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Morphological differences between '*subrugosa*' and '*gregaria*' morphs of adult *Munida* (Decapoda: Anomura: Galatheidae) from the Beagle Channel, southern South America

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Munida subrugosa and *M. gregaria* are very abundant in the southern hemisphere, especially off New Zealand and South America. The specific identity of both species is still controversial and accurate identification is needed for conservation or ecological purposes. In this study we used univariate and multivariate methods to determine the morphological differences between both species/morphs. Analyses of covariance of ten morphological variables regressed individually on the carapace length demonstrated that the carapace (including rostrum) and eyestalks (EL) were longer, and the anterior carapace (ACW), the rostrum basis (RBW), and dactylus (DaW) and propodus (PW) of the third maxilliped were wider in *M. gregaria* than in *M. subrugosa*. In contrast, the carapace, mandible and eyestalk were wider and the rostrum was longer in *M. subrugosa* compared to *M. gregaria*. A stepwise discriminant analysis found that five body measurements namely DaW, EL, PW, RBW and ACW, were useful to discriminate between both species/morphs. The difference between the two discriminant functions provides an objective decision rule for the classification of both species/morphs. We also present the linear relationships of wet and dry masses on size, for use in biomass estimations of *Munida* spp. as prey.

INTRODUCTION

In the southern hemisphere, *Munida subrugosa* (White, 1847) and *M. gregaria* (Fabricius, 1793) occur in great abundance, mainly in the continental shelves off New Zealand and southern South America (Matthews, 1932; Rayner, 1935; Zeldis & Jillett, 1982; Zeldis, 1985). In southern South America *Munida* spp. may constitute ~50% of the macrobenthic biomass (Arntz & Gorny, 1996) and represent the most abundant decapods in coastal waters off Tierra del Fuego (~55°S 67°W), occurring at densities as high as 27 individuals$\cdot$m^{-2} (Gutt et al., 1999). In benthic samples from the Beagle Channel, *Munida* spp. represent ~90% of decapods (Pérez Barros et al., 2004) and *M. subrugosa* normally outnumbers *M. gregaria* (Tapella et al., 2002a). High densities and multiple commercial applications of related galatheids, *Pleuroncoden monodon* (H. Milne-Edwards, 1837), *P. planipes* Stimpson, 1860, and *Cervimunida johni* Porter (1903) (see Aurioles Gamboa & Balart, 1995) suggest that these species also have the potential to become economically important (Rayner, 1935; Lovrich et al., 1998).

The specific identity of both species is still controversial. Williams (1973, 1980) reprised the original ideas of Lagerberg (1906) and Chilton (1909), and suggested that off New Zealand *M. subrugosa* is the benthic morph of the *M. gregaria*. '*Munida gregaria* is the juvenile pelagic form that after ca. 4 molts acquires the morphological characteristics of *M. subrugosa*' (Williams, 1980). The abundance of food at the surface and the availability of a suitable bottom would determine the duration that these animals remain pelagic (Chilton, 1909). However, in southern South America both morphological forms have been considered as two distinct species, since they have subtle characteristic differences (Rayner, 1935; Retamal, 1981, 2000; Boschi et al., 1992). Moreover, in the Beagle Channel adults of both morphological forms have been caught in benthic samples (Tapella, 2002), whereas it is very rare to find such pelagic juvenile aggregations as occur in coastal waters off south-eastern New Zealand (Jillett & Zeldis, 1985). Since the specific identity of both species is still controversial, hereafter we will refer both species as species/morphs.

Both species/morphs are prey of a wide variety of top predators (see Romero, 2003 for a review). In the Atlantic continental shelf, *Munida* spp. are preyed on by several particularly interesting species, which are either a target of fisheries (e.g. king crabs, squid, fish) or have special conservation value (e.g. whales, albatrosses, penguins). In some cases *Munida* spp. constitute the main food item (e.g. Sanchez & Prensky, 1996; Arata & Xavier, 2003; Gibbons et al., 2003; Phillips et al., 2003). Consequently, studies on predator diet may request accurate specific identification, sizing and estimation of prey mass in stomach contents. However, specific identification of *Munida* spp. as prey may constitute a difficult task, and several authors do not identify correctly any of both species/morphs. Since in the continental shelves *M. subrugosa* and *M. gregaria* are reported to have different habits—benthic

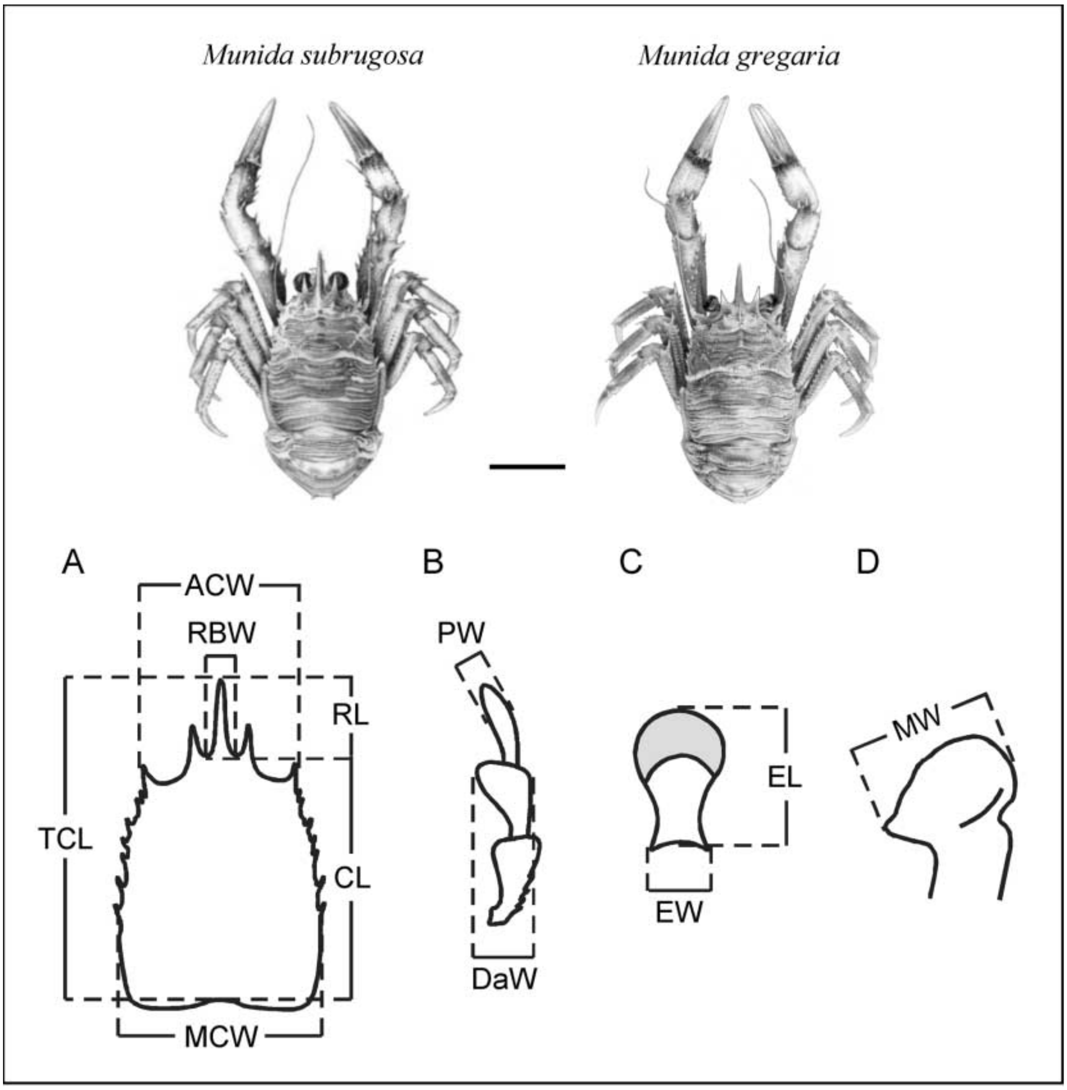

Figure 1. General aspect of *Munida subrugosa* and *M. gregaria* (above). Measurements made on (A) the carapace; (B) the third maxilliped; (C) the eyestalk; and (D) mandible. TCL, total carapace length; CL, carapace length; ACW, anterior carapace width; MCW, maximum carapace width; RL, rostrum length; RBW, rostrum basis width; DaW, dactylopodus width; PW, propodus width; EL, eyestalk length; EW, eyestalk width; MW, mandible width. Measurements were drawn on *M. subrugosa*. For the above drawings. Scale bar: 1 cm.

or pelagic, respectively (e.g. Matthews, 1932; Williams 1980)—accurate identification tools are needed to elucidate predator feeding habits, e.g. diving depths or foraging strategies.

In this paper we quantified the morphological differences between both species/morphs (*Munida subrugosa* and *M. gregaria*) and provide a discriminant function that allows the identification of each species/morph from easy-to-take morphometric measurements. Furthermore, we offer size–weight relationships that permit biomass estimations.

MATERIALS AND METHODS

Study site and sampling

Adult specimens of *Munida subrugosa* and *M. gregaria* were collected from the Beagle Channel, near Ushuaia (55°S 68°W) during May 1999, and February and March 2000. Samples were taken at depths from 10 to 42 m with an epibenthic trawl of 1.7 m mouth width and 10 mm mesh size net (Tapella et al., 2002b). After sampling, all crabs were fixed in 4% buffered formalin seawater, except a random sub-sample of ~110 crabs which were taken alive to the laboratory. Crabs were sorted by species/morph and sex. Species/morph classifications were based on the following characteristics: (1) wider rostrum base in *M. gregaria*; (2) longer ocular peduncles in *M. gregaria*; and (3) meropodite of the third maxilliped in *M. subrugosa* bears a distal spine (Retamal, 1981). Sex determination was based on the presence and shape of pleopods. In males the first two pairs of pleopods are modified to form gonopods, the remaining three pairs are small and flap-like. In females the first pair is absent and the remaining four pairs are elongated and with long setae for egg-carrying. All animals were gonadally mature, i.e. males and females were >8.0 and >9.9 mm carapace length (CL), respectively (Tapella et al., 2002b).

Table 1. *Regressions of body measurements on the crab sizes (carapace length) of 57* Munida subrugosa *(12.0–28.6 mm CL) and 55* M. gregaria *(13.6–28.2 mm CL) from the Beagle Channel, Argentina.*

Munida subrugosa (*Ms*)			*Munida gregaria* (*Mg*)			F slopes	F ordinates
Regression	r^2	F	Regression	r^2	F	H_o: *Ms*=*Mg*	H_o: *Ms*=*Mg*
TCL=0.565+1.293 CL	0.98	3080.87*	TCL=0.719+1.229 CL	0.99	6007.76*	4.74	87.90*
ACW=0.825+0.572 CL	0.98	2526.38*	ACW=1.366+0.556 CL	0.98	2325.55	0.95	11.26*
MCW=−1.033+0.860 CL	0.99	4881.98*	MCW=−1.356+0.851 CL	0.98	2848.76*	0.21	40.34*
RBW=0.239+0.130 CL	0.92	622.04*	RBW=0.545+0.143 CL	0.87	372.78*	1.90	232.08*
RL=0.463+0.465 CL	0.89	452.54*	RL=0.054+0.424 CL	0.94	898.72*	2.19	119.13*
DaW=0.075+0.047 CL	0.51	62.16*	DaW=0.703+0.037 CL	0.54	69.20*	1.53	196.78*
PW=0.041+0.091 CL	0.60	88.17*	PW=0.676+0.088 CL	0.70	137.38*	0.04	133.29*
EL=1.385+0.112 CL	0.89	430.65*	EL=2.287+0.114 CL	0.79	216.11*	0.06	645.14*
EW=0.705+0.083 CL	0.89	438.66*	EW=0.501+0.087 CL	0.86	338.97*	0.32	29.52*
MW=0.255+0.103 CL	0.95	1134.40*	MW=0.116+0.101 CL	0.95	954.39*	0.06	79.74*

r^2, coefficient of determination; F, F-statistic of the lineal regression; *, $P<0.001$. TCL, total carapace length; ACW, anterior carapace width; MCW, maximum carapace width; RBW, rostrum basis width; RL, rostrum length; DaW, dactylopodus width; PW, propodus width; EL, eyestalk length; EW, eyestalk width; MW, mandible width.

Morphometry

In order to quantify the morphological differences between both species/morphs, 11 different body parts were measured (Figure 1). Size-ranges of studied *M. subrugosa* and *M. gregaria* were 12.0–28.6 mm CL and 13.6–28.2 mm CL, respectively. Carapace length, total carapace length (TCL), maximum carapace width (MCW) and anterior carapace width between antero-lateral spines (ACW) were recorded with a digital caliper to the nearest 0.1 mm. Rostral basis width (RBW), rostral length (RL), widths of the third maxilliped propodus (PW) and dactylus (DaW), eyestalk width (EW) and length (EL) and mandible width (MW) were measured with an ocular micrometer mounted on a stereomicroscope to the nearest 0.08 mm. For each species, linear regressions of each morphometric measurement on crab size (CL) were calculated, and their slopes and ordinates were compared by analysis of covariance (Sokal & Rohlf, 1995).

To determine which morphometric measurements are appropriate to predict group membership, a backward stepwise discriminant analysis was performed (Morrison, 1976; Wilkinson, 1990). Thus, the discriminant functions were built by two successive discriminant analyses. In the first step, all morphometric measurements were included and used to determine which one contributes most to allow discrimination between the species/morphs. In the second step, those morphometric measurements that contribute least to the discrimination between species ($P>0.05$) were excluded, and the discriminant functions that predict which species/morph pertain were built using the rest of the morphometric measurements.

Biomass

In order to provide linear relationships between body size and weight of crabs, CL, and wet and dry masses (WW and DW, respectively) of fresh sub-sampled crabs were recorded. All crabs were weighed to the nearest 0.01 g with a Sauter RC 2022 balance. Crabs were dried to constant weight at 55°C. The predictive regressions (Sokal & Rohlf, 1995) between log-CL and log-WW and log-DW for both species and sexes were calculated, and their slopes and ordinates were compared with an analysis of covariance (Sokal & Rohlf, 1995).

RESULTS

Morphometry

All morphometric measurements of *Munida subrugosa* and *M. gregaria* were positively correlated with animal size. Ordinates of linear functions of each morphometric measurement and body size were different between both species/morphs (Table 1). As indicated by the significantly

Table 2. *Discriminant analysis for 11 morphometric measurements performed on 55* Munida subrugosa *and 57* M. gregaria *from the Beagle Channel, Argentina. Measurements with * were considered to be important for discrimination between both species and were used to run the second discriminant analysis to provide the discriminant functions.*

Body measurements	F	*P*
Dactylopodus width*	120.111	<0.001
Eyestalk length*	77.878	<0.001
Propodus width*	72.495	<0.001
Rostrum basis width*	29.897	<0.001
Anterior carapace width*	4.253	0.042
Rostrum length	3.151	0.079
Carapace length	2.290	0.133
Eyestalk width	0.594	0.443
Maximum carapace width	0.503	0.480
Total carapace length	0.086	0.770
Mandible width	0.004	0.948

F and *P*, are F-statistic and probability of discriminant analysis, respectively.

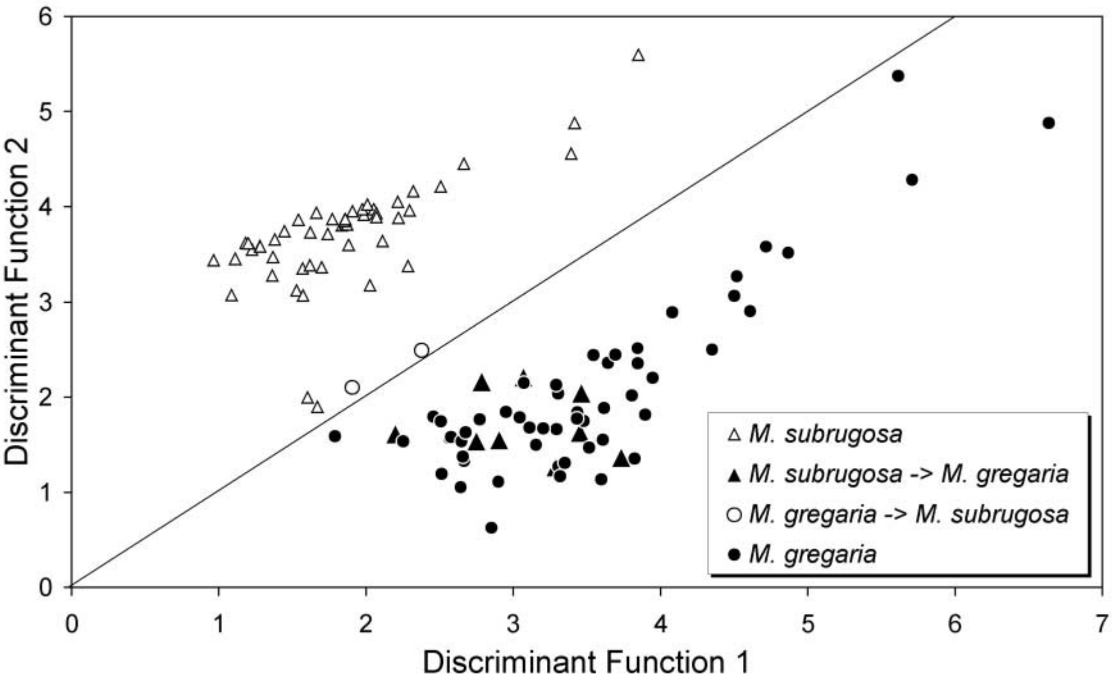

Figure 2. Scatterplot of loading scores of the two functions generated with the discriminant analysis performed on *Munida subrugosa* and *M. gregaria*. The line represents 1:1 and separates the two groups of points. Triangles and circles are specimens identified visually as *M. subrugosa* and *M. gregaria*, respectively. Closed triangles are *M. subrugosa* that changed to *M. gregaria*, and open circles are *M. gregaria* that changed to *M. subrugosa* after the discriminant analysis.

Table 3. *Regressions of the logarithm of wet and dry weight (WW and DW, respectively) on the logarithm of crab sizes (carapace length, CL) of* Munida subrugosa *and* M. gregaria *from the Beagle Channel, Argentina. Sample sizes were 32 males (13.3–28.0 mm CL) and 30 females (14.4–24.1 mm CL) for* M. subrugosa*; and 24 males (15.4–28.1 mm CL) and 23 females (16.2–26.5 mm CL) for* M. gregaria.

Species	Biomass	Sex	Equation of regression	r^2	F	F slopes H_o: F=M	F ordinates H_o: F=M
Munida subrugosa	Wet weight	M	$\log WW=-3.335+3.150 \log CL$	0.99	5735.21*	8.160*	–
		F	$\log WW=-3.034+2.914 \log CL$	0.98	1557.44*		
	Dry weight	M	$\log DW=-4.181+3.397 \log CL$	0.99	2808.28*	14.660*	–
		F	$\log DW=-3.552+2.894 \log CL$	0.95	577.07*		
Munida gregaria	Wet weight	M	$\log WW=-3.242+3.053 \log CL$	0.99	1633.86*	6.919	0.888
		F	$\log WW=-2.903+2.800 \log CL$	0.99	2158.89*		
		C	$\log WW=-3.052+2.911 \log CL$	0.99	3284.47*	–	–
	Dry weight	M	$\log DW=-3.638+2.958 \log CL$	0.96	521.44*	3.881	0.114
		F	$\log DW=-3.128+2.566 \log CL$	0.93	300.19*		
		C	$\log DW=-3.355+2.741 \log CL$	0.97	737.08*	–	–

r^2, coefficient of determination; F, F-statistic of the lineal regression; *, $P<0.01$; C, common regression line.

larger ordinates of the linear functions (Table 1), the carapace (TCL) and eyestalks (EL) were longer, and the-anterior carapace (ACW), the rostrum basis (RBW), dactylus (DaW) and propodus (PW) were wider in *M. gregaria* than in *M. subrugosa*. In contrast, the carapace (MCW), mandible (MW) and eyestalk (EW) were wider and the rostrum (RL) was longer in *M. subrugosa* as compared to *M. gregaria*.

The stepwise discriminant analysis performed on 57 and 55 *Munida subrugosa* and *M. gregaria* respectively, proved to be effective in separating the two species/morphs. In the first discriminant analysis, six out of 11 morphometric measurements (RL, CL, EW, CW, TCL and MW) were least important ($P>0.05$) for discrimination between *M. subrugosa* and *M. gregaria* and were eliminated from the second analysis (Table 2). The second discriminant analysis was performed with the five best morphometric measurements (DaW, EL, PW, RBW and ACW), and resulted in the following discriminant functions (DF_1 and DF_2) that predict the species/morph of a crab:

$$\begin{aligned} DF_1 = {} & 2.080\ ACW - 8.487\ RBW - 9.494\ DaW \\ & -12.201\ PW + 23.694\ EL - 28.697 \end{aligned}$$

$$\begin{aligned} DF_2 = {} & 0.175\ ACW - 5.299\ RBW - 0.282\ DaW \\ & -12.282\ PW + 26.421\ EL - 38.470 \end{aligned}$$

The null hypothesis that two groups composed of both species/morphs were equivalent were rejected (Wilks' lambda F=41.2, $P < 0.001$), and the discriminant functions served to generate two statistically different groups (Figure 2). After the application of both discriminant functions to our dataset, nine of 57 specimens classified visually as *M. subrugosa* changed to *M. gregaria*, and two out of 55 *M. gregaria* changed to *M. subrugosa* (Figure 2).

Biomass

Wet and dry weight of *M. subrugosa* and *M. gregaria* crabs were positively correlated with crab size (Table 3). In *Munida subrugosa*, linear regressions that describe the relationship between both log-WW and log-DW on log-body size were different between sexes. Slopes of linear regressions of both log-WW and log-DW on log-body size were steeper in male than in female *M. subrugosa* (Table 3). In contrast, in *M. gregaria* linear regressions of log-weight on log-body size were similar for males and females (Table 3).

DISCUSSION

Our study provides objective functions that allow separation of species/morphs of *Munida* spp. based on morphological distinctions. Results of discriminant and covariance analyses indicate that morphological characteristics used for the visual identification of both species/morphs are appropriate. The ten morphometric measurements used in this study exhibited differences between both species/morphs (Table 1), and the five best were used to create two discriminant functions (Table 2). With a minimum of training in identification and with both species/morphs available for morphological comparisons it is relatively easy to distinguish them visually with a ~90% success rate (cf. Figure 2). Rostrum carapace width and eyestalk length were the clearest visible differences, and were also identified among the discriminant variables. In the presence of only one species/morph or in doubtful cases, after the corresponding measurements are taken, we recommend use of the following discriminant functions:

If $DF_1 - DF_2 > 0$ then *Munida subrugosa*

If $DF_1 - DF_2 < 0$ then *Munida gregaria*

Misclassification between the visual method and the discriminant function was acceptably low. However, the number of individuals that were visually originally assigned to *M. subrugosa* and switched to *M. gregaria* after the discriminant analysis was four times higher than changes in the opposite direction. This indicates that the probability of wrong classification as *M. subrugosa* is higher than as *M. gregaria*.

Specific identification of galatheids is considered problematic. For example, subtle morphological differences that match with mitochondrial nucleotide sequences were required to justify the creation of different species of *Raymunida* (Macpherson & Machordom, 2001). Two different populations of *M. tenuimana* (Sars, 1872) containing individuals with some differential characters were proposed to be undergoing speciation (Rice & de Saint Laurent, 1986). Many species of *Munidopsis* appear to be morphologically very similar, leading to confusion about their systematic status (Creasey et al., 2000).

There is still conflicting evidence that *Munida subrugosa* and *M. gregaria* may either belong to the same species, or to different ones. A few studies carried out off New Zealand suggest that *M. gregaria* and *M. subrugosa* are actually the same species. After planktonic larval development during spring, the pelagic post-larval stages remain in the water column for ~6 months, after which adult features are wholly or partially acquired (Zeldis, 1985). Williams (1973) demonstrated empirically that once settled on the bottom, juvenile pelagic animals—supposedly *M. gregaria*—change their morphology over a series of moults until they conform to the description of *M. subrugosa*. Yet, if juvenile *M. gregaria* remain pelagic for an extended period, they may grow to a large size, retaining pelagic morphology as benthic adults (Zeldis, 1985). Furthermore, live larvae from hybridization experiments carried out with *M. subrugosa* and *M. gregaria* caught in the Beagle Channel suggest that at least some reproductive isolation barriers do not exist between both species/morphs (F. Tapella, unpublished data). Alternatively, such ontogenetic change in morphology and habits seems not to hold true for the South Atlantic waters for two reasons. Firstly, juvenile stages of ~3 mm CL of *M. subrugosa*, presumably younger than 1 y old, were found in benthic samples (Tapella, 2002). Secondly, megalopae of both species/morphs were found and distinguished from plankton samples off the Atlantic shelf of South America, south to 42°S (Bacardit, 1986). Therefore, the specific status of these species/morphs needs resolution by means of detailed genetic, larval morphology and reproductive studies.

Munida subrugosa and *M. gregaria* have a wide distribution in the continental shelf off southern South America. Previous studies suggest that *M. subrugosa* plays a key role in making primary production and detritus available to top predators of cold-temperate and subantarctic environments (Romero, 2003; Romero et al., 2004). Hence, its ecological role in subantarctic coastal waters is likely to be similar to that of euphausiids in the Southern Ocean (Romero et al., 2004). Therefore, it is indispensable to have appropriate conversion equations between body mass and different morphometric measurements, along with correct identification. Any of our linear regressions shown in Table 1 could provide size estimation for both species/morphs using only one body part. When used along with regressions of weight on size (Table 3), these functions enable estimations of biomass.

The correct identification of either of the two species/morphs can give information about feeding habits and distribution of their predators; even though the information about their vertical distribution is fragmentary and still largely lacking, *Munida subrugosa* is reportedly benthic (Tapella, 2002) whereas juvenile, and occasionally adult, stages of *M. gregaria* are found in the water column (Matthews, 1932; Jillett & Zeldis, 1985; Zeldis, 1985). In the Atlantic continental shelf, off Patagonia (south 42°S), distributions of *M. gregaria* and *M. subrugosa* greatly overlap (Rayner, 1935), but detailed distributional studies related to environmental conditions are still necessary. However, *M. gregaria* is seemingly associated with river mouths or waters with relative low salinities, such as those of the Strait of Magellan (cf. Rayner, 1935; Guerrero & Piola, 1997). Similarly, at the scale of the Beagle Channel (200 km length, 4 km width) both species/morphs exhibit markedly different distributions. *Munida gregaria* is practically restricted to estuarine bays at <50 m depth, whereas *M. subrugosa* occurs in the entire channel and down to 150 m depth (Tapella et al., 2002b). Thus, by knowing which species/morph is present in the diet, one can draw different conclusions about foraging sites, depths or environments of their predators.

Morphological differences found in this study can be associated with specific feeding adaptations of these galatheids. *Munida subrugosa* has two distinct and simultaneous feeding habits: foraging on algae or preying upon small crustaceans or worms; and as a deposit feeder by sweeping the uppermost benthic layer, rich in organic matter (Romero et al., 2004). In this study, we found that in *M. subrugosa* the mandible is wider and the distal extreme of the third maxilliped is narrower than in *M. gregaria*. Mandibles are used for cutting large pieces of food whereas the shovel shaped end of the third maxilliped makes this mouthpart suitable for digging up the mud (Garm & Hoeg, 2000, 2001). Consequently, we hypothesize that a wider maxilliped in *M. gregaria* may be an adaptation to deposit feeding. By contrast, a wider mandible should confer the ability to process larger food portions, giving *M. subrugosa* more scope for foraging/preying. These morphological differences probably reflect an attempt to avoid a trophic niche overlap and explain the differential distribution in the Beagle Channel of both species/morphs.

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