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Pattern of shell occupation by the hermit crab *Pagurus exilis* (Anomura, Paguridae) on the northern coast of São Paulo State, Brazil

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Pattern of shell occupation by the hermit crab *Pagurus exilis* (Anomura, Paguridae) on the northern coast of São Paulo State, Brazil

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Abstract

The purpose of this study was to determine the shell occupation pattern of *Pagurus exilis* using the percentage of shell types that were occupied and the morphometric relationship between hermits and occupied shells. Specimens were collected monthly from July 2001 to June 2003. A total of 1737 individuals were collected, occupying 19 gastropod shell species. *Buccinanops gradatum* (82%) was the most occupied shell, followed by *Natica isabelleana* (6.4%), *Stramonita haemastoma* (3.2%), and *Cymatium parthenopeum* (2.2%). There was a differential shell utilization pattern between sexes; males occupied larger and heavier shells while the non-ovigerous females occupied the lightest ones. *Pagurus exilis* occupied more bare shells instead of incrustated ones. *Buccinanops gradatum* was the most occupied shell species as a function of its availability in the survey, and this occupation is strongly associated with the higher internal volume presented by these shells.

Keywords: Brazil, hermit crab, *Pagurus*, shell occupation, Southern Atlantic

Introduction

Hermit crabs, like other animals, compete for resources for growth or successful reproduction, such as territory or nest sites, to maximize their fitness (Yoshino and Goshima 2001). One of these resources is the gastropod shells that represent a limiting factor to these populations (Bollay 1964). The association between hermit crabs and shells influences the majority of the hermit crabs' biological aspects and may affect their susceptibility to predation, protection against mechanical abrasion, tolerance to environmental stress such as temperature and salinity oscillations, growth, reproduction, and

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fecundity of females (Bollay 1964; Reese 1969; Fotheringham 1976; Davenport et al. 1980; Hazlett 1981; McLean 1983; Scully 1983; Raimondi and Lively 1986; Lancaster 1988; Mantelatto et al. 2002; Litulo 2005).

Mechanisms underlying the pattern of shell selection and occupation by hermit crabs have been found to be determined by factors such as competition (Bertness 1980), shell type (Reese 1962), shell size (Vance 1972a, 1972b), shell internal volume (Conover 1978; Siu and Lee 1992; Mantelatto and Dominciano 2002), and shell availability (Reese 1962; Bertness 1980; Emmerson and Alexander 1986; Reddy and Biseswar 1993; Garcia and Mantelatto 2000). The latter is greatly influenced by the relative abundance of different live gastropods and their mortality rates (Ohmori et al. 1995; Mantelatto and Meireles 2004).

Sufficient and adequate-sized shells are scarce to the hermit crab populations (Scully 1979), mainly in areas where these animals are abundant. Such shell limitation may cause the occupancy of inadequate-sized shells by hermit crabs (Angel, 2000; Garcia et al. 2003). Furthermore, inadequate shells may enhance predation and desiccation risks (Angel 2000) and reduce growth rates (Markham 1968; Fotheringham 1976). Presence of epibionts covering the shells may also influence shell selection and occupation (Martinelli and Mantelatto 1998) but only a few studies have focused on the relation between epibiont occurrence and shell occupation by hermit crabs (Conover 1976; Martinelli and Mantelatto 1998; Sandford 2003).

Hermit crabs have also been included in numerous reports of decapods from Central and South America (see Haig and Harvey 1991 for review). However, few species have received more than brief attention such as the species studied here. *Pagurus exilis* (Benedict, 1982) is distributed along the Western Atlantic, from Rio de Janeiro (Brazil) to Mar del Plata (Argentina). Despite the considerable number of studies on the biogeography and systematics of *P. exilis* (see Melo 1999 for review), information on biological aspects is scant. There are only the studies of Scelzo and Boschi (1969), Espósito et al. (forthcoming), and Mantelatto et al. (forthcoming), on post-embryonic development, population biology and shell selection under laboratory conditions, respectively.

In this study the pattern of shell occupation by *P. exilis* from the Caraguatatuba region (SP), Brazil, was investigated. In order to detect the shell variables that best describe this association, the percentage of shell type occupation and the morphometric relationship between hermit crabs and occupied shells was characterized. This information is important to understand the biology of this hermit crab on the northern coast of São Paulo State.

Material and methods

Specimens were collected monthly over a 2-year period (July 2001 to June 2003) in the Caraguatatuba region (23°34' and 23°51'S; 45°10' and 45°26'W), northern coast of São Paulo State. Samples were taken by a fishery boat during daytime with a double-rig trawl net (20 mm mesh size in the net body and 15 mm in the cod end) at seven different depths (from 5 to 35 m) in order to make the capture effort as efficient as possible. After collection the animals were frozen and transported to the laboratory where they were removed from their shells, counted, weighed, and measured for the shield length (SL). Sex was checked by the gonopore position.

Shell species occupied by the hermit crabs were identified according to Rios (1994), and their aperture width (SAW) and length (SAL), and dry weight (SDW) were measured. Shell internal volume (SIV) was measured according to Bertness (1981a), modified by Mantelatto and Garcia (2000), determining the volume of sand (diameter 0.25–0.125 mm)

required to fill the empty shell. External occurrence of epibionts on shells was first verified, identified, and then the percentage of each type (group) of epibionts calculated in relation to the total shells collected.

The Kolmogorov–Smirnov test (KS) was utilized to verify the normality of the hermit crabs' frequency distribution, while regression analysis and Spearman correlation were utilized to estimate the relations between variables (shell versus hermit crab dimensions); the chi-square test was used to test the percentage of occupied shells and ANOVA on Ranks Test was utilized to evaluate the size of occupied shells (Zar 1996). The level of significance adopted was 0.05. Voucher specimens collected are deposited in the Crustacean Collection of the Biology Department of the Faculty of Philosophy, Sciences and Letters of Ribeirão Preto, University of São Paulo, Brazil (DB/FFCLRP/USP, accession numbers 1201–1204).

Results

A total of 1737 individuals was obtained throughout the study period: 1170 (67.4%) males, 285 (16.4%) non-ovigerous females, and 282 (16.2%) ovigerous females. Size frequency distribution of individuals revealed a unimodal pattern with a non-normal distribution (total: KS=0.038; males: KS=0.057; non-ovigerous females: KS=0.279; ovigerous females: KS=0.069; $P<0.003$) (Figure 1).

Pagurus exilis occupied 19 gastropod shell species. *Buccinanops gradatum* was significantly the most occupied (82%, $\chi^2=1120.7$), followed by *Natica isabelleana* (6.4%), *Stramonita haemastoma* (3.2%), and *Cymatium parthenopeum* (2.2%) (Table I). *Buccinanops gradatum* was also significantly the most occupied in relation to sex of individuals (males: 81.1%, $\chi^2=698.6$; non-ovigerous females: 81.7%, $\chi^2=199.3$; ovigerous females: 85.8%, $\chi^2=210.9$), while the pattern of occupation in relation to the other shell species varied (Table I). The second most significantly occupied shell by the males was *N. isabelleana* (8.1%, $\chi^2=21.4$), and by the females was *C. parthenopeum* (ovigerous: 3.9%, non-ovigerous: 4.2%).

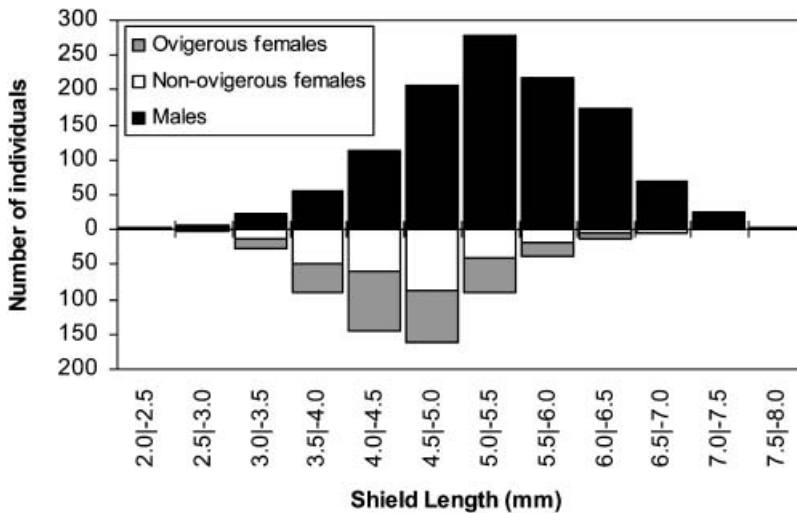


Figure 1. *Pagurus exilis*: size frequency distribution for the individuals collected.

Table I. *Pagurus exilis*: gastropod shell species and percentage of occupation.

Gastropod shell species	MA		NOF		OF		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
<i>Buccinanops deformis</i> (King, 1831)	2	0.17	–	–	–	–	2	0.12
<i>Buccinanops gradatum</i> (Deshayes, 1844)	949	81.11	233	81.75	242	85.82	1424	81.98
<i>Chicoreus tenuivaricosus</i> (Dautzenberg, 1927)	10	0.85	6	2.11	2	0.71	18	1.04
<i>Comus clerii</i> Reeve, 1844	1	0.09	1	0.35	–	–	2	0.12
<i>Cymatium parthenopeum</i> (von Salis, 1793)	16	1.37	12	4.21	11	3.90	39	2.25
<i>Dorsanum moliniferum</i> (Valenciennes, 1834)	5	0.43	5	1.75	2	0.71	12	0.69
<i>Fusinus brasiliensis</i> (Grabau, 1904)	20	1.71	6	2.11	7	2.48	33	1.90
<i>Natica cayennensis</i> Recluz, 1870	3	0.26	–	–	–	–	3	0.17
<i>Natica isabelleana</i> Orbigny, 1840	95	8.12	7	2.46	10	3.55	112	6.45
<i>Olivancillaria urceus</i> (Roding, 1798)	4	0.34	3	1.05	–	–	7	0.40
<i>Phalium granulatum</i> (Born, 1778)	2	0.17	–	–	–	–	2	0.12
<i>Pleurotomella aguayoi</i> (Carcelles, 1953)	4	0.34	1	0.35	1	0.35	6	0.35
<i>Polinices hepaticus</i> (Roding, 1798)	2	0.17	–	–	–	–	2	0.12
<i>Polinices lacteus</i> (Guilding, 1834)	5	0.43	–	–	2	0.71	7	0.40
<i>Prunum martini</i> (Petit, 1853)	3	0.26	–	–	–	–	3	0.17
<i>Stramonita haemastoma</i> (Linnaeus, 1767)	41	3.50	9	3.16	5	1.77	55	3.17
<i>Tonna galea</i> (Linnaeus, 1758)	6	0.51	2	0.70	–	–	8	0.46
<i>Trophon pelseneeri</i> Smith, 1915	1	0.09	–	–	–	–	1	0.06
<i>Zidona dufresnei</i> (Donovan, 1823)	1	0.09	–	–	–	–	1	0.06
Total	1170	100	285	100	282	100	1737	100

n, number of individuals; MA, males; NOF, non-ovigerous females; OF, ovigerous females.

In general, the ovigerous females occupied a lower diversity of shell species ($n=9$) than males ($n=19$) and non-ovigerous females ($n=11$) (Table I). In relation to the size of individuals the pattern of shell species occupation was more diversified in the intermediary size classes (3.5–6.5 mm SL) (Figure 2).

All regression analyses showed significant correlation ($P<0.05$); however, the regressions between hermit crabs and shell aperture width (SAW), and shell internal volume (SIV) gave the highest correlation values (Table II) and were considered the shell features that best characterized the association between *P. exilis* and the occupied shells.

From the total ($n=1737$) analysed shells, 42.2% ($n=733$) had epibionts covering the external surface. These were classified as: barnacles (*Octalasmis* spp. and *Balanus* spp.) (25.9%), bryozoans (*Conopeum* spp. and *Ascophora* spp.) (19.1%), polychaete tubes (Family Sabellidae) (13.1%), bivalve molluscs (*Chama* spp.), and polyplacophorans (*Ischnochiton* spp.) (1.2%). In some shells more than one group of epibionts was registered. No significant difference was observed between the occupation of shells with epibionts and the sex of hermit crabs ($P>0.05$). Less than 50% of the more common shells carried by *P. exilis* (*B. gradatum*, *C. parthenopeum*, and *N. isabelleana*) presented epibionts.

Significant differences in dimensions were observed between the four most occupied shell species (*B. gradatum*, *N. isabelleana*, *S. haemastoma*, and *C. parthenopeum*). The mean values of dry weight (SDW) and aperture width (SAW) of *B. gradatum* and *S. haemastoma* shells did not show significant differences between each other ($P>0.05$), but they were significantly ($P<0.05$) larger than *N. isabelleana* and *C. parthenopeum*. The mean aperture

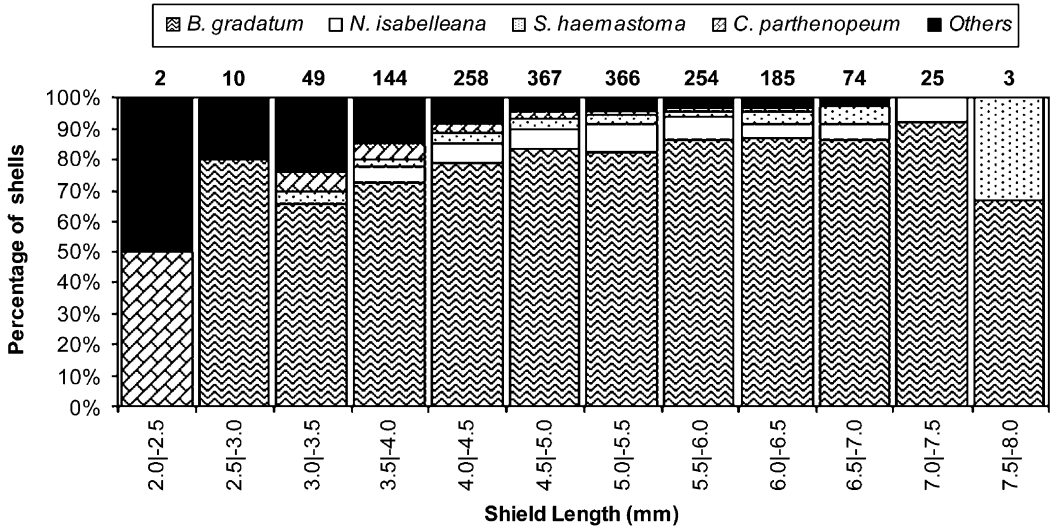


Figure 2. *Pagurus exilis*: percentage of the four most occupied shells as a function of the hermit crab size frequency distribution (numbers above columns represent number of individuals in each size class).

Table II. *Pagurus exilis*: regression equations for the two most occupied shell species.

Shell species	<i>n</i>	Relationship	Linear equation, $Y=aX^b$	Transformed, $\ln Y=\ln a+b \ln X$	<i>r</i>
Total	1736	SL \times SAL	$SAL=5.80 SL^{0.65}$	$\ln SAL=1.76+0.65 \ln SL$	0.59*
	1736	SL \times SAW	$SAW=1.96 SL^{0.84}$	$\ln SAW=0.67+0.84 \ln SL$	0.73*
	1736	SL \times SDW	$SDW=0.08 SL^{1.86}$	$\ln SDW=-2.53+1.86 \ln SL$	0.58*
	1518	SL \times SIV	$SIV=0.04 SL^{2.20}$	$\ln SIV=-3.22+2.20 \ln SL$	0.67*
	1736	WW \times SAL	$SAL=18.48 WW^{0.19}$	$\ln SAL=2.92+0.19 \ln WW$	0.64*
	1736	WW \times SAW	$SAW=8.56 WW^{0.24}$	$\ln SAW=2.15+0.24 \ln WW$	0.76*
	1736	WW \times SDW	$SDW=2.29 WW^{0.58}$	$\ln SDW=0.83+0.58 \ln WW$	0.67*
	1518	WW \times SIV	$SIV=1.78 WW^{0.69}$	$\ln SIV=0.58+0.69 \ln WW$	0.78*
<i>B. gradatum</i>	1423	SL \times SAL	$SAL=5.04 SL^{0.74}$	$\ln SAL=1.62+0.74 \ln SL$	0.69*
	1423	SL \times SAW	$SAW=2.02 SL^{0.82}$	$\ln SAW=0.70+0.82 \ln SL$	0.75*
	1423	SL \times SDW	$SDW=0.08 SL^{1.94}$	$\ln SDW=-2.53+1.94 \ln SL$	0.63*
	1246	SL \times SIV	$SIV=0.04 SL^{2.19}$	$\ln SIV=-3.22+2.19 \ln SL$	0.69*
	1423	WW \times SAL	$SAL=18.81 WW^{0.23}$	$\ln SAL=2.93+0.23 \ln WW$	0.77*
	1423	WW \times SAW	$SAW=8.53 WW^{0.24}$	$\ln SAW=2.14+0.24 \ln WW$	0.79*
	1423	WW \times SDW	$SDW=2.48 WW^{0.62}$	$\ln SDW=0.91+0.62 \ln WW$	0.71*
	1246	WW \times SIV	$SIV=1.82 WW^{0.70}$	$\ln SIV=0.60+0.70 \ln WW$	0.79*
<i>N. isabelleana</i>	112	SL \times SAL	$SAL=8.01 SL^{0.32}$	$\ln SAL=2.08+0.32 \ln SL$	0.41*
	112	SL \times SAW	$SAW=4.20 SL^{0.42}$	$\ln SAW=1.44+0.42 \ln SL$	0.44*
	112	SL \times SDW	$SDW=0.17 SL^{0.95}$	$\ln SDW=-1.77+0.95 \ln SL$	0.40*
	93	SL \times SIV	$SIV=0.30 SL^{0.76}$	$\ln SIV=-1.20+0.76 \ln SL$	0.35*
	112	WW \times SAL	$SAL=14.37 WW^{0.12}$	$\ln SAL=2.67+0.12 \ln WW$	0.51*
	112	WW \times SAW	$SAW=9.02 WW^{0.14}$	$\ln SAW=2.20+0.14 \ln WW$	0.48*
	112	WW \times SDW	$SDW=0.99 WW^{0.39}$	$\ln SDW=-0.01+0.39 \ln WW$	0.53*
	93	WW \times SIV	$SIV=1.29 WW^{0.39}$	$\ln SIV=0.25+0.39 \ln WW$	0.60*

n, number of individuals; SL, shield length; WW, wet weight of hermit crabs; SAL, shell aperture length; SAW, shell aperture width; SDW, shell dry weight; SIV, shell internal volume. *Significant correlation ($P<0.05$).

length (SAL) of *B. gradatum*, *S. haemastoma*, and *C. parthenopeum* shells did not show significant differences between each other ($P > 0.05$), but they were significantly larger ($P < 0.05$) than *N. isabelleana*. *Buccinanops gradatum* had significantly larger internal volume than the other shells ($P < 0.05$).

Significant differences ($P < 0.05$) were detected in relation to the sex of the total number of individuals and the size of occupied shells. Males occupied significantly larger shells in relation to aperture length and width, internal volume, and dry weight than females; ovigerous females occupied the lightest shells; among females (ovigerous and non-ovigerous) there were no significant differences ($P > 0.05$) in occupation regarding the aperture length and width, and the shell internal volume. Nevertheless, analyzing the individuals according to the size classes males showed significant differences in relation to females (ovigerous or not) only at some classes (4.5|–5.0, 5.5|–6.0 and 6.0|–6.5; $P < 0.05$).

Discussion

Hermit crabs represent a promising crustacean group for study because establishment of these animals in different habitats derives from the evolution of adaptative population strategies (Mantelatto and Sousa 2000). These crustaceans are ideal organisms in which to investigate the relationship between energy gain and resource choice because it is easy to measure and manipulate the empty shells of dead gastropods that the crabs occupy as a movable habitat (Yoshino et al. 1999).

The population dynamics of hermit crabs is closely tied to the species of gastropods that are present in the habitat. *Pagurus exilis* occupied 19 gastropod shell species. Some of these occupations were considered accidental (*Buccinanops deformis*, *Conus clerii*, *Phalium granulatum*, *Polinices hepaticus*, *Prunum martini*, *Trophon pelsenerii*, and *Zidona dufresnei*), because of the low occupancy rates.

Buccinanops gradatum shells were significantly the most frequently occupied (82%), evidencing a low shell species occupation regarding gastropod species diversity. Also, the fact that this shell species is the most available in nature (A. L. Meireles, personal communication) and that it is the preferred one in laboratory conditions (Mantelatto et al. forthcoming) lead us to conclude that *P. exilis* occupies the most available and preferred shell species in nature. In Argentina, this hermit crab species showed high number of shell species occupation, and the species most occupied (*Buccinanops cochlidium*) corresponded to only 29% of the total individuals collected (M. Scelzo, personal communication). Some of these differences are part of a broad range of adaptations to reproduce and survive successfully in different areas that are strongly related to gastropod shell utilization. Furthermore, the diversity of hermit crab species in a specific locality is related to the latitudinal distribution not only of the gastropods supplying the shells, but to that of other species of hermit crabs competing for those shells (Mantelatto and Garcia 2000).

Studies with different hermit crabs species inhabiting other areas on the northern coast of Brazil demonstrated that the shell types utilized may vary. At Anchieta Island, Faria (2004) reported that *Cerithium atratum* (Born, 1778) was the shell most occupied (89.3%) by *Pagurus criniticornis* (Dana, 1852), showing a low shell species occupation. Conversely, *Paguristes tortugae* Schmitt, 1933 (Mantelatto and Dominciano 2002), *Paguristes erythropus* Holthuis, 1959 (Garcia 2003), and *Pagurus brevidactylus* (Stimpson, 1859) (Mantelatto and Meireles 2004) also at Anchieta Island, showed a high shell species occupation (Table III). Furthermore, the different use of resources among competing species is a principal

Table III. *Pagurus exilis*: gastropod shell utilization by hermit crab species from the northern coast of São Paulo State, Brazil.

Species	<i>n</i>	Most occupied shells	Best relationship	Locality	Reference
<i>Calcinus tibicen</i> (Herbst, 1791)	15	Pa (35%), Ao (19%), Ca (14%)	WW × SDW	Anchieta Island	Garcia and Mantelatto (2000)
	8	Sh (71%), Ln (16%), Pa (7%)	SL × SDW	Ubatuba	Mantelatto and Garcia (2000)
<i>Dardanus insignis</i> (Saussure, 1858)	13	Ou (28%), Bg (25%)	SL × SAW	Ubatuba	Fernandes-Góes (1997)
	14	Ou (48%), Bg (14%)	WW × SIV	Ubatuba	Fernandes-Góes (2000)
<i>Isocheles sawayai</i> Forest and Saint Laurent, 1967	5	S (80%), B (13%)	SL × SAW	Ubatuba	Pinheiro et al. (1993)
<i>Loxopagurus</i> <i>loxochelis</i> (Moreira, 1901)	6	Ou (53%),Bg (39%)	WW × SDW	Ubatuba	Martinelli and Mantelatto (1999)
<i>Paguristes erythropus</i> Holthuis, 1959	23	Pa (21%), Sh (15%), Sp (14%)	SL × SIV	Anchieta Island	Garcia (2003)
<i>Paguristes tortugae</i> Schmitt, 1933	1	S (100%)	SL × SWW	Ubatuba	Negreiros-Fransozo and Fransozo (1992)
	21	Pa (35%), Ca (28%)	SL × SDW	Anchieta Island	Mantelatto and Dominciano (2002)
<i>Pagurus brevidactylus</i> (Stimpson, 1859)	17	Ca (48%), Mn (42%)	SL × SIV	Anchieta Island	Mantelatto and Meireles (2004)
<i>Pagurus criniticornis</i> (Dana, 1852)	16	Ca (89%)	SWW and SIV	Anchieta Island	Faria (2004)
<i>Pagurus exilis</i> (Benedict, 1892)	19	Bg (82%)	SW × SIV; SW × SAW	Caraguatatuba	Present study
<i>Petrochirus diogenes</i> (Linnaeus, 1758)	12	Tg (61%), Zd (16%)	WW × SAW; SL × SAW	Ubatuba	Bertini and Fransozo (2000)

n, total number of occupied shells; Ao, *Astraea olfersii* (Philippi, 1844); B, *Buccinanops*; Bg, *Buccinanops gradatum*; Ca, *Cerithium atratum*; Ln, *Leucozonia nassa* (Gmelin, 1791); Mn, *Morula nodulosa* (C. B. Adams, 1845); Ou, *Olivancillaria urceus*; Pa, *Pisania auritula* (Link, 1807); S, *Stramonita (Thais)*; Sh, *Stramonita haemastoma*; Sp, *Strombus pugilis* Linnaeus, 1758; Tg, *Tonna galea*; Zd, *Zidona dufrseni*; SL, hermit shield length; SW, hermit shield width; WW, hermit wet weight; SAW, shell aperture width; SDW, shell dry weight; SWW, shell wet weight; SIV, shell internal volume.

mechanism to allow species coexistence, since the species can avoid negative effects from competition (Rosenzweig 1981). Hermit crabs' shell competition occurs mainly between individuals of similar size, independently of whether they are of the same species or not (Garcia 2003).

If a relationship exists between the pattern of hermit crab population and the resources, we may consider that the gastropod assemblage and its mortality rates will determine the shell types available to hermit crabs. Such availability may be influenced by species coexistence, which in turn is associated with the avoidance of resource overlap and competition.

Previous studies have shown that shell aperture width (SAW), shell weight (SW) and internal volume (SIV) to be the most important variables in shell occupation pattern by hermit crabs (Table III). In the present study the most occupied shells, *B. gradatum*, had the highest shell aperture width, weight and internal volume values, as well as the highest correlation coefficients of the shell aperture width and internal volume in relation to hermit

crab dimensions. These features, together with its availability in nature and the hermits' preference in laboratory conditions (Mantelatto et al. forthcoming) might contribute to explaining the observed high occurrence of *P. exilis* in *B. gradatum*.

Shell utilization pattern is related to habitat as a result of differences in local shell supply, i.e. gastropod assemblage and hermit crab community. In the present study there was a decrease in shell species diversity occupation by the small-sized hermit crabs which may be related to resource partition, or to low small gastropod species diversity in the area. On the contrary, *P. tortugae* and *P. brevidactylus* showed a decrease in shell species diversity occupation when there was an increase in hermit crab size (Mantelatto and Dominciano 2002; Mantelatto and Meireles 2004). Considering that small hermit crabs are more susceptible to predation (Yoshino et al. 2002) and less likely to win an adequate shell than large ones, for *P. exilis* growing as fast as possible to a size unendangered by predation, and to achieve reproductive size, would be advantageous for its population dynamics.

Depending on their sex or condition, animals might make different selections due to differences in the relative importance of each demand. The adequacy of shells that hermit crabs occupy affects aspects of crab growth and reproduction (Yoshino et al. 1999). Large shells allow growth while moderately small shells may restrict growth (Fotheringham 1976) although they promote allocation of energy to reproduction (Bertness 1981b).

Male crabs may select shells that will result in faster growth and females may select shells based on their benefit to egg production (Harvey 1990). The occupation of the largest shells by the males has been reported in other studies (Garcia and Mantelatto 2000; Mantelatto and Meireles 2004), and this occurs as a function of the size difference attained by the different sexes, as the males' investment on reproduction is lower than for females. Male *Pagurus exilis* attained larger sizes than females, evidencing sexual size dimorphism (Espósito et al. forthcoming) as reported for *Pagurus* species such as *P. criniticornis*, *P. brevidactylus*, *P. excavatus* (Herbst, 1791), and *P. filholi* (De Man, 1887) (Faria 2004; Mantelatto et al. 2005; Macpherson and Raventos 2004; Goshima et al. 1998, respectively).

Males of *P. exilis* occupied the largest shells and a great diversity of species whereas ovigerous females occupied fewer shell species and the lightest shells. Females might have more advantage in occupying lighter shells because of their energy expenditure in reproduction (Gherardi 1991). Furthermore, the benefits of having a heavier and/or a larger shell are higher in males, which could be more exposed to predation during intra-sexual contests for a female. Furthermore, reproductive success of females depends on their fecundity which is influenced by the quality of the shell they use. Therefore, in the period close to reproduction females may be expected to place a higher value on a shell and therefore to be more aggressive for a shell than in other seasons, and they more often win a contest (Yoshino and Goshima 2002). This may be applied partially to the population studied, according to the sexual differences shown in shell occupation among the hermit crab size classes.

Some shell features, such as the presence of anemones (Brooks and Gwaltney 1993; Sandford 2003), hydroid colonies (Buckley and Ebersole 1994; Sandford 2003), holes produced by gastropods (Pechenik and Lewis 2000), and the utilization of damaged shells, may affect (enhance and/or diminish) the hermit crabs' mortality and fitness. *Pagurus exilis* presented a low percentage of occupation ($n < 50\%$) of shells when they were colonized by epibionts. Barnacles were the most abundant, but their occurrence was low (25.9%) compared to the total number of analysed shells. These results differ from other species studied in the same region, which revealed more than 70% colonization by epibionts (Martinelli and Mantelatto 1998; Garcia 2003).

The occupation of colonized shells, especially by hydroid colonies, can potentially minimize predation levels, increase fitness, and reduce competition with other shell-seeking hermit crabs (Brooks and Mariscal 1985). However, certain hermit crabs still prefer bare shells to those colonized by hydroids. In this study we may assume that *P. exilis* may prefer the occupancy of bare shells instead of encrusted ones. A further investigation on shell selection in laboratory experiments may help to elucidate this point.

This study demonstrated that, despite the number of shell species occupied by *P. exilis*, there must exist a shell preference for *B. gradatum* which may be related to its features that best provide adequacy to the hermits and favour population maintenance and survivorship along the western Atlantic coast of Brazil.

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