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"GREGARIA" TO "SUBRUGOSA," THAT IS THE QUESTION: SHAPE CHANGES UNDER LABORATORY CONDITIONS IN THE PELAGIC MORPHOTYPE OF THE SQUAT LOBSTER *MUNIDA GREGARIA* (FABRICIUS, 1793) (DECAPODA: ANOMURA: MUNIDIDAE)

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ABSTRACT

Munida gregaria (Fabricius, 1793) is one of the few species of squat lobsters (Anomura, Munididae) with two morphotypes, one with a post-metamorphic pelagic phase that eventually settles to the bottom ("gregaria") and a second that is exclusively benthic ("subrugosa"). This study provides the first information on the growth of the pelagic morphotype of *M. gregaria* and its relation with changes in morphology in southern South America. Specifically, we studied growth at molt and duration of the intermolt period in the laboratory and analyzed changes in morphology through growth by means of geometric morphometry techniques. Fifty squat lobsters were sampled from shoals in the Beagle Channel, Tierra del Fuego and kept in individual flasks during 29 months. The carapace of each exuvia was photographed and analyzed using 2D geometric morphometry analysis. Changes in shape associated with growth in the gregaria morphotype were gradual, adjusted to a linear function, and occurred mainly in the anterior portion of the carapace. After two years and at least eight molts, however, individuals of the gregaria morphotype were still clearly distinguishable from a typical individual of the subrugosa morphotype. These results suggests that once sexual maturity is attained, pelagic individuals of *M. gregaria* do not transform from gregaria to subrugosa, and retain the gregaria morphology.

KEY WORDS: Beagle Channel, geometric morphometry, swarms, Tierra del Fuego

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INTRODUCTION

The squat lobsters *Munida gregaria* (Fabricius, 1793) and *M. subrugosa* (White, 1847) (family Munididae) have been considered two different species based on their morphology (e.g., Boschi et al., 1992; Hendrickx, 2000). The absence of reciprocal monophyly for four genes (16S, COI, ND1, ITS1; Pérez-Barros et al., 2008), however, supported their synonimy (Baba et al., 2008). Moreover, there was no evidence of behavioral prezygotic barriers to gene flow (Pérez-Barros et al., 2011), of intrinsic postzygotic isolation (measured as the number of hatched larvae from homo- and heterotypic mating couples) (Pérez-Barros, 2008), or of trophic polymorphism (Pérez-Barros et al., 2010) between both morphotypes (former species).

Munida gregaria is the only recorded species of Munididae with two morphotypes, one with a post-metamorphic pelagic phase that eventually becomes benthic, and a second with an exclusively benthic one. Both morphotypes have been referred to by the names of both former species, "gregaria" and "subrugosa," respectively, hereafter gregaria and subrugosa. Several hypotheses have been proposed regarding the relationship of these morphotypes (Thomson, 1899; Williams, 1973; Bacardit, 1986; Chilton, 1909; Pérez-Barros et al., 2011), yet the mechanisms involved in their origin and maintenance still need to be elucidated.

The idea that the gregaria morphotype of *M. gregaria* is a juvenile (immature) morphotype and that the subrugosa morphotype is the adult has been discussed by several authors (Thomson, 1899; Chilton, 1909) and suggested by Miers (1876). Hutton (1878), however, was the first to point out that gregaria had a pelagic habit while subrugosa was benthic. Hutton argued that the difference in habitat, added to the occurrence of small individuals with the specific morphology of the subrugosa maxilliped, gave support to the hypothesis that they were dealing with two different species (Chilton, 1909). Notwithstanding, Thomson (1899), after studying the maxillipeds of both morphotypes determined that the differences were not enough to consider them

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as different species, and that he would rather treat gregaria as a stage in the development of subrugosa (Thomson, 1899; Chilton, 1909). Chilton (1909) proposed that the species had two morphotypes, and that under certain circumstances, e.g., absence of a suitable substrate for settlement, the immature pelagic morphology could extend in time, and that individuals could even become sexually mature without losing the immature gregaria characters. If environmental conditions are adequate for settlement, individuals would settle to the bottom, and after successive molts the morphology of their maxillipeds, a diagnostic character of the two morphotypes according to Chilton (1909), will resemble those of the subrugosa, i.e. short, less foliaceous, and in-folded.

Williams (1973: 209) studied the effect of the environment on the morphology of *M. gregaria* and concluded that the characters used to distinguish both former species (*Munida gregaria* and *M. subrugosa*) could be altered by a change of environment, “a change from a pelagic existence to the benthic one is accompanied by the alteration of existing ‘gregaria’ features to ‘subrugosa’ features.” According to these results, all recently metamorphosed juveniles were pelagic, having the morphology of gregaria, and during their development, after their settlement to the bottom, changed to the morphology of subrugosa (e.g., Williams, 1980; Zeldis, 1985). Ecological evidence around southern South America nevertheless challenges her observations and do not support such “transformation” (Pérez-Barros et al., 2008), i.e. the existence of two morphologically distinguishable megalopae in the plankton (Bacardit, 1986; Varisco, 2012), as well as the occurrence of small benthic specimens of the subrugosa morphotype and large benthic specimens of the gregaria morphotype (Tapella, 2002). Tapella and Lovrich (2006) showed that for benthic animals >12 mm carapace length ten morphological characters distinguish both morphotypes. The anterior carapace and the posterior portion of the rostrum are wider and the carapace and rostrum are shorter in gregaria than in subrugosa.

In order to test whether carapace shape changes of *M. gregaria* are related to sexual maturity, the individual variation in size and shape at different stages of development was assessed. We used geometric morphometry following the general approach of Rojas-Quiroga (2013) in recently settled, wild individuals (i.e. juveniles), tracked their molt cycle, and used the exuviae of reared specimens as a singular independent datum to test for changes in shape and size of the carapaces. We provide evidence that *Munida gregaria* has two morphotypes and hypothesize that there is no change in the morphology from one morphotype to another.

MATERIALS AND METHODS

Collection and Rearing of Individuals

Samples of shoaling individuals were taken with a nektonic net with a mouth diameter and 10 mm mesh size in Bahía Ushuaia, Beagle Channel, Tierra del Fuego (54°51′S 68°15′W) during May 2007. Nektonic hauls were carried out at different depths (10-25 m) for several minutes and squat lobsters were transported to the Centro Austral de Investigaciones Científicas, transferred to individual plastic flasks (1 l) and kept during 29 months (May 2007-October 2009) with aerated seawater at 8 ± 0.5°C with an artificial photoperiod of 12:12 h (light/darkness) and salinity of 30 psu. Water was changed every two days and individuals (21 females, 29 males; survival rate 26% at the end of the experiment) were fed three times a week with Tetra Color granules *ad libitum*. The presence of exuviae was checked daily, and if present, they were removed from the flask and fixed in 6% formalin sea-water. The carapace of the exuvia of each individual was carefully separated and photographed (see below) and images were used for later determinations of body size and geometric morphometry. Because some carapaces deteriorated during some molt events, the number of exuviae available during the experiment varied from 5 to 11 for each individual.

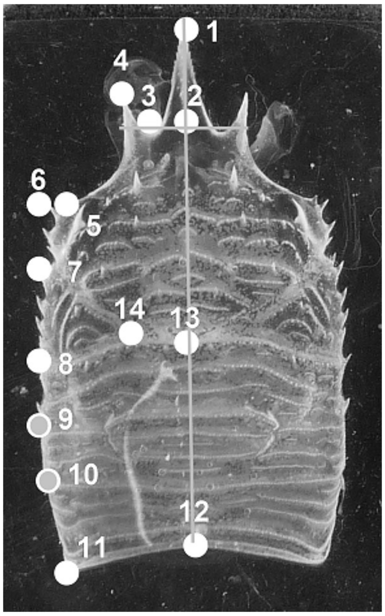

Fig. 1. Landmark configuration on the exuvia of the gregaria morphotype of *Munida gregaria*. Full and empty circles represent anatomical landmarks and semilandmarks, respectively.

Data Collection and Image Analysis

A total of 315 carapace exuviae belonging to 43 molting specimens of the gregaria morphotype were used in the study (mean initial size 8.99 mm carapace length (CL); size range 7.44-10.95 mm CL. The CL, used as a standard measure of the body size, was measured as the straight line from the eye-orbit (landmark 3 in Fig. 1) to the midpoint of the posterior carapace (landmark 12 in Fig. 1) using tools of the Image Pro Plus 6.0 software. The carapaces of exuviae (henceforth exuviae) were photographed using a calibrated digital Panasonic DMC-FZ35 camera with 12 megapixels and 18× optical zoom, according to the standard procedure reported by Rojas-Quiroga (2013). Each exuvia was located in the center of the image (with most of the image margins not occupied by the exuvia) to avoid marginal distortions. In order to minimize the light reflection, each exuvia was submerged in glycerin in a Petri dish and photographed setting the picture plane parallel to its coronal plane (Fig. 1). Each image included a grid of known dimensions and was scaled and digitalized using tpsUtil and tpsDig software (Rohlf, 2012, 2013). The shape and size of exuviae were analyzed using 2D geometric morphometric analysis (Bookstein, 1991). To scrutinize the existence of a transformation from the gregaria to the typical subrugosa morphotype, carapaces of 22 individuals of the subrugosa morphotype (18.7-26.7 mm CL), also caught in the Beagle Channel, were photographed.

Molt Increment

The carapace lengths of successive exuviae corresponding to a molt event were considered pre-molt and post-molt sizes, respectively. For individuals that molted during all the study period both the molt increment and the percentage increment were estimated. Molt increment was assessed by means of Hiatt model (Hiatt, 1948) and expressed as follows: $L_{t+1} = aL_t + b$, where L_t is the pre-molt CL at stage t, L_{t+1} is post-molt CL at the following stage, a is the slope and b is the y-intercept of the regression line. The percentage increment was estimated as:

$$(\text{post-molt CL} - \text{pre-molt CL}) \times \text{pre-molt CL}^{-1} \times 100.$$

Morphometric and Statistical Analyses

Given that deviations from symmetry were discarded in a previous analysis, only the left side of each exuviae was digitized (see Rufino et al., 2004). In consequence, a landmark configuration of twelve landmarks and two semi-landmarks (Fig. 1) was used to capture the general shape of each exuviae. This landmark configuration allowed both, to apply simpler statistical analyses and to compare with the shape used previously (e.g. Rojas Quiroga, 2013). Semi-landmarks were slid according to a sliding algorithm that minimizes the bending energy (Gunz et al., 2005) in tpsRelw software (Rohlf, 2010). Landmarks 1, 4, and 6 marked the top of the rostrum, postocular spine, and anterolateral spine, respectively. Landmark 2 was located in the intersection of the midline and the line that passes through the valleys formed between the rostrum and postocular spines; landmarks 3 and 5 in the two valleys formed between the rostrum and postocular spine and between the postocular spine and ocular zone, respectively; and marks 7 and 8 at the junction between cervical and postcervical grooves; semi-landmarks 9 and 10 between landmarks 8 and 11; landmark 11 marked the lateral posterior extreme of the carapace; landmarks 12 and 13 were placed at the intersection of the midline and the posterior extreme and the cervical groove, respectively and landmark 14 was placed in the anteriormost point of the intersection between cervical and post-cervical grooves (Fig. 1).

A Generalized Procrustes Analysis was performed to obtain pure-shape information (procrustes coordinates; with translation, rotation and scale effects removed) and size information was conserved in the Centroid Size (CS) value, which was computed as the square root of the sum of the squares of the distances from all landmarks configurations to their centroid, using tpsRelw software (Rohlf, 2010).

The changes in shape along with the size changes (growth) of exuviae were evaluated by means of a multivariate regression of procrustes coordinates on log-transformed centroid size ($\ln \mathrm{CS}$). The strength of association was assessed by the percentage of shape variance explained by size, whereas the statistical significance was tested with permutation test against the null hypothesis of independence (Good, 2000) using MorphoJ software (Klingenberg, 2011). The regression routine computes a regression score for each exuvia and the scatterplot of the regression scores against the log CS provides a graphical means to examine the shape change as unit of size change (Drake and Klingenberg, 2008). Afterwards, the multivariate regression was replicated by adding 22 exuviae of adult specimens of the subrugosa morphotype. In this case, exuviae were assumed as a symmetric object (symmetry was not tested) and were included in order to assess the growth change (shape vs. size) of both morphotypes jointly.

RESULTS

Growth

The relationship between pre-molt and post-molt size was similar in both sexes. Significant linear relationships of positive slopes between pre- and post-molt sizes were determined for each sex (Table 1, Fig. 2). The mean of molt events of *Munida gregaria* was similar between males (10.5 ± 2.94 molt events) and females (10.6 ± 4.36 molt events) and at the end of the experiment both sexes reached similar sizes: 16.31 and 16.51 mm CL for males and females, respectively.

Individuals of *M. gregaria* that completed all molt events during the study period showed similar growth rates (Fig. 3, Table 2). The percentage increment showed a tendency to decrease towards the end of the experiment with a mean of 7.37 ± 3.74 and 4.38 ± 2.26 at the beginning and end of the study, respectively. The intermolt period increased from the first molting event (44 ± 13.9 days) towards the last molts (144.4 ± 44.9 days) (Fig. 4). For all individuals and molts, the mean intermolt period was 85.8 ± 35.4 days (Fig. 4).

Morphological Changes

In both morphotype regressions, changes in shape were observed with increase in individual size (Fig. 5). These patterns indicate a relationship between shape variables and growth (Fig. 5). The multivariate regression of the exuviae shape on the size of the gregaria morphotype was highly significant after 10,000 permutations ($P < 0.001$) and allometry accounted for 23.58% of the total shape variation.

Changes in shape associated with growth in gregaria were gradual, adjusted to a linear function, and occurred mainly in the anterior zone (Fig. 6). These changes included an elongation of the postocular and anterolateral spines as well as a narrowing and deepening of the valley formed between the rostrum and the postocular spine. A subtle difference in the posterior region of the carapace was also observed, which became wider with increasing size. Throughout growth, the shape of the gregaria morphotype showed a tendency to approach the shape of an adult of the subrugosa morphotype (Fig. 5). After two years and at least eight molts, however, individuals of gregaria were still clearly distinguishable from a typical individual of the subrugosa morphotype (Fig. 7).

The shape of the average subrugosa had a narrower ocular orbit than the average gregaria, approaching the shape of both the postocular and anterolateral spines (Fig. 8). Moreover, the depression formed between the rostrum and the postocular spine was deeper in gregaria than in subrugosa. The posterior area of the cephalothorax was proportionally wider in gregaria than in subrugosa, with a displacement of landmark 12 (medium carapace posterior point) towards the anterior region.

DISCUSSION

Results of this study provide the first information on growth of the pelagic morphotype of *Munida gregaria* and its relation with changes in morphology in southern South America. Studies on absolute growth of squat lobsters are limited (Gramitto and Froglia, 1998; Company and Sardà, 2000; Tapella, 2002; Arancibia et al., 2005; Varisco and Vinuesa, 2015) and our study is the first that links data on growth with changes in morphology in Munididae. The patterns observed on the Hiatt lines (Fig. 2, Tables 1 and 2) and the relationship between post-molt and duration of the intermolt period (Fig. 4) showed that individual growth follows the general pattern for crustacean decapods: a lengthening of the intermolt period and a decreasing of the increment at molt (Hartnoll, 1982). Our results provide evidence that changes in morphology are gradual but that

Table 1. Growth of the gregaria morphotype of *Munida gregaria* expressed as Hiatt functions for males and females.

	Regression equation	n	r^2	F	P
Females	Post-molt LC = 0.98 pre-molt LC + 1.08	75	0.97	2603.65	<0.0001
Males	Post-molt LC = 0.85 pre-molt LC + 2.55	77	0.96	1651.98	<0.0001

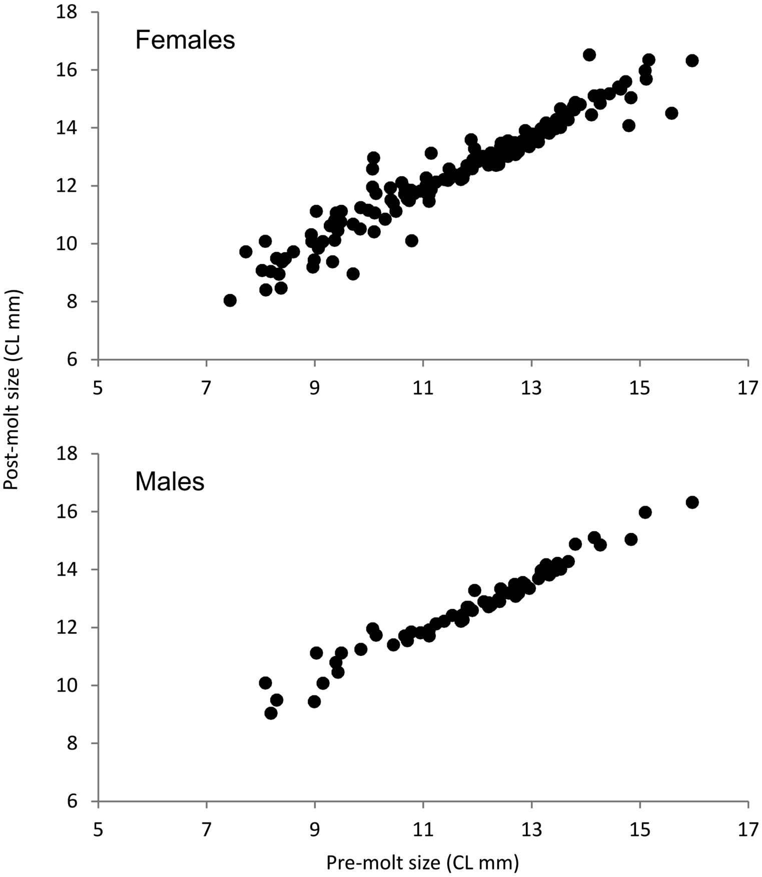

Fig. 2. Growth in the pelagic morphotype of *Munida gregaria* as Hiatt functions.

there is no transformation from one morphotype to another throughout at least eight molts and 30 months.

Most individuals attained the size of gonadal maturity, at 8.0 and 9.9 mm CL in males and females, respectively (Tapella et al., 2002) at the start of our experiment or during it. After reaching sexual maturity, energy allocation changes and part of the energy assigned to growth is diverted to reproduction with the consequent marked decrease in the percent size increment per molt. As reported by Chang et al. (2012) confinement and time of captivity likely affected growth of *M. gregaria* during our experiment still this effect would have been similar in all individuals at the same experimental conditions. These results should therefore be further used with caution. Notwithstanding, the experiment

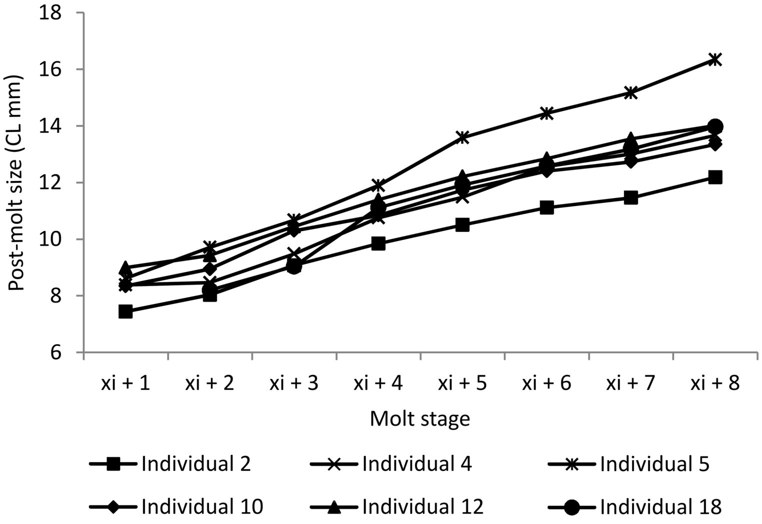

Fig. 3. Individual growth of the specimens that molted each molt period. X_i is the molt stage at the beginning of the experiment.

Table 2. Growth of the gregaria morphotype of *Munida gregaria* expressed as Hiatt functions for individuals that completed all molt events during the study period. CL denotes confidence limits of the slope.

Individual	Regression equation	r^2	*F*	*P*	CL (5%)	CL (95%)
2	Post-molt LC = 0.94 pre-molt LC + 1.3	0.98	302.46	<0.0001	0.80	1.07
4	Post-molt LC = 0.99 pre-molt LC + 0.87	0.95	102.77	<0.001	0.74	1.24
5	Post-molt LC = 0.97 pre-molt LC + 1.42	0.98	315.61	<0.0001	0.83	1.11
10	Post-molt LC = 0.90 pre-molt LC + 1.79	0.97	141.48	<0.001	0.71	1.09
12	Post-molt LC = 0.96 pre-molt LC + 1.12	0.98	307.33	<0.0001	0.82	1.10
18	Post-molt LC = 0.86 pre-molt LC + 2.42	0.99	380.58	<0.0001	0.74	0.97
21	Post-molt LC = 0.87 pre-molt LC + 2.54	0.98	203.91	<0.0001	0.72	1.03

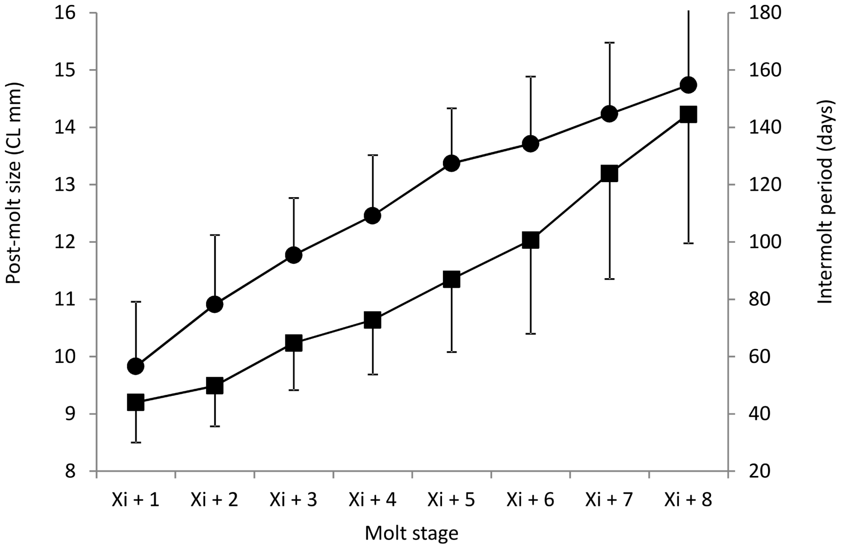

Fig. 4. Duration of intermolt period (squares) of *Munida gregaria* and its relationship with post-molt size (circles). Bars denote standard deviation. X_i is the molt stage at the beginning of the experiment.

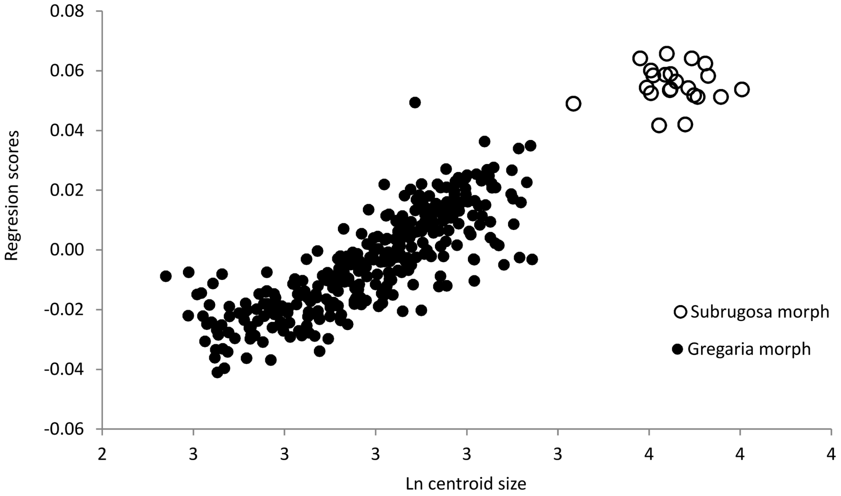

Fig. 5. Multivariate regression of procrustes coordinates (shape variables) on ln-transformed centroid size.

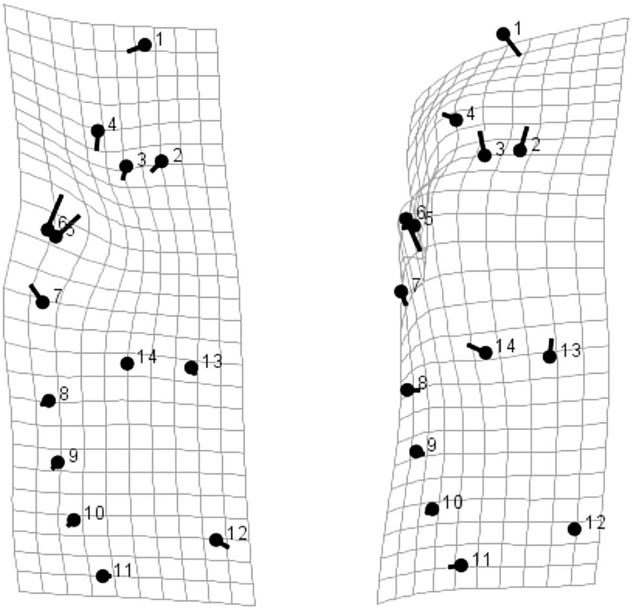

Fig. 6. Changes in shape along the growth of the gregaria morphotype of *Munida gregaria*. Transformation grids of extreme sizes. Left: smallest exuviae (7.44 mm CL), rigth: biggest exuviae (16.32 mm CL). Numbers denote landmarks. For a clearer visualization, the size of grids was doubled.

shows that the duration of the intermolt period increased with the number of molts and with post-molt size.

Some changes in shape were observed through the period in the anterior region of the carapace of the pelagic individuals of *M. gregaria*. At the end of the experiment, after 30 months and eight molt cycles, individuals had nevertheless retained the typical morphology of gregaria. These changes in shape seemed to approach the subrugosa morphotype but did not match the subrugosa morphology at the end of the experiment (Fig. 7). Rojas-Quiroga (2013) studied the ontogenetic trajectories of gregaria and subrugosa morphotypes and concluded that shapes tend to converge to a single morphotype, but the difference in size allows distinguishing the two morphotypes. Rojas-Quiroga (2013) used different individuals of different sizes, whereas the present study followed the ontogenetic trajectory of the very same individuals.

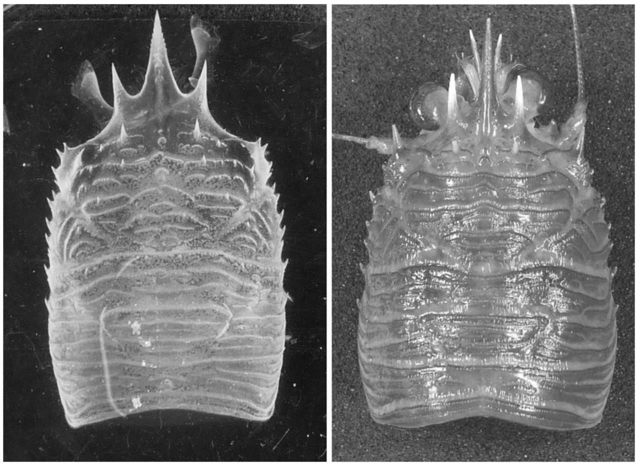

Fig. 7. Exuviae of the gregaria morphotype of *Munida gregaria* at the end of the experiment (left). Typical carapace of the subrugosa morphotype of *Munida gregaria* (right).

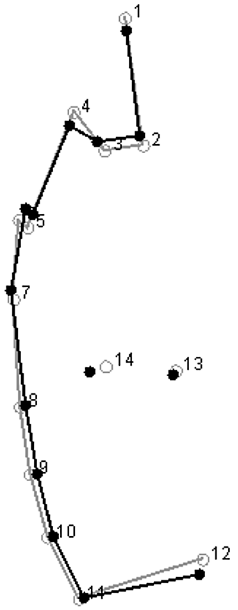

Fig. 8. Average shape of the gregaria morphotype of *Munida gregaria* (grey) and of the subrugosa morphotype (black). Numbers denote landmarks.

These results and the observation that during the studied period all individuals of *M. gregaria* probably reached the size of gonadal maturity suggests that once the sexual maturity is attained, pelagic individuals of *M. gregaria* do not transform from gregaria to subrugosa, but retain the gregaria morphology. The absence of a transformation nevertheless does not limit the chance of settlement of these individuals as part of benthic community after molting to maturity (e.g., Tapella, 2002; Ravalli et al., 2012). In this context, transformation from gregaria to subrugosa does not occur after molt to maturity.

The processes that trigger the occurrence of two morphotypes in *M. gregaria* remain unknown. The existence of megalopae of the two morphotypes (Rayner, 1935; Roberts, 1973; Varisco, 2012) and the information provided by our study suggest that future studies should be focused on late zoeal development since the degree of morphological variability increases in the late larval stages (Anger, 2001). The presence and higher abundance of the megalopae of gregaria than that of subrugosa found in the Gulf of San Jorge, Argentina (46°12′S 67°29′O) (Varisco, 2012) was coincidental with and attributed to an increase in primary production (Varisco and Vinuesa, 2010). This high abundance was also concurrent with the increase of both, the abundance of gregaria morphotype in the benthos (Ravalli et al., 2012) and the occurrence of pelagic swarms of *M. gregaria* in the Patagonian continental shelf between 42 and 55°S (Varisco and Vinuesa, 2010; Diez et al., 2012, in press). A match/mismatch between *Munida gregaria* larval supply and food quality rather than food quantity could perhaps be related to the dominance of either morphotype (Toupoint et al., 2012). We hypothesize that the occurrence of different morphotypes is a complex process that is probably governed by demographic and environmental factors acting together, along with the ability of this species to exploit resources in both, the water column and the benthic environment.

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