Fecundity, defined as the number of eggs carried per female, was estimated in three sub-samples of ovigerous females of different sizes. Eggs were separated from the ovigerous setae after cutting the basis of each pleopod, in order to eliminate the weight of the appendages. Each ovigerous mass was put on a sieve and placed on blotting paper to remove excess water. The total egg mass weight (EMW) was measured for each female using an analytical balance to the nearest 0.1 mg. Three subsamples were separated on a microscope slide, weighed (w_i), and eggs in each subsample were counted. So, the total number of eggs was calculated for each sub-sample (e_i). For each female, fecundity (F) was obtained by the following formula:

$$F = \sum_{i=1}^{3} \left(\frac{EMW \cdot e_i}{w_i} \right) / 3$$

Number of eggs were counted directly under stereoscopic microscope when present in small numbers (< 400).

The size of the clutch was also analyzed macroscopically in relation to pleon storage capacity, and arbitrarily classified in the following categories: SC: small-sized clutch, with very few eggs, IC: medium-sized, incomplete clutch. CC: complete clutch.

Embryogenesis

Embryonic development was determined under stereoscopic microscope according to a previous study in *Pleuroncodes monodon* (Palma and Arana, 1997). A final stage involving partial or total larvae hatching was included.

A cytological analysis was done on eggs from 10 females collected in June 1999, to determine the presence of non-vitelline cells during the cleavage process. Eggs were embedded in paraffin, serially cut at a thickness

of 8 μm and stained with hematoxilin-eosin. Likewise, the eggs of 20 females with incomplete clutches collected in June and July 2002 were squashed and stained with Sudan Black B to identify vitelline granules (lipids) and non-stained, proliferative cells.

RESULTS

A total of 10,868 specimens of both sexes were collected from 40 fishing tows using bottom trawl nets (Table 1). No squat lobsters were captured from seven tows at depths below 80 m in June and July 1999, and from other two made in coastal waters between 25 and 30 m deep in March and April 2000. Of the total males collected, 1987 (38.7%) were found at depths below 60 m, and among these, 95.7 % were larger than 21 mm CL (N = 1902). Among females, 77.7% (n = 4451) were captured in waters below 60 m.

Dimorphism and Sex Proportion

In San Jorge Gulf, largest males were approximately 76 mm TL and 29.8 mm CL, whereas largest females were 71 mm TL and 25.3 mm CL. The overall sex proportion was 0.91, but there were variations in the predominance of males or females at different depths along the study period (Table 1). The G-statistics revealed highly significant differences in sex proportion between sixteen tows.

Ovarian Maturation and Egg-Laying

The presence of eggs on pleopods is a common indicator of fecundation and duration of embryo development, and also an indirect indicator of the ovarian regeneration period and resumption of oogenesis. Figure 2 shows the percentage of ovigerous females in relation to the total females collected during the monthly samplings between December 1998 and 2000. In both years, ovigerous females were present between June and late November or early December. There were two peaks of occurrence, a major one between July and August and a minor one between September and October. The sharp decline of ovigerous females in September was related to larval hatching. These results suggest that there were two cohorts of females at different maturation stages, or that some of the females laid twice during the reproductive season.
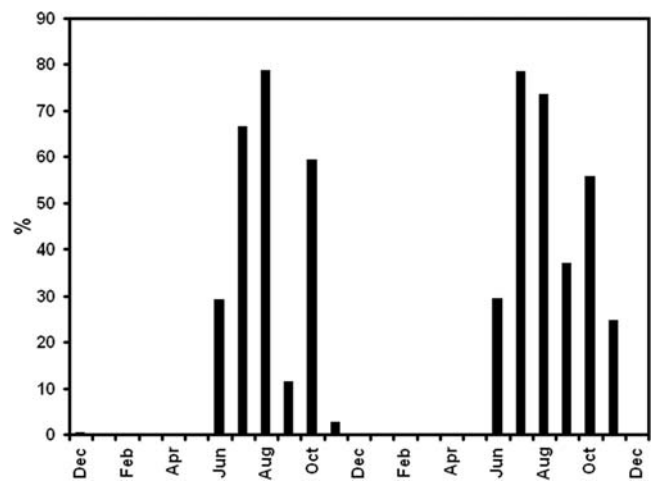

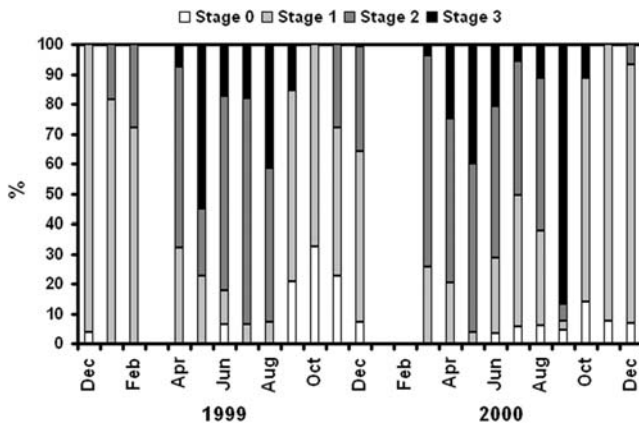Fig. 2. Percentage of ovigerous females between December 1998 and December 2000.

Fig. 3. Stages of ovary development during the monthly sampling periods.

The analysis of the ovary (Fig. 3) indicates that the secondary vitellogenesis started at the beginning of 1999 and that the gonad was fully mature between April and May (stage 3), However, a large proportion of females with developing ovaries were found in May (stages 1 and 2). In June, when egg extrusion was observed in part of the population, females showed a rapid regeneration of the ovary, as reflected by the lack of predominance of stage 1 and by the onset of vitellogenesis (stage 2). Oögenesis was here a short-term process that took place between June and August. In September, a second egg-laying event was observed in coincidence with a large proportion of females showing gonad regeneration, and females with no macroscopically detectable ovary. From October onwards, gametogenic activity resumed gradually and continued until May-June of the next year. In 2000, a first oöcyte extrusion was again recorded in June, but the second one occurred in October, followed by a gradual and steady resumption of gametogenic activity. However, some non-ovigerous females with mature ovaries and close to egg-extrusion were found too between June and August.

Post-ovigerous females of *M. gregaria* cannot be recognized after complete hatching because, in contrast to other decapod species, funicles and empty egg cases are not retained until the next moult, probably enabling free movement of the pleon for swimming. Oögoniae and previtellogenic oöcytes were always present in the ovaries. Measurements of vitellogenic oöcytes in developing ovaries of females sampled between December 1998 and December 1999 were as follows: the mean diameter of oöcytes ranged between 0.32 (SD: ± 0.08) mm and 0.85 (SD: ± 0.05) mm. A decrease in mean oöcyte diameters, which was only recorded in June and September, would indicate the occurrence of egg-laying events and resumption of gametogenic activity from September or October onwards.

Embryogenesis

The embryonic developmental stages observed for *M. gregaria* in San Jorge Gulf are described as follows:

Stage I: Egg dark green (orange in fixed specimens), spherical, yolk uniformly distributed, no visible structures or differentiated cells (no signs of embryonic development). Mean diameter: 0.64 mm. Mean volume: 0.12 (SD: ± 0.09) mm^3.

Stage II: Egg green. Beginning of cell differentiation, embryo appears as a transparent or whitish small body at one pole of the egg. Mean diameter: 0.77 mm. Mean volume: 0.19 (SD: ± 0.05) mm^3.

Stage III: Egg light green, less spherical in shape. Ocular pigmentation is visualized as a dark thin curve. Mean diameter: 0.84 mm. Mean volume: 0.21 (SD: ± 0.06) mm^3.

Stage IV: Egg whitish or yellowish, ovoid in shape. Red chromatophores scattered over the body. Well-developed eyes, black in colour. Mean diameter: 0.88 mm. Mean volume: 0.26 (SD: ± 0.08) mm^3.

Stage V: Embryos were close to hatching and some were recently hatched. This stage is characterized by incomplete clutches.

Figure 4 shows the stages described above and their percentage of occurrence in ovigerous females. In both years studied, eggs in stage I were present from June onwards; their percentage decreased thereafter until September or October, and then decreased again until November or December, according to the year.

Eggs laid in June completed development between August and September and those laid in September and October completed development in November and December, respectively. The duration of embryogenesis varied according to the time of oviposition. In 1999, laying started at the beginning of June, as determined by the appearance of embryos at stage II, and females with already hatched larvae were first seen at the end of August, which indicates that embryogenesis lasted approximately 90 days. The second egg-laying event took place in mid-September, ovigerous females carried embryos close to hatching in November, and non-ovigerous females were found in mid-December, indicating a developmental period of about 70-80 days. In 2000, a similar cycle was repeated with a massive egg-laying event in June and hatching in September and a second laying at early October and hatching in mid-December (Fig. 4).

Broods at different developmental stages were observed only in some of the females. The female of *M. gregaria* has no structures for spermatophore retention, and hence another mating is expected for a new oviposition. In most of the cases, eggs were at stage I and II, and their occurrence between July and August suggested the presence of incomplete clutches in part of the population.

Fecundation, Egg-Laying and Fecundity

Clutch size analysis indicated that the first clutch was generally small, suggesting that it would be completed during the reproductive season. Incomplete clutches were mainly found between June and July in both studied years and showed a tendency to disappear in the following samplings (Fig. 5).

In December 2000, there were a large proportion of females with embryos undergoing hatching. The absences of partial clutches during the second egg-laying event indicate that it lasts for a short period.

The analysis of fecundity was difficult due to the incomplete clutches laid in June and July and to the low number of
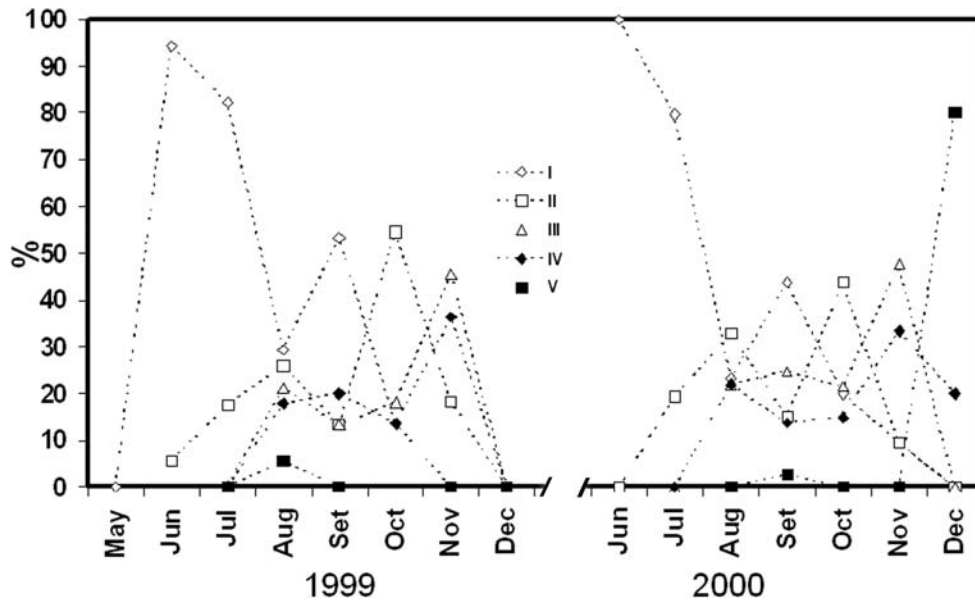
Fig. 4.   Stages of embryogenesis during the two-year study period.

eggs, which were barely visible and with no signs of development. No embryonic cells were observed in the cytological analysis of eggs made in 1999, suggesting that the initial egg deposition would only consist of non-fertilized eggs.

The Sudan Black B technique for lipids applied in eggs from females with incomplete clutches collected in June and July 2002 indicated the presence of embryonic cells in 16 of the clutches. In June 2000, the species showed a similar behaviour to that observed in June 1999. In July 2000,

females had complete or almost complete clutches, as observed for August 1999.

Figure 6 shows the results of the fecundity analysis conducted in 468 females, between June and October 1999. Fecundity varied between 5 and 7545 eggs/crab in females measuring between 22 and 19.7 mm CL, respectively. Seventy-one out of 184 females examined in June carried less than 100 eggs. In August, there were only 6 females with low fecundity values (F < 500).
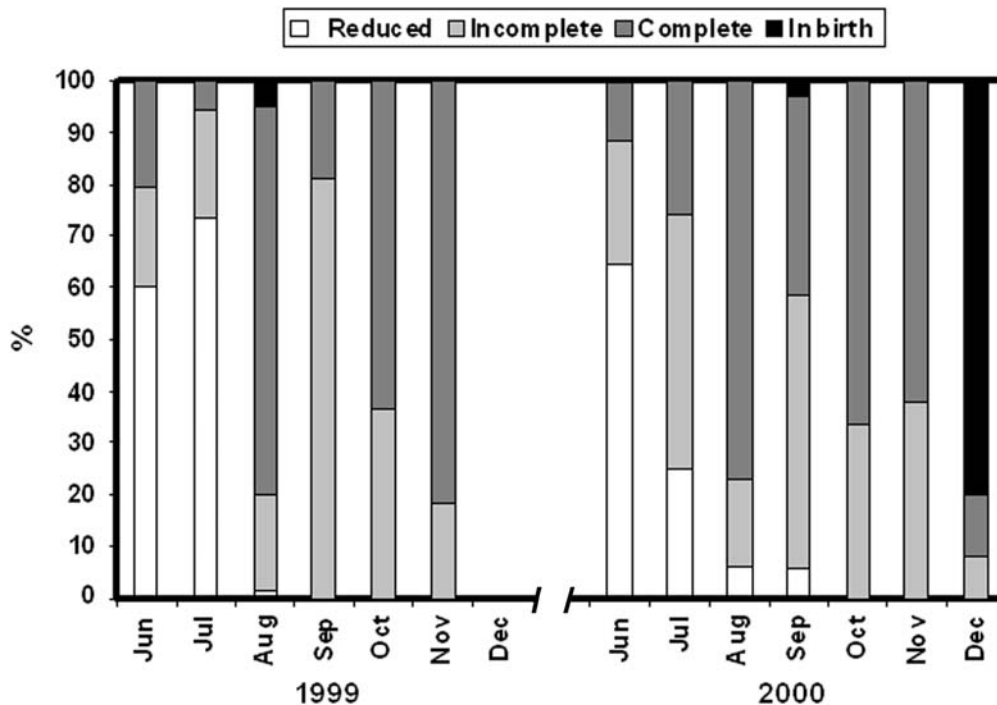

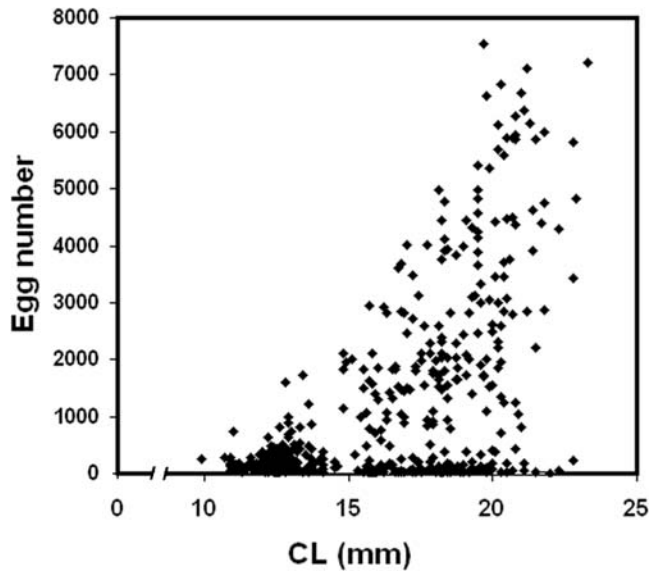Fig. 5.   Clutch sizes observed during the two-year study period.

Fig. 6.   Fecundity of females.

First Sexual Maturity

The study of the ovarian development allowed to estimate the size at which females attain maturity, and owing to the very extended reproductive period, to distinguish between non-ovigerous females laying eggs within the same period and those reaching maturity the following year.

In samples collected in June and July 1999 and June 2000, the relation between body size and the developmental stages of the ovary was analysed in females from 6.8 to 14 mm CL. Immature females were present until the interval 11-11.9 mm CL. Taking into account that females with ovaries in an advanced stage of development attain maturity within the reproductive period, the first sexual maturity of the female population in San Jorge Gulf is attained at a mean size of 9.3 mm CL (Fig. 7).

The analysis of the deferent ducts was made in males between 3.6 and 29 mm CL. Spermatophores were not found in individuals of up to 8.2 mm CL, above which all males were physiologically mature. The size for 50% physiological maturity was 7.4 mm CL.

DISCUSSION

Size represents the most conspicuous dimorphic feature of the mature squat lobster, with males bearing a larger carapace and chelipeds than females. In males, the chelipeds show a positive allometry with respect to body size, while in females the allometry is negative or isometric (Tapella et al., 2002b). Previous studies conducted in different populations of *M. gregaria* reported a male/female ratio of about 1:1. In the surroundings of Malvinas Is. and Patagonian coasts, Rayner (1935) reported a proportion of 1.033 (N = 457) and in the Magellan Strait a similar value was obtained (Rodríguez and Bahamonde, 1986). In the population of *M. gregaria* from San Jorge Gulf, overall sex proportion was 0.91 with a slight predominance of females, but differences in the proportion of males or females at different depths during different periods (Table 1) support the occurrence of migrations related to reproduction. During the reproductive period, larger males were very abundant in more coastal waters, but they disappeared at the beginning of October, after reproduction. Migrations towards shallow waters at the onset of the reproductive period have been mentioned for other galatheids such as *Pleuroncodes monodon* (Palma and Arana, 1997) and *Pleuroncodes planipes* (Serrano-Padilla and Aurioles-Gamboa, 1995). In the Magellan Strait, Rodríguez and Bahamonde, (1986) reported that the squat lobster population was found in
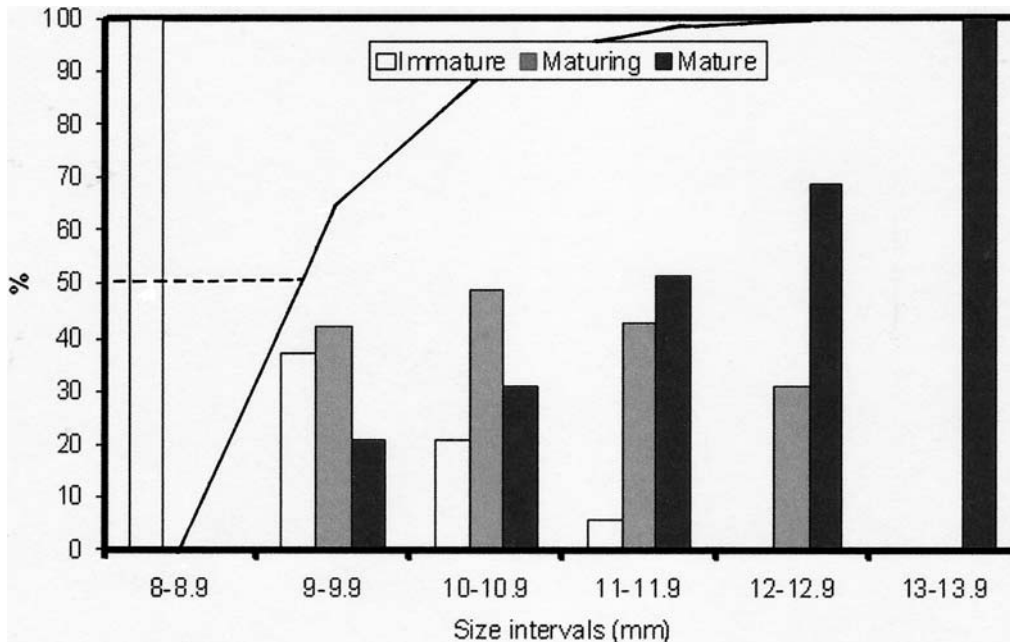

Fig. 7.   Relation between female reproductive stage and body size at the beginning of reproductive period. Line drawing indicates the amount of females with mature ovaries and with eggs on pleopods.

shallow waters in spring and moved to deeper waters in summer. According to the authors, this bathymetric migration takes place after moult and mating and may account for the small number of squat lobsters in shallow waters during March and April. In San Jorge Gulf, vertical migrations are suggested by increased captures of large males and females in shallow waters during June and July, in coincidence with the reproductive period, and by the absence of individuals at depths below 80 m. This behaviour might increase the probability of encounters between adult males and females, and would lead to the mating of small females, which reach first sexual maturity at 9-12 mm CL and are present in coastal waters from June and August (see Fig. 3).

Migration to deep water and away from the coast during summer would be indicated by the lack of squat lobsters in two coastal tows, but further data are needed to confirm this behaviour. However, if that were the case, such migration would not take place after mating, but after larval hatching and moulting, and would represent a dispersal movement.

All studied species of the genus *Munida* exhibit an annual reproductive cycle. In females, fecundation is followed by breeding and the moult starts after larval hatching (Wenner, 1982; Zeldis, 1985; Hartnoll et al., 1992; Sanz-Brau et al., 1998 and Tapella et al., 2002b). The earliest data on the reproduction of the squat lobster in Malvinas Is. and Patagonian waters were provided by Rayner (1935). This author inferred the occurrence of larval hatching in March, but the findings of well-developed embryos in females collected during September and October indicated that they were close to hatching. Data obtained from isolated samplings performed during spring and autumn in the Magellan Strait showed larval hatching between October and January, suggesting breeding of embryos between April and November (Rodríguez and Bahamonde, 1986). A recent study conducted in the Beagle Channel documented that the reproductive cycle started in May, with the occurrence of ovigerous females until November (Tapella et al., 2002b). Although the squat lobster population from San Jorge Gulf also showed an annual reproductive cycle, it differed from those described for the Magellan Strait (Rodríguez and Bahamonde, 1986) and the Beagle Channel.

In San Jorge Gulf, there are two major egg-laying periods, the first one between June and August that probably includes polyandry, and the second one in September or early October, which seems to be a single event. Ovary development of females laying from June to early July coincides with embryogenesis. Therefore, ovigerous females with mature or almost mature ovaries (stage 3) occur simultaneously with late embryonary stages (stages III and IV). Thus, they are able to mate immediately after larval hatching. In the Beagle Channel, females had partial clutches of about 300 eggs at the beginning of the reproductive cycle, between May and June 1998 and 1999, with lower values of fecundity in May (98.1 and 82% for each year, respectively), and higher values in June (Tapella et al., 2002b). These authors regarded the occurrence of incomplete clutches as puzzling, and speculated that one female would copulate with many males, and that partial broods may constitute a chemical signal for male attraction for mating.

In San Jorge Gulf, the presence of non-fertilized eggs in initial partial clutches may serve as an attractant signal for adult males that are found in deeper waters and away from the coast. The presence of non-embryonated eggs in incomplete clutches represents a clear evidence of this phenomenon. Embryos from the first egg-laying hatch between late August and late September, whereas those laid between late September and early October hatch in late November or December. These processes would account for the occurrence of ovigerous females between June and November or December.

Temperature is the main factor influencing the metabolism of marine Crustacea. It acts at any stage of the life cycle and has notorious effects on both the reproductive organs and embryonic development. The differences in temperature between Beagle Channel and San Jorge Gulf range from 4 to 8°C, and even more. As a result, *M. gregaria* inhabiting the gulf shows two spawnings within the same reproductive period. A similar finding has been reported for *Carcinus maenas*, with two or three spawnings in the same intermolt in Belgium (d'Udekem d'Acoz, 19939) and only one in Norway (Van der Meeren, 1992), Maine, USA (Berryl, 1982) and San Jorge Gulf (Vinuesa, in press), in colder waters.

M. gregaria from Beagle Channel has only one spawning time, and its eggs are larger and contain more organic matter than those of *M. gregaria* from San Jorge Gulf (Tapella et al., 2005). The authors conclude that larvae birth coincides with plankton blooms. On the other hand, at these latitudes larvae do not require of a high energy content for survival, because of large food availability.

During 2004, the by-catch of *M. gregaria* by Patagonian fisheries was calculated to be about 2000 ton (E. Godelman, personal communication, 2006). This fact makes it hard to think of a monospecific fishery of this species. In order to make better use of this resource, it would be desirable to carry out studies focused on the utilization of the by-catch and to stop discards at sea, as currently performed.

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