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## The hermit crab *Sympagurus dimorphus* (Anomura: Parapaguridae) at the edge of its range in the south-western Atlantic Ocean: population and morphometry features

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*Sympagurus dimorphus* is one of the 12 hermit crab species recorded for Argentinean waters. Despite the high abundance registered in some scallop fishing grounds, its biology remains little known. In the present study, we analysed some population features of *S. dimorphus* living in symbiosis with *Epizoanthus paguricola* from a series of samples taken in the Argentine Sea, south-western Atlantic Ocean. Our results showed that *S. dimorphus* was commonly found from 40°S to lower latitudes, in a patchy distribution along the shelf-break front. The overall sex ratio was 1:1. The smallest ovigerous female measured 6 mm in cephalothoracic shield length and this size was used as parameter to define the size of juveniles. The sex ratio size class pattern corresponded to Type IV or anomalous curve. *S. dimorphus* is a dimorphic species, as evidenced by the larger size of the males and the positive allometric growth of the right cheliped. The species also showed asymmetry, with the left uropod always larger than the right one. To the best of our knowledge, this is the first report on population features and relative growth for a member of the genus, based on long-term sampling. This species presents a patchy distribution along the shelf-break of Argentina. Its density tended to decrease over the five-year sampling period regarding the recruitment of hermits associated with colonies of zoanths. In addition, the relatively homogeneous nature of this refuge does not seem to influence the growth of the hermit crab, which presents sexual dimorphism in relation to the sex/size conditions.

**Keywords:** Argentina; hermit crabs; population dynamics; relative growth; sex ratio

### Introduction

Population traits such as sex ratio, size frequency and recruitment are important biological parameters, and are essential for understanding decapod populations and to provide for their natural renewal. This is particularly true for many deep-water species that are known from only one or a few localities, and population aspects of many of these species are still undescribed. Some of the intriguing hermit crabs in particular, distinctive for sheltering their fragile and uncalcified abdomen in gastropod shells, afford an opportunity to study these aspects.

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The genus *Sympagurus* Smith, 1883 is a prominent group of hermit crabs that includes some species that live in close symbiosis with members of Anthozoa (actinians and zoanthids) that can produce a pseudoshell (a structure built by the zoanthid after it settles, which mostly preserves the shell-like morphology of the gastropod, including a columellar axis) (see Schejter and Mantelatto 2011 for details). Although 17 recognised species of *Sympagurus* inhabit the lower continental shelf and upper slope regions of most world oceans at depths from 80 to 2537 m (Lemaitre 2004), details on their populations are still unknown.

In Argentina, 12 hermit crab species have been recorded (Boschi et al. 1992; Boschi 2000), although only a few of them inhabit deep shelf waters (Bremec et al. 2003). Among these deep-water hermits, *Sympagurus dimorphus* Studer, 1883 is prominent because of its high abundance in some fishing grounds (Bremec et al. 2003; Schejter and Mantelatto 2011), but its biology remains little known. The juveniles and megalopae were described by Lemaitre and McLaughlin (1992). *S. dimorphus* is distributed in the southern hemisphere from 22°S to 57°S, at depths of 91–1995 m (Lemaitre 1989, 2004; Lemaitre and McLaughlin 1992) and is found in the Argentine Sea living in the benthic community dominated by the Patagonian scallop *Zygochlamys patagonica* (King, 1832), around the 100 m isobath (Bremec et al. 2003). Over its distributional range, *S. dimorphus* inhabits gastropod shells and is also found associated with zoanthid colonies (Lemaitre 1989, 2004; Ates 2003; Bremec et al. 2003).

As an initial step to improve the knowledge of this species, we previously described in detail the symbiosis between *S. dimorphus* and the shell-like colonies of *Epizoanthus paguricola* associated with gastropod shells (Schejter and Mantelatto 2011). Stemming from this promising scenario for investigation, the objectives of the present study were to: analyse and compare the distribution and density of *S. dimorphus* populations from a series of samples taken between 2002 and 2006 along the shelf-break front of the Argentine Sea; study the sex ratio and size–frequency distribution of the species; and characterise the relative growth of the hermit crabs living associated with *E. paguricola* colonies.

## Materials and methods

The study area lies between 36.9833–43.9166°S and 54.6500–60.1833°W, at depths of 81–141 m (Figure 1), in Argentinean waters, south-western Atlantic Ocean, where the fishing grounds for the Patagonian scallop (*Zygochlamys patagonica*) are located. The mean bottom temperature in this area is almost constant, ranging from 5 to 9°C during the year depending on latitude, over the sampling area (Bogazzi et al. 2005).

Population parameters of *S. dimorphus* were estimated from data from samples of the benthic community collected during Patagonian scallop stock assessment cruises carried out by the R/V ‘Capitán Cánepa’ of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) during 2002 (April, July), 2003 (June, November), 2004 (July, August), 2005 (March, October) and 2006 (April, May) using a non-selective dredge (2.5 m aperture width, 10 mm mesh size). Sampling sites were approximately the same each year, as required for projects for scallop stock assessment purposes. These benthic community samples are collected as part of a long-term

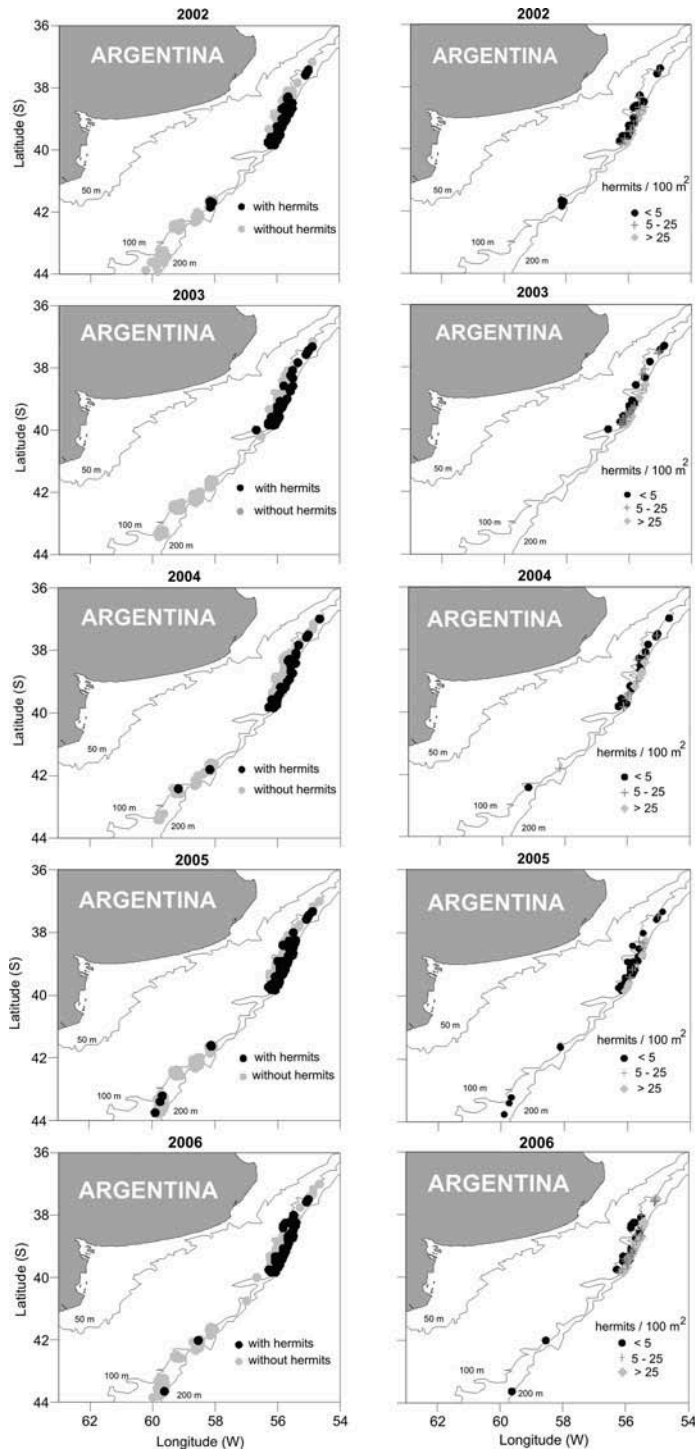


Figure 1. *Sympagurus dimorphus*. Densities (number of individuals/100 m<sup>2</sup>) in the sampling areas from 2002 through 2006. Left column shows presence/absence data including all sampling sites, and right column shows densities on a relative scale.

project of ecosystem monitoring (Schejter et al. 2013). Density (number of individuals/100 m<sup>2</sup>) was estimated considering the number of hermit crabs in the haul over the sampling area. The sampling area of each haul was estimated using the time of the haul (10 minutes), the speed of the vessel (mean speed = 3.6 knots), and the width (2.5 m) and efficiency (43% according to Valero 2002) of the dredge. The value used was estimated for the Patagonian scallop, but we used the same value for faunal analysis since no estimates for individual species have yet been calculated. A two-way analysis of variance (ANOVA) test evaluated the population density among the periods.

For the morphometric and sex ratio analyses, we used only part of the all hermit crab population sampled. To this end, hermit crabs from benthic community samples taken during the 2005 and 2006 cruises were sorted and preserved in 5% formaldehyde after routine community composition analyses conducted in the Benthos Laboratory (INIDEP). Specimens were counted and checked in relation to the sex and their cephalothoracic shield length (CL); the length and width of the propodus of the major (right) cheliped (CHL and CHW) were measured using a vernier caliper with a precision of 0.01 mm. Small individuals and the length of the exopods of the right and left uropods (RUL/LUL) were measured under a stereomicroscope. Individuals were grouped in size classes. The mean size of the specimens and the number of individuals were compared among the areas and periods sampled. A two-way ANOVA test evaluated the variation in sizes of individual crabs among the sample areas. In case of non-parametric data, the Kruskal–Wallis test was used (Zar 1996).

Morphometric relationships were considered for CHL, CHW, RUL and LUL, and compared with CL, which was chosen as the reference dimension for hermit crab size. The pattern of allometry, as the power function  $Y = aX^b$ , was established by  $b$  value ( $b = 1$  isometry,  $b < 1$  negative allometry,  $b > 1$  positive allometry). Values of  $b$  between 0.9 and 1.1 were considered indicative of isometry ('conservative definition'; Clayton 1990, p. 285).

The asymmetry index ( $AI$ ) was calculated for the uropods according to van Valen (1962), with  $AI = (L - R)/(L + R)$ , where L and R correspond to the measurements of the left and right exopod, respectively. This index varies from +1 (left longer) to -1 (right longer), with 0 indicating perfect symmetry. Values were obtained from hermit crabs inhabiting *E. paguricola* pseudoshells. Data were taken considering that the morphology of the pseudoshell may be influenced by the type of initial gastropod shell found at the 'apex' of the *E. paguricola* colony (see explanation in Schejter and Mantelatto 2011). The pseudoshell structure is morphologically similar to a gastropod shell, but made by the symbiotic cnidarian, and starts from a small empty gastropod shell occupied by *S. dymorphus* during the early life phase. The identification of the initial gastropod shells followed could be done after breaking up the cnidarian colony. Common mollusks species present in the area are mentioned in Bremec et al. (2003).

The relationship between size class and sex ratio was analysed according to Wenner (1972). The  $t$ -test was used to compare the sizes of males and females. In the case of non-parametric data, the Mann–Whitney Rank Sum test was used. The Kolmogorov–Smirnov (KS) test was performed to verify the normality of the population data according to the size of the individuals.

Table 1. *Sympagurus dimorphus*. Mean densities of hermit crabs (number of individuals/100 m<sup>2</sup>) considering the entire sampling area (TOTAL) and only the sites where hermits were collected (POSITIVE SITES); ranges of densities at all sites per year are also shown. Numbers in parenthesis indicate the number of sampled sites.

Density Year	Total (individuals/100 m <sup>2</sup> )	Positive sites (individuals/100 m <sup>2</sup> )	Range (individuals/100 m <sup>2</sup> )
2002	6.64 (133)	22.64 (40)	0–314.92
2003	5.30 (137)	20.75 (35)	0–128.63
2004	3.29 (113)	12.40 (30)	0–93.78
2005	5.32 (143)	15.22 (50)	0–186.99
2006	4.74 (142)	13.94 (48)	0–81.49

## Results

*Sympagurus dimorphus* is a frequent species on the Patagonian scallop fishing grounds in the Argentine Sea. Variations in densities (individuals/100 m<sup>2</sup>) in the sampling areas and years were recorded (Figure 1). Hermits were commonly found from 40°S to lower latitudes (~37°S), and sporadically south of 40°S. The mean density of hermits (individuals/100 m<sup>2</sup>) over the entire area and/or the ‘positive’ sites (stations where *S. dimorphus* was recorded) and the range varied among the years, is shown in Table 1. However, there was no significant difference among the mean densities in the sampling periods ( $H = 1.8929$ ;  $p > 0.05$ ). The highest density found in the study (314.92 ind/100 m<sup>2</sup>) was recorded during 2002, at a site located at 39,8333°S and 56,0722°W, at 130 m depth.

For the morphometric and sex ratio analyses, a total of 241 individuals of *S. dimorphus* were sampled: 118 males (48.9%) and 123 females (51.1%), of which 67 were ovigerous (54.5%) and 56 were non-ovigerous females (45.5%). The overall sex ratio was 1:1. The pattern corresponding to the sex ratio size class analysis established by Wenner (1972) corresponded to a Type IV or anomalous curve (Figure 2).

Males were significantly larger ( $10.501 \pm 4.684$  mm CL; range: 3.2–14 mm) than non-ovigerous females ( $8.083 \pm 2.838$  mm CL; range: 4.6–10 mm) and ovigerous females ( $8.682 \pm 2.625$  mm CL; range: 6–11 mm) ( $U = 2742.500$ ;  $p < 0.001$ ). The smallest ovigerous female caught measured 6 mm CL; this size was used as the parameter to define the minimum size of maturity. Regarding the abundance of individuals by size class, an unequal sex ratio was observed in almost all the classes, with a marked increase in the abundance of females in the intermediate classes, and a skewed ratio favouring males in the larger classes (Figures 2 and 3). The studied samples also included 18 juveniles (7.47%), of which 8 were females and 10 were males. A non-normal (K-S distribution = 0.101;  $p < 0.001$ ) and bimodal distribution pattern was found for the size–frequency distribution of the total population, clearly caused by modes of females at 8–9 mm CL and of males at 11–12 mm CL (Figure 2).

Cheliped growth was found to be positive allometric in males, while females were negative allometric for length and width measurements. Juveniles were grouped for this estimation, and showed isometry for length and positive allometry for width (Figure 4, Table 2). Uropod growth was found to be negative allometric for both sexes (Table 2). Asymmetry was also detected, with the left uropod always larger than

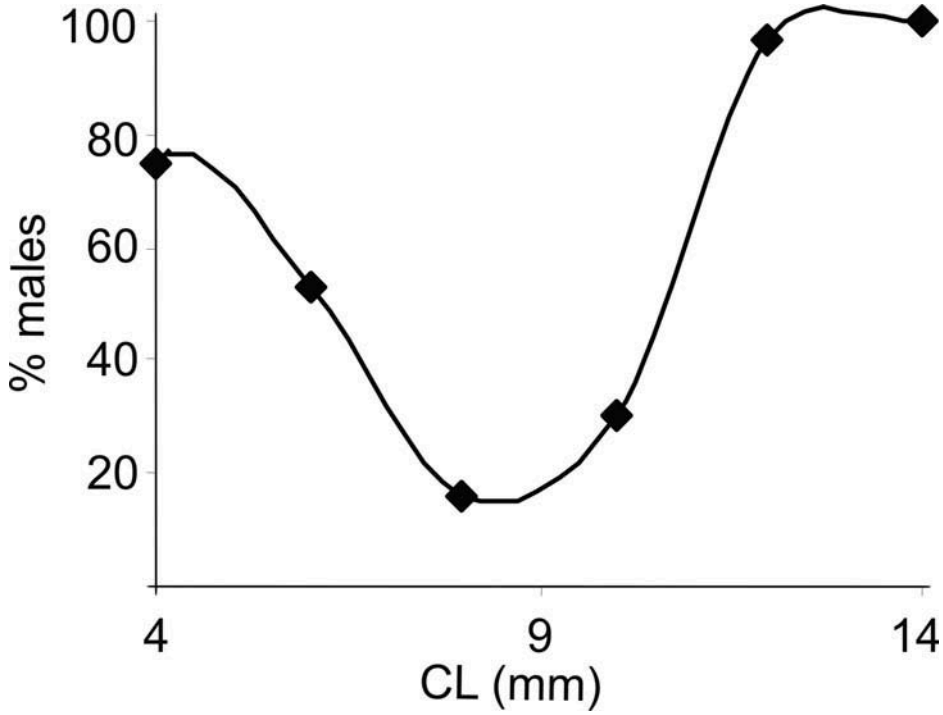


Figure 2. *Sympagurus dimorphus*. Sex ratio as the percentage of males in relation to size (CL = cephalothoracic shield length) for hermits collected in 2005 and 2006.

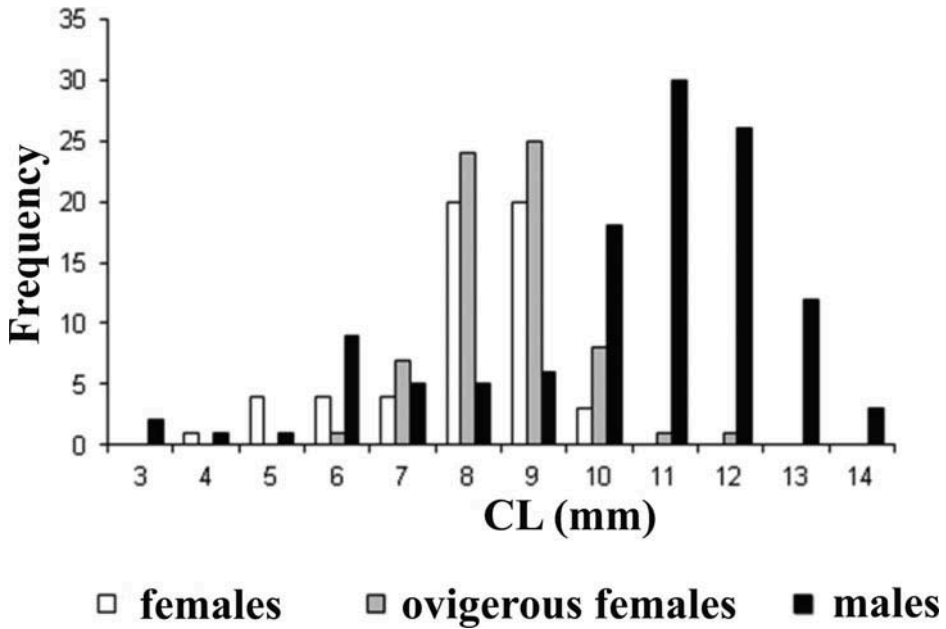


Figure 3. *Sympagurus dimorphus*. Size frequency distribution (CL = cephalothoracic shield length) for the total of males and females (non-ovigerous and ovigerous) collected.



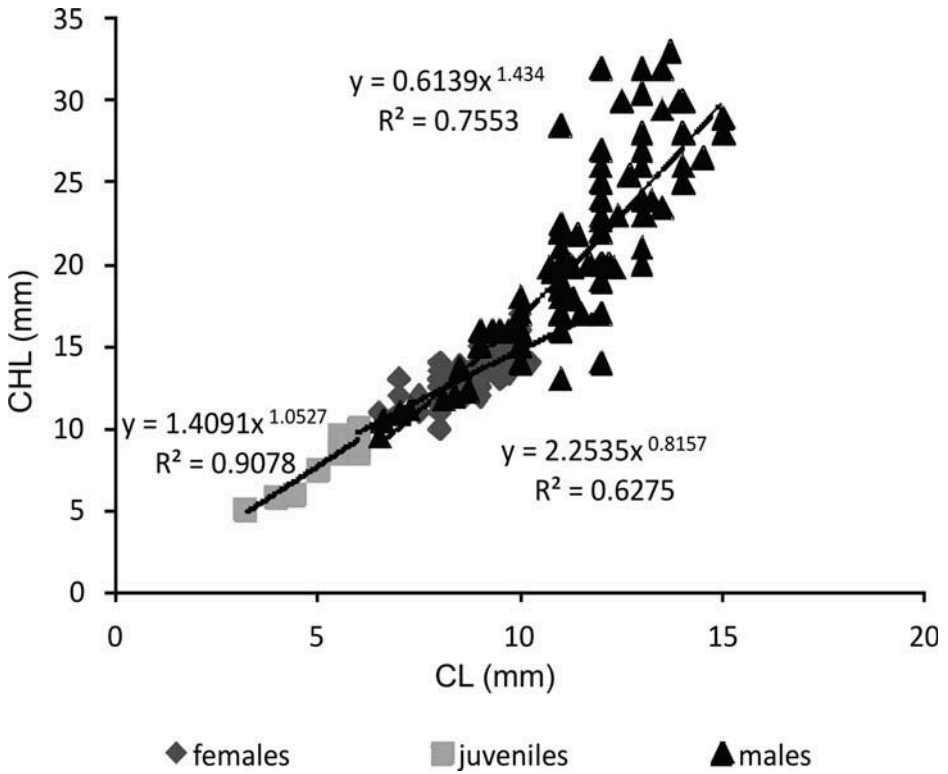


Figure 4. Relative growth of the major cheliped propodus length (CHL) in relation to cephalothoracic shield length (CL) in males, female and juveniles ( $\leq 6$  mm CL). Regression equations and coefficient of determination for a potential function are shown.

Table 2. *Sympagurus dimorphus*. Regression equations. CL: cephalothoracic shield length; CHL and CHW: major cheliped propodus length and width; LUL and RUL: length of the exopod of the left and right uropod, respectively;  $r^2$ : coefficient of determination; A: allometry – (=) isometry, (-) negative, (+) positive; juv: juveniles; tot: total of individuals examined (males, females and juveniles) for the character.

<i>n</i>	Relationship	Power function $y = ax^b$	Linear equation $\ln Y = \ln a + b \ln x$	$r^2$	A
106 ♂	CHL × CL	CHL = 0.61 CL <sup>1.434</sup>	$\ln \text{CHL} = -0.487 + 1.434 \ln \text{CL}$	0.75	+
100 ♀	CHL × CL	CHL = 2.25 CL <sup>0.8157</sup>	$\ln \text{CHL} = 0.812 + 0.815 \ln \text{CL}$	0.62	-
15 juv	CHL × CL	CHL = 1.40 CL <sup>1.05</sup>	$\ln \text{VHL} = 0.342 + 1.05 \ln \text{CL}$	0.90	=
106 ♂	CHW × CL	CHW = 0.86 CL <sup>1.130</sup>	$\ln \text{CHW} = -0.142 + 1.13 \ln \text{CL}$	0.73	+
100 ♀	CHW × CL	CHW = 1.95 CL <sup>0.744</sup>	$\ln \text{CHW} = 0.671 + 0.744 \ln \text{CL}$	0.54	-
15 juv	CHW × CL	CHW = 0.88 CL <sup>1.144</sup>	$\ln \text{CHW} = -0.126 + 1.144 \ln \text{CL}$	0.85	+
239 tot	LUL × CL	LUL = 0.373 CL <sup>0.757</sup>	$\ln \text{LUL} = -0.984 + 0.757 \ln \text{CL}$	0.68	-
239 tot	RUL × CL	RUL = 0.902 CL <sup>0.799</sup>	$\ln \text{RUL} = -0.103 + 0.799 \ln \text{CL}$	0.86	-

Table 3. *Sympagurus dimorphus*. Asymmetry index of the uropods: mean and standard deviation of sexes (total) and of individuals inhabiting pseudoshells made by *Epizoanthus paguricola* (with three different gastropods species at the ‘apex’).

	<i>n</i>	Mean	Standard deviation
Total females	123	0.455	0.0462
Total males	116	0.446	0.0532
in Naticidae	155	0.461	0.0784
in <i>Epitonium magellanicum</i>	32	0.442	0.0494
in Volutidae	15	0.435	0.0518

the right one. The results discriminated by sex and by initial pseudoshell gastropod are presented in Table 3.

### Discussion

To the best of our knowledge, no information on population structures of hermit crabs living in deep waters and obtained through systematic collections is available for species in Argentinean waters. We reported on population features for *Sympagurus dimorphus* based on a long-term data series. Considering that the Magellanic Region corresponds to the southernmost distribution limit known for this species, comparisons with other populations distributed anywhere else would be desirable in the future.

Data from this study showed that the density (number of individuals/100 m<sup>2</sup>) varied slightly over the five-year sampling period (2002 through 2006), although significant differences among mean densities were not detected. This is the first profile obtained for this species and should be considered as a baseline condition for future comparative analyses. The disturbance caused by the scallop trawling on the benthic ecosystem (i.e. the trawling disturbance itself and the damage to non-target species caused by the onboard sorting process; Escolar et al. 2013) is a continuous external factor that modifies these benthic systems and may produce either increases or decreases in the abundance and biomass of invertebrates, as already mentioned by Bremec et al. (2011) for an area located between 39° and 39°50′ S, from 1995 to 2007.

The description of animal distribution patterns or arrangements in space has considerable ecological meaning, not only by affecting sampling programmes and data analyses, but also for describing the conditions under which a population is found in a particular area (Southwood 1978). Physical factors are assumed not only to determine the distribution of the animals in deep waters, but also to regulate their abundance within this range. *Sympagurus dimorphus* is able to exist in the study area because of its association with the zoanths, as not enough suitable empty gastropod shells are available for its use (Schejter and Mantelatto 2011). The patchy distribution of this species in the study area was evident, since the estimated densities varied widely between neighbouring sampling sites (L. Schejter, personal observation). Whether this patchy distribution might be due to the distribution of resources or of larvae (either hermit crabs or zoanths) is unclear, and this question is outside the scope of this study. It is necessary to consider that the sampling design used here was developed to assess the Patagonian scallop stock for fishery purposes, not specifically

for the sampling or study of the benthic community species. The present research on *S. dimorphus* could be considered a byproduct of the benthic community assessment in the scallop fisheries context.

Several factors are apparently determining and maintaining through time the particular distribution recorded for *S. dimorphus* in the study area, located on the shelf break off Argentina. The population structure described here agrees with those of other species, and the sex ratio size class analysis corresponds to the Type IV or 'Anomalous pattern' described by Wenner (1972). The probability curve in this case could arise from an overlapping of two different modal size classes in a population (males and females). Crustaceans with this pattern mostly change little in size distribution with season or locality, implying that this specific relationship between males and females is more a function of the physical size of the animals than of any other feature. At least four possible explanations have been provided to explain this distribution, including differences in longevity, migration, mortality or growth rate between the sexes (Wenner 1972). We suggest that the pattern observed here for *S. dimorphus* (Figure 2) could be explained since the mean size of adult males is notably larger than that of females, and the dip in the probability curve could result from the accumulation of adult females in that size class. Although it has not been tested, of the explanations for the observed pattern listed above, we consider that the difference in growth rate is the most probable cause.

Aspects of relative growth have been scarcely investigated in hermit crabs when compared with other decapods, and the patterns found have proved to be influenced by the gastropod shell that they inhabit (Bertness 1981; Lancaster 1988). Studies of the size structure, relative growth and shell preferences have been conducted for: *Pagurus exilis* (Mantelatto et al. 2007), *P. criniticornis* (Meireles et al. 2008), *Dardanus insignis* (Branco et al. 2002; Fernandes-Góes et al. 2005), *Loxopagurus loxochelis* (see Ayres-Peres and Mantelatto 2008 for review) in Brazilian waters; for *P. comptus* in Chilean waters (Soto and George-Nascimento 1991; Soto et al. 1999); and for *Propagurus gaudichaudii* and *D. insignis* in Uruguayan waters (Carranza and Horta 2008; Carranza et al. 2008). All of these species also inhabit Argentinean waters. For the species of *Sympagurus*, no previous data were available on population aspects.

All the individuals examined in this study inhabited *Epizoanthus paguricola* pseudoshells. Considering the relatively homogeneous nature of this refuge, the soft structure of the zoanthid colony does not seem to influence the normal growth of any part of the hermit crab (as evident asymmetries were found for other hermit crab species inhabiting different refuges), despite the variability in the shape of the pseudoshell, as was recorded previously (Schejter and Mantelatto 2011). Sexual dimorphism in this species is apparent in the larger size of males and the positive allometric growth found in the relationships of the right (major) cheliped in males, compared with the slightly negative allometric growth recorded for females. These are common dimorphic characteristics, also found in other hermit crabs with similar body dimensions, such as *Paguristes erythropus* (Biagi and Mantelatto 2006) and *Loxopagurus loxochelis* (Mantelatto and Martinelli 2001). The larger size of the male cheliped for a given CL of the hermit crab agrees with the larger aperture size of the *E. paguricola* pseudoshell, as was noted previously (Schejter and Mantelatto 2011). It has been proposed that the larger size of the cheliped in adult male hermit crabs could be related to behavioural differences such as territorial defence, intraspecific fights and

courtship behaviour (Hartnoll 1974; Gherardi and Nardone 1997). An appropriate shell choice has also been related to this dimorphic characteristic in some species (Martinelli and Mantelatto 1999), which is not the case for the populations studied here.

Unfortunately, the details of population aspects of members of Parapaguridae are critical and the available information does not allow further discussion. Detailed population studies of these species are needed for a better understanding of the life cycles of this scarcely studied group of hermit crabs.

Summarising, this is the first report on population features for a member of the genus *Sympagurus* based on long-term sampling and includes relative growth parameters. *Sympagurus dimorphus* presented a patchy distribution along the shelf-break of Argentina and its density remained constant over the five-year sampling period. In addition, the relatively homogeneous nature of this refuge (pseudoshell) did not seem to influence the growth of the hermit crab, which showed sexual dimorphism in relation to the sex/size conditions.

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### Disclosure statement

No potential conflict of interest was reported by the author(s).

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