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Research Article

Composition, density, and shell use of hermit crabs (Crustacea: Paguroidea) from subtidal boulder fields in southeastern Brazil

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ABSTRACT. Hermit crabs are common and abundant members of the intertidal community and in sublittoral bottoms, where they play a fundamental role in the trophic chain. This study aimed to determine the composition of the hermit crab fauna, to quantify the density in the natural environment, and to register shells use by main species from subtidal boulder fields, in an island off the southeastern Brazilian coast. Monthly samples were taken from March 2010 to February 2011 on boulder fields on Couves Island, Ubatuba, Brazil, during scuba diving daytime sessions. Three hundred and eighty-three crabs were collected by hand, in a quadrat of 20 m^2 belonging to five species: *Calcinus tibicen*, *Dardanus venosus*, *Pagurus brevidactylus*, *Paguristes tortugae*, and *Petrochirus diogenes*. The highest densities were recorded for *P. brevidactylus* and *P. tortugae*. Hermit crabs occupied shells of 15 gastropod species. *Cerithium atratum*, *Gemophos auritulus*, and *Morula nodulosa* comprised more than 80% of the occupation. The heterogeneity of boulder fields of Couves Island, composed almost entirely of small refuges and crevices, favors the exploration of hermit crab species recorded here, which are characterized by small size. These results, combined with the findings of further studies, can contribute to the development of effective monitoring programs for decapod crustacean species.

Keywords: Paguridae, Diogenidae, rocky bottom, shell occupancy, scuba dive, southeastern Brazil.

INTRODUCTION

Anomurans are a diverse decapod group, currently comprising 7 superfamilies, 20 families, over 200 genera, and 2500 species (Tudge *et al*., 2012; Bracken-Grissom *et al*., 2013). Hermit crabs are grouped into the superfamily Paguroidea, which includes more than 1100 species described worldwide (McLaughlin *et al.*, 2010). Besides being a diverse group, hermit crabs are common and abundant members of the intertidal community and sublittoral bottoms, where they play a fundamental role in the trophic chain (Hazlett, 1981; Negreiros-Fransozo *et al*., 1997; Iglesias & Raso, 1999). Abundance and density of hermit crabs can be very heterogeneous due to the tendency of many species to live in clusters (Gherardi & Vannini, 1992, 1993; Turra & Leite, 2000). Therefore, hermit crab density can vary widely and reach tens or hundreds of individuals per m^2 in tropical and subtropical regions (Gherardi, 1990; Siu & Lee, 1992; Barnes, 1997).

In Brazilian waters, some significant studies on the composition of hermit crab species have been performed by Hebling *et al.* (1994), Negreiros-Fransozo *et al*. (1997), Fransozo *et al.* (1998), and Leite *et al*. (1998) in the region of Ubatuba. Except by the latter study, where animals were manually captured along a perpendicular transects to the water line, all the other studies used material obtained by a shrimp fishery boat equipped with double-rig nets used for trawling, a method which is frequently used in Brazilian fishery of penaeid shrimps in coastal waters (Castilho *et al.*, 2008; Prantoni *et al.*, 2013). This method is efficient, but also significantly impacts the bottom community (Pauly *et al.*, 2002; Worm & Lenihan, 2014), because it generates a series of direct and indirect impacts, especially due to its low selectivity (Kaiser & Spencer, 1996; Rumohr & Kujawski, 2000; Worm & Lenihan, 2014).

In contrast, the use of scientific scuba diving to study decapods is an important addition to complement

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the traditional methodologies employed; it can be used for creating a decapod checklist and generally represents an important tool to study and monitor decapod assemblages in reef environments (Giraldes *et al*., 2012, 2015). During the last decade, an increasing number of studies in Brazil with decapods were made using scuba diving (Bouzon & Freire, 2007; Alves *et al.*, 2012; Giraldes *et al.*, 2015; Soledade *et al.*, 2015).

The following information is crucial for monitoring natural populations and communities: density of the organisms found in their natural environment (Costa *et al.*, 2012); resources explored by each species [*e.g.*, food (Chong & Sasekumar, 1981; Kyomo, 1999); feed and shelter sites (Wieters *et al.*, 2009); shells (Floeter *et al.*, 2000; Sallam *et al.*, 2008)], and additional population parameters [*e.g.*, reproductive period (Cobo, 2002); fecundity (Bertini & Baeza, 2014); geographical and ecological distribution (Bertini *et al.*, 2004)]. For hermit crabs, such information becomes even more relevant for species that have been explored by the Brazilian marine ornamental trade (*e.g.*, Gasparini *et al.*, 2005; D.F.R. Alves *pers. comm.*), without regulation and supervision, almost exclusively by extraction, reinforcing the importance of basic studies on these decapods.

This study investigated the composition of the hermit-crab fauna and quantified its density in subtidal boulder fields of an insular region in southeastern Brazil. In addition, since shells are a limiting resource for most hermit crab populations (Kellogg, 1976), shell occupancy was recorded.

MATERIALS AND METHODS

This study was conducted from March 2010 to February 2011 at Couves Island (23°25'25"S, 44°52' 03"W), in the coast of State of São Paulo, southeastern Brazil, nearly 6 km from the municipality of Ubatuba (Fig. 1). The samples were taken from the sheltered face of the island, on subtidal boulder fields, at depths of 5 to 10 m. Sampling was performed during scuba diving daytime sessions. The crabs were actively collected in a quadrat of 20 m^2 (2×10 m), settled monthly and randomly on subtidal rocky bottoms. We selected the boulder fields according to the definition provided by Le Hir & Hily (2005), which recommended using heterogeneous areas of rock, gravel, and soft sediment, thus favoring the formation of cavities and sheltered sediments. During diving sessions, the microhabitats occupied by each hermit crab were recorded (*e.g.*, on rocks or anthozoan colonies, crevices, fissures, cavities, and rocky/sand interface) to increase our information about the ecological distribution of these species.

Hermit crabs were identified according to Melo (1999), and their taxonomic status was determined following McLaughlin *et al*. (2010). Shell species were identified according to Rios (1994), and in some cases with help of specialists. Specimens were measured for cephalothoracic shield length (CSL = from the tip of the rostrum to the groove at the posterior edge) using a caliper (to the nearest 0.1 mm) under a stereoscopic microscope.

Specimens were sexed by the number of pleopods, *i.e.*, four unpaired pleonal appendages for female and three pleopods on the left side for males, as well as by the gonopore position, on the fifth and third pair of pereopods for females and males, respectively (Tudge *et al*., 2012). Individuals were grouped into three demographic categories: males (M), females (F), and ovigerous females (OF). The relative abundance (RA) was calculated for each species by the formula RA = n/N, where n is the number of specimens of each species obtained during the sample period, and N is the total number of specimens. Crab density was accessed for the number of individuals per m^2. Comparisons between densities were carried out with the Kruskal-Wallis test (Zar, 1999). Shell occupancy was analyzed by correspondence analysis (CA) with the software Statistica® 8.0 (StatSoft, 2007). Density index and CA was performed with species that represented more than 1% of all sampled specimens.

RESULTS

The hermit crabs collected on boulder fields of Ilha das Couves were represented by one Paguridae, *Pagurus brevidactylus* (Stimpson, 1859), and four Diogenidae, *Calcinus tibicen* (Herbst, 1791), *Dardanus venosus* (H. Milne Edwards, 1848), *Paguristes tortugae* Schmitt, 1933, and *Petrochirus diogenes* (Linnaeus, 1758). A total of 383 individuals were collected. The highest relative abundance values were recorded for *P. brevidactylus* (RA = 0.559) and *P. tortugae* (RA = 0.405), while low relative abundance index values were obtained for *C. tibicen* (RA = 0.021), *D. venosus* (RA = 0.013), and *P. diogenes* (RA = 0.003). The most abundant species, *P. brevidactylus* (Fig. 2a), was represented by 214 specimens (115 males, 90 females, and 67 ovigerous females). Specimen size ranged from 1.0 to 3.5 mm CSL, with a mean size of 2.0 ± 0.4 mm CSL. This species was collected mainly on rocks and associated with Anthozoa such as *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860).

One hundred and fifty-five specimens of *P. tortugae* (Fig. 2b) were collected (69 males, 30 females, and 56 ovigerous females), with mean size 4.1 ± 1.4 mm CSL, ranging from 1.1 to 7.3 mm CSL. Specimens were collec-

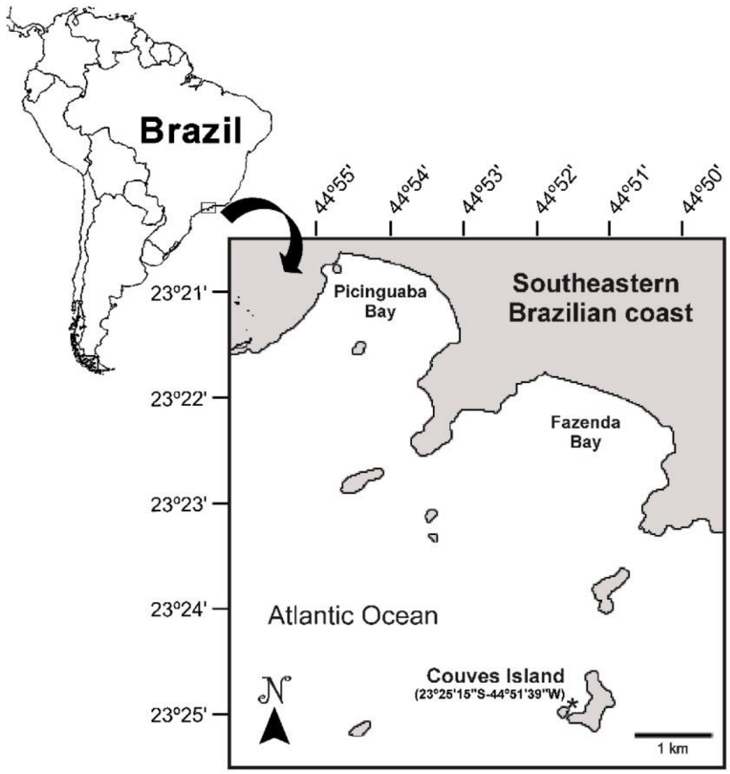

Figure 1. Sampling location of Couves Island, Ubatuba, São Paulo, southeastern Brazilian coast (asterisk indicates the sampling location).

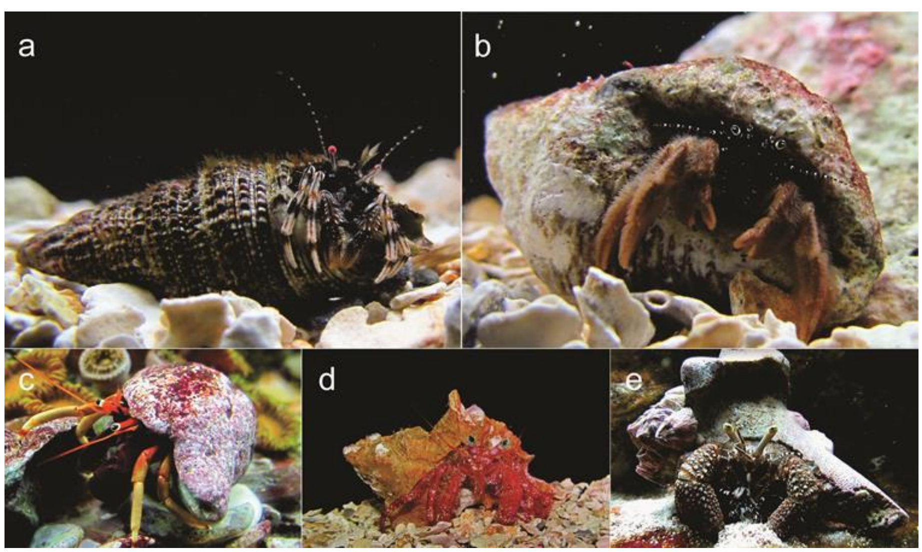

Figure 2. *Ex situ* hermit crabs from Couves Island boulder fields in southeastern Brazilian coast. a) *Pagurus brevidactylus* (Stimpson, 1859), b) *Paguristes tortugae* Schmitt, 1933, c) *Calcinus tibicen* (Herbst, 1791), d) *Dardanus venosus* (H. Milne Edwards, 1848), e) *Petrochirus diognes* (Linnaeus, 1758) (Photos: D.F.R. Alves).

collected mainly in fissures and sheltered sites, often showing clustering behavior. Eight specimens of *C. tibicen* (Fig. 2c) were collected (1 male, 3 females, and 4 ovigerous females), with mean size 3.1 ± 2.7 mm CSL, ranging from 1.9 to 6.7 mm CSL. Five specimens of *D. venosus* (Fig. 2d) were obtained (2 males and 3 females), with mean size 5.1 ± 1.6 mm CSL, ranging from 4.5 to 6.6 mm CSL. Specimens of both species were collected in cavities and sheltered sites. One male specimen of *P. diogenes* (Fig. 2e) was collected at 10 m depth, on rocky/sand interface, and with 33 mm CSL.

Significant differences were recorded between hermit-crab species densities (Kruskal-Wallis test, H = 36.90504; $P < 0.001$). The highest density means were obtained for *P. brevidactylus* (0.892 ± 0.61 ind m^{-2}) and *P. tortugae* (0.646 ± 0.25 ind m^{-2}), whereas the lowest density means were recorded for *C. tibicen* (0.033 ± 0.07 ind m^{-2}) and *D. venosus* (0.021 ± 0.07 ind m^{-2}) (Fig. 3).

The hermit crabs occupied shells of 15 gastropod species (Table 1; Figs. 4-6). Shells of *Cerithium atratum* (Born, 1778), *Gemophos auritulus* (Link, 1807), and *Morula nodulosa* (C.B. Adams, 1845) were used most frequently and comprised combined more than 80% of the shells occupied by all hermit crab species. Correspondence analysis (CA) (Fig. 7) indicated a major correspondence of *P. tortugae* and the use of a great variety of gastropod shells, especially of *G. auritulus* and *C. atratum*. Results also revealed that *D. venosus* (Fig. 7) and *P. diogenes* (Table 1) occupied shells of *Olivancillaria urceus* (Röding, 1798) and *Adelomelon becki* (Broderip, 1836), respectively, species not explored by the other hermit crab species.

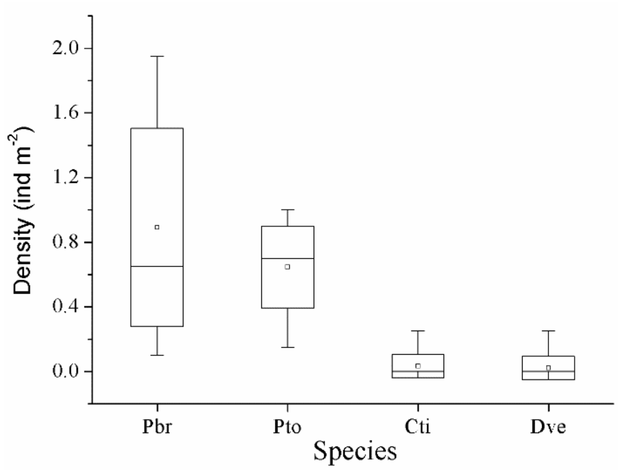

Figure 3. Hermit crab density of boulder fields from Couves Island, southeastern Brazilian coast. Pbr: *Pagurus brevidactylus*; Pto: *Paguristes tortugae*, Cti: *Calcinus tibicen*, Dve: *Dardanus venosus.* Square = mean, box = standard deviation, line = minimum and maximum.

DISCUSSION

The hermit crab fauna from boulder fields at Couves Island, Brazil, was numerically dominated by *P. brevidactylus* and *P. tortugae*. This statement is confirmed by results obtained from RA and density analysis. Similar results have been reported by Mantelatto & Garcia (2002) for the infralittoral zone of Anchieta Island, São Paulo, Brazil. However, they have registered some species that were not recorded in the present study, *i.e.*, *Dardanus insignis* (De Saussure, 1858), *Paguristes erythrops* Holthuis, 1959, *Pagurus criniticornis*, and *Pseudopaguristes calliopsis* (Forest & De Saint Laurent, 1968). The absence of these species in the present study is probably due by the fact that they are typically found in non-consolidated bottoms; since the sample procedures of the present study aimed to collect hermit crab species from boulder fields, these species were not really expected to be obtain here. In this sense, *Petrochirus diogenes* was recorded by one specimen in both studies, indicating that the occurrence of this hermit crab is occasional and uncommon in these environments, corroborating information provided by Melo (1999) that *P. diogenes* is a typical inhabitant of non-consolidated bottoms.

Of all species captured around Couves Island, *P. brevidactylus* and *P. tortugae* had the highest density levels. It is commonly believed that these species are part of the decapod fauna in southeastern Brazil, especially in the rocky sublittoral as described by Melo (1999) and observed by Mantelatto & Garcia (2002) and by Lima *et al.* (2014) for the coast of São Paulo State. In contrast, for *C. tibicen* and *D. venosus*, low densities were recorded in this study. The low density of *C. tibicen* may be associated with the type of environment these individuals normally occupy in that region. Species of the genus *Calcinus* are also found in subtidal regions (Haig & McLaughlin, 1983; Gherardi, 1990). They are most common in the littoral region, as observed for *Calcinus latens* (Randall, 1840) and *C. laevimanus* (Randall, 1840) by Barnes (1997) in Quirimba Island, Mozambique, *C. tibicen* by Fransozo *et al.* (2003) in Ubatuba, Brazil, and for *C. californiensis* Bouvier, 1898 by Arce & Alcaraz (2011) in Troncones, Mexico.

For *D. venosus* the low density could be the result of many factors. These include the following: 1) the likely fact that this species inhabits the interface between the rocky and the non-rocky sublittoral and/or greater depths, in higher densities (Mantelatto & Garcia, 2002; Almeida *et al.*, 2007); 2) its large body size, compared with other documented species, may be a limiting factor regarding the density of this hermit crab possibly because of the lower availability of larger shells in the environment, or the smaller number of refuge sites (crevices or indentations in rocks) that can be used to escape the action of a disturbing agent; 3) the need for a larger feeding area. According to the foraging theory, it is assumed that the energy requi-rements of larger organisms are proportionally higher,

Table 1. Shell occupancy by hermit crab species from Couves Island, southeastern Brazilian coast. n: total number of occupations, Pbr: *Pagurus brevidactylus*, Pto: *Paguristes tortugae*, Cti: *Calcinus tibicen*, Dve: *Dardanus venosus*, Pdi: *Petrochirus diogenes*.

Species	n	Pbr	Pto	Cti	Dve	Pdi
Adelomelon beckii (Broderip, 1836)	1					1
Cerithium atratum (Born, 1778)	77	41	30	6		
Coralliophila aberrans (C.B. Adams, 1850)	1	1				
Fusinus brasiliensis (Grabau, 1904)	1		1			
Gemophos auritulus (Link, 1807)	57	5	52			
Leucozonia nassa (Gmelin, 1791)	4	2	2			
*Lithopoma olfersii (*Philippi, 1846)	14	4	8	2		
Modulus modulus (Linnaeus, 1758)	1	1				
Monoplex parthenopeus (Salis Marschlins, 1793)	8		8			
Morula nodulosa (C.B. Adams, 1845)	144	127	17			
Olivancillaria urceus (Röding, 1798)	1				1	
Pisania pusio (Linnaeus, 1758)	23	3	20			
Siratus tenuivaricosus (Dautzenberg, 1927)	2		2			
Stramonita haemastoma (Linnaeus, 1767)	10		7		4	
Tegula viridula (Gmelin, 1791)	2	1	1			

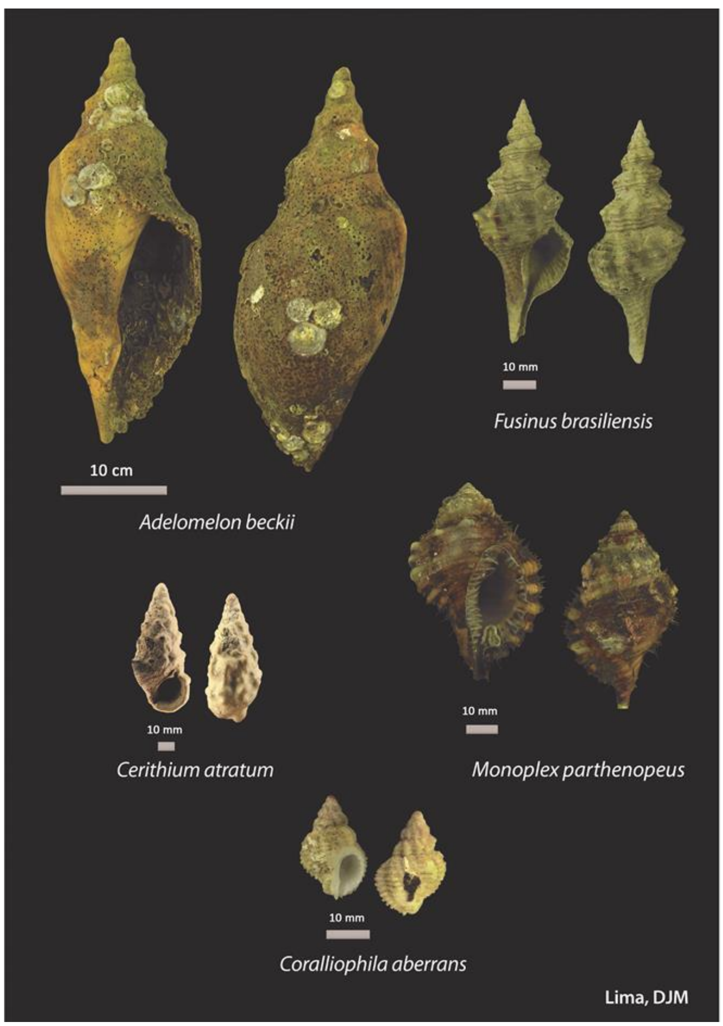

Figure 4. Gastropod shell species of the genus *Adelomelon*, *Fusinus*, *Cerithium*, *Cymatium*, and *Coralliophila* occupied by hermit crabs from Couves Island, southeastern Brazilian coast (Photos: D.J.M. Lima).

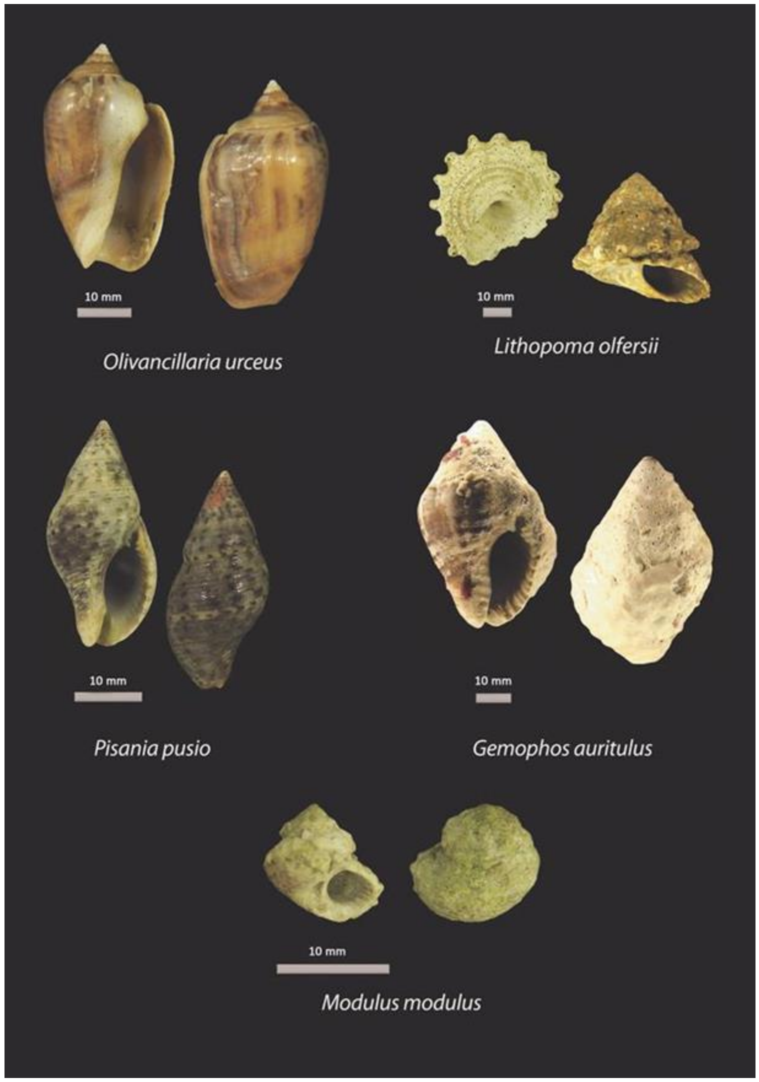

Figure 5. Gastropod shells species of the genus *Olivancillaria*, *Lithopoma*, *Pisania*, *Gemophos*, and *Modulus* occupied by hermit crabs from Couves Island, southeastern Brazilian coast (Photos: D.J.M. Lima).

which may directly affect species density (McNab, 1963; MacArthur & Levins, 1964; Krebs, 2008).

The hermit crabs were observed to forage typically on the rocky surface and in anthozoarian colonies (*e.g.*, *Palythoa caribaeorum*) or in crevices and shelters between rocks, forming aggregations with a variable number of individuals and species. Although we did not use any experimental method to evaluate clustering, this type of distribution is common and extensively documented in the literature, both for *in situ* and laboratory studies (*e.g.*, Gherardi, 1990; Turra & Leite, 2000). In hermit crab species that live in littoral zones, clustering can be understood as a strategy to protect the animals from environmental and biological stress, such as hydrodynamic forces, dissection, and predation (Meesters *et al.*, 2001; Le Hir & Hily, 2005). Although hydrodynamic forces exert more influence on littoral zones, with a tendency to lose energy with the increase of depth (Denny, 1988), these forces can influence the upper layer (up to a depth of 1 m) (Riedl, 1970) of subtidal zones. Besides that, clustering can be related to the "shell exchange markets" hypothesis, proposed by Gherardi & Vannini (1993), favoring the encounters between males and females and acting as a source of shell resource (Turra & Leite, 2000).

The hermit crabs sampled in the present study used mainly shells of three gastropods, *C. atratum*, *G. auritulus*, and *M. nodulosa*. Similar results were recorded by Mantelatto & Garcia (2002) and Meireles *et al.* (2003) for the hermit crab fauna from Anchieta Island; such pattern can be related to the high availability of these shells in shallow marine subtidal waters along the northeastern coast of São Paulo State (Meireles *et al.*, 2003). Previous studies regarding the

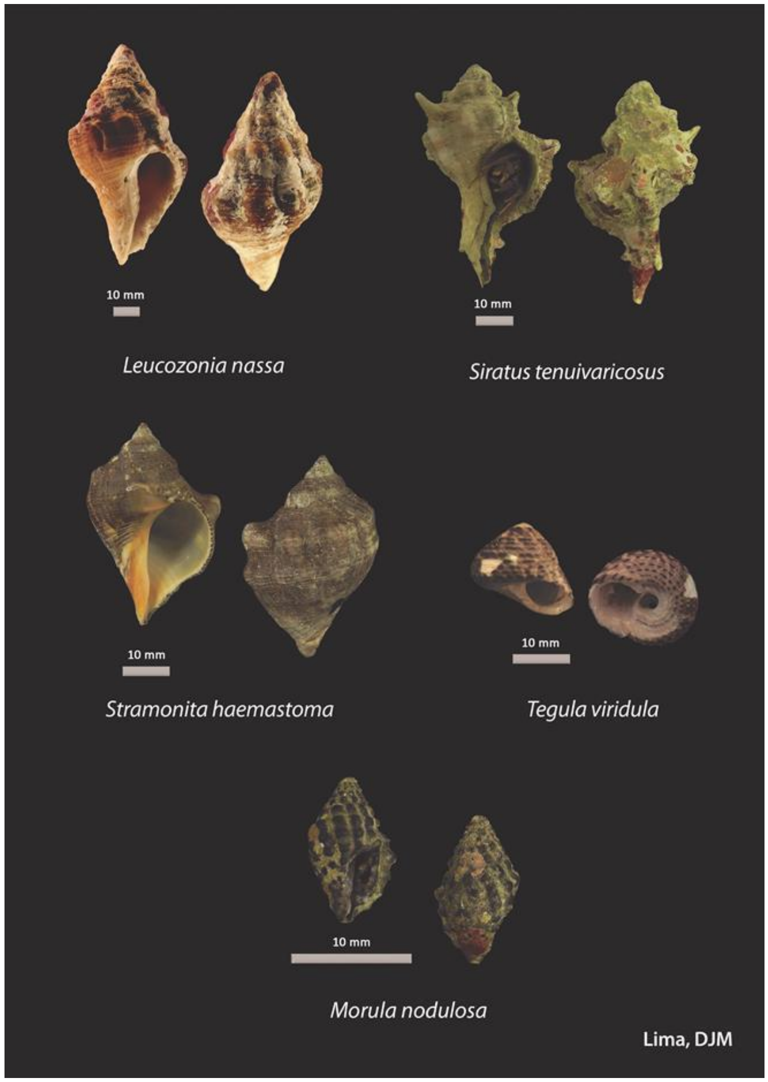

Figure 6. Gastropod shells species of the genus *Leucozonia*, *Siratus*, *Stramonita*, *Tegula*, and *Morula* occupied by hermit crabs from Couves Island, southeastern Brazilian coast (Photos: D.J.M. Lima).

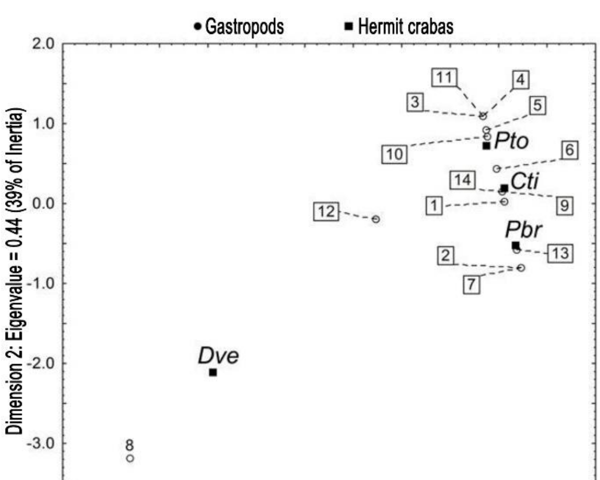

Figure 7. Correspondence analysis between hermit crab species and shell occupancy. Pbr: *Pagurus brevidactylus*, Pto: *Paguristes tortugae*, Cti: *Calcinus tibicen*, Dve: *Dardanus venosus*. 1 *Cerithium atratum*; 2 *Coralliophila aberrans*; 3 *Monoplex parthenopeus*; 4 *Fusinus brasiliensis*; 5 *Gemophos auritulus*; 6 *Lithopoma olfersii*; 7 *Modulus modulus*; *Olivancillaria urceus*; 9 *Leucozonia nassa*; 10 *Pisania pusio*; 11 *Siratus tenuivaricosus*; 12 *Stramonita haemastoma*; 13 *Morula nodulosa*; 14 *Tegula viridula*.

use of shells by hermit crabs pointed out that available shells are a scarce resource under natural conditions (Vance, 1972; Spight, 1977), and the occupation is therefore more related to shell availability than shell adequacy (Bertness, 1982).

Although shells of at least 12 gastropod species were available (Table 1), hermit crab specimens used mainly the three species listed above. We recorded an overlap in the shell use by hermit crabs from Couves Island, however, the results of the correspondence analysis indicated a preference in shell use (Fig. 7). Such pattern can be related to the use of the most adequate shells (*i.e.*, which reduce their predation risk, provide space for crab growth, enhance fecundity, and modulate reproductive activity) (see Turra & Leite, 2001). A good shell adequacy to the crabs can be associated with strong and significant relationships between shell parameters (*e.g.*, width, aperture length, and weight) and crab size (Scully, 1983). The higher occupation of *C. atratum* and *M. nodulosa* shells, high- and medium-spired, respectively, supports the hypothesis that hermit crabs tend to use spired and elongated shells for better protection against predation and physical stress (Turra & Denadai, 2001; Turra & Leite, 2003).

CONCLUSIONS

The hermit crab fauna sampled on subtidal boulder fields from Couves Island is mainly composed of small-sized species, which can be understood as a strategy, by increases the use of available refuges between rocks and other consolidated substrates. The hermit crab density recorded in this study was lower than in previous studies carried out in adjacent areas, which could be explained by the sampling method used, in particular when compared with studies carried out in non-consolidated subtidal regions. Shell occupancy overlap was found for almost all hermit crab species; however, the pattern of occupation indicates preferences in shell choice, where *P. brevidactylus*, *P. tortugae*, *C. tibicen* and *D. venosus* used mainly shells of *M. nodulosa*, *G. auritulus*, *C, atratum*, and *S. haemastoma* respectively. Although the shell occupancy seemed to be more related to shell availability than shell adequacy, hermit crabs preferred adequate shells. Finally, further studies regarding the composition and aspects of the structure and dynamics of hermit crab populations and communities are needed, because many species have been commercially extracted and exploited for marine ornamental trade without any regulation or supervision by governmental agencies.

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