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Shell occupation and ectosymbionts of two hermit crab species in the South Atlantic: a comparative analysis

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This study characterized shell occupation by two species of hermit crabs and analysed the occurrence of ectosymbionts on their shells, in a comparative way. The hermit crabs Clibanarius antillensis *and* Calcinus tibicen *were selected for this comparative study because of their abundance and wide distributions. Specimens were collected manually during spring low tides every 2 months, from February 2011 to January 2012 in north-eastern Brazil (03°S), and in south-eastern Brazil (23°S). The populations showed different patterns of shell occupation and ectosymbiont coverage. The plasticity of these ecological traits is discussed in a broad context and possibly correlated to habitat differences.*

Keywords: Brazil, *Clibanarius antillensis*, *Calcinus tibicen*, Diogenidae, symbiosis, habitat differentiation, gastropod shells

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INTRODUCTION

Hermit crabs are curious and conspicuous organisms that inhabit mostly intertidal environments of the world. These crustaceans use gastropod shells as a shelter to protect themselves against predators and desiccation (Reese, 1969; Bertness, 1981; Hazlett, 1981). The main factors that affect shell occupation in the field are related to availability and shell attributes such as weight, shape, architecture and internal volume (Hazlett, 1981). Adaptation to a particular shell species may differ among hermit crab species, reflecting numerous selective pressures, which may be associated with different habitats (Bertness, 1981; Garcia & Mantelatto, 2000). Furthermore, gastropod shells occupied by hermit crabs are an important substrate for settlement of ectosymbionts (epizoans and epiphytes) (Brooks & Mariscal, 1986; Wahl, 1989; Williams & McDermott, 2004). Ectosymbiont presence can influence many aspects of shell occupation, including shell selection and shell exchange (Grant & Pontier, 1973; Hazlett, 1981, 1984).

Most studies of ecological aspects of hermit crabs are restricted to certain localities. In Brazil, knowledge of shell occupation by hermit crabs in the field has accumulated in the last 15 years, and several studies have been conducted particularly on species/populations from the southern region (Mantelatto & Garcia, 2000; Mantelatto & Dominciano, 2002; Mantelatto & Meireles, 2004; Biagi *et al.*, 2006; Fantucci *et al.*, 2008). Considering that Brazil has an extensive coastline and a high diversity of habitats (Dominguez, 2006), in addition to a high richness and wide distribution of hermit crabs species, comparative studies could be useful for understanding intraspecific adaptations to different environmental conditions (Stearns, 1992; Wehrtmann *et al.*, 2012).

Here we present a comparative study in two regions of the Brazilian coast to evaluate the patterns of shell occupation in the field and the occurrence of ectosymbiotic organisms on the shells of two hermit crab species, comparing two different populations of each species, in order to further investigate the adaptation of species in different habitats. We chose to study *Clibanarius antillensis* Stimpson, 1859 and *Calcinus tibicen* (Herbst, 1791) (Melo, 1999), which are abundant in rocky beaches, especially in the mesolittoral portion, and have a wide geographic distribution, occurring from the Atlantic coast of the United States to southern Brazil (Melo, 1999).

MATERIALS AND METHODS

Site description and sampling methods

Two diogenid species of hermit crabs were selected for the study, *Clibanarius antillensis* Stimpson, 1859 and *Calcinus tibicen*

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Fig. 1. Study areas: (A) Pedra Rachada Beach, Paracuru, Ceará, north-eastern region; (B) Araçá Beach, São Sebastião, São Paulo, south-eastern region; (C) Grande Beach, Ubatuba, São Paulo, south-eastern region.

(Herbst, 1791). Specimens were randomly captured manually during about 1 h by one person in low-tide periods in order to obtain specimens of different sizes, every 2 months from February 2011 to January 2012. Sampling was carried out in three different intertidal areas, in two geographic regions (Figure 1).

The first area, in north-eastern Brazil, is Pedra Rachada Beach, Paracuru, state of Ceará (03°23′52″S 39°00′47″W), where both species were collected. This beach has a sandstone reef about 3 km long, interrupted by sandbanks, with many species of algae and a wide diversity of marine invertebrates (Matthews-Cascon & Lotufo, 2006). The second area is Araçá Beach, São Sebastião, São Paulo state in south-eastern Brazil (23°49′41″S 45°25′22″W), where only individuals of *C. antillensis* were collected. This area is protected lowland in a bay, which contains one of the last remaining mangrove stands along the São Sebastião Channel. The environment is formed by sandy-mud sediments, gravels and mangrove roots, and is entirely uncovered at low tide (Amaral *et al.*, 2010). The third area is Grande Beach, Ubatuba, São Paulo (23°27′98″S and 45°03′49″W), where only individuals of *C. tibicen* were collected. This area has a sloping rocky profile with cracks and irregular surfaces, exposed to strong wave action (Mantelatto & Fransozo, 1998).

Laboratory analysis

After collection, the hermit crabs were placed in plastic bags and taken to the laboratory, where they were immediately frozen. There, they were carefully removed from their shells. The gastropod shells were identified according to Rios (2009), counted, and measured for aperture length (SAL) and width (SAW). The sex of hermit crabs was checked by the gonopore position (on the basis of the third pereopods in females and the fifth in males) and measured for the shield length (SL), i.e. the distance from the edge of the rostrum to the V-shaped groove in the posterior margin. The measurements were made with a vernier caliper (±0.01 mm accuracy).

The species of ectosymbionts that composed the fouling community were separated and identified to the lowest possible taxonomic level. Where this identification was not possible, ectosymbionts were classified in greater taxonomic groups and their frequency of occurrence was evaluated. We used a qualitative classification adopted from Ayres-Peres & Mantelatto (2010), which consisted of recording the presence or absence, and when possible, the position of these organisms on the surface of the shell. Most of the surfaces were completely covered, so it was not possible to describe the exact boundaries of many fouling organisms. In addition, we analysed the prevalence of ectosymbionts in occupied shells according to the terminology of Overstreet (1978) and Margolis *et al.* (1982) and checked the range of the number of ectosymbiont groups in colonized shells. We established the prevalence of fouling, consisting of the proportion of infested hosts, as the percentage of colonized shells by each ectosymbiont group. The abundance, i.e. the number of symbionts per host, and the intensity, i.e. the number of symbionts per infested host were not evaluated.

For damaged shells, the frequency and location of the damage were recorded. Damage location was characterized according to the position on the shells: aperture (including the siphon channel and internal/external lips), body whorl, spire and protoconch. Damage included mainly cracks, breaks and perforations.

Voucher specimens of hermit crabs were deposited in the carcinological collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS catalogue numbers 5744–5747).

Statistical procedures

The Pearson correlation was employed to determine the relationships among the SL, SAL and SAW. The G-Test was utilized to determine possible differences in shell occupation among males, non-ovigerous and ovigerous females. The Chi-square test was used to assess the crabs' occupancy of damaged and undamaged shells. All analyses were performed with a significance level (α) of 95% (Zar, 2010).

RESULTS

Shell occupation

Clibanarius antillensis

In total, 851 hermit crabs were sampled: 507 (59.6%) in the north-eastern region, occupying five species of gastropod shells, with *Cerithium atratum* and *Tegula viridula* being the shell species most occupied; and 344 (40.4%) in the south-eastern region, occupying eight species of gastropod shells, *C. atratum* being the most occupied (Table 1). Ovigerous females occupied the shell species *C. atratum* in both areas.

Table 1. Gastropod shell species occupied by the hermit crab *Clibanarius antillensis* in the two study areas in north-eastern and south-eastern Brazil.

Shell species	North-eastern								South-eastern							
	Males		NOVF		OVF		Total		Males		NOVF		OVF		Total	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	
Astralium latispina (Philippi, 1844)	2	0.64	0	0.00	0	0.00	2	0.4	1	0.46	0	0.00	0	0.00	1	0.29
Cerithium atratum (Born, 1778)	158	50.8	46	79.31	138	100	342	67.45	176	81.48	57	96.62	68	100	301	87.5
Chicoreus brevifrons (Lamarck, 1822)	0	0.00	0	0.00	0	0.00	0	0.00	2	0.92	0	0.00	0	0.00	2	0.58
Monoplex parthenopeus (Salis-Marschlins, 1793)	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.29
Leucozonia nassa (Gmelin, 1791)	10	3.22	3	5.18	0	0.00	13	2.56	1	0.46	0	0.00	0	0.00	1	0.29
Pisania pusio (Linnaeus, 1758)	4	1.29	1	1.72	0	0.00	5	0.99	0	0.00	0	0.00	0	0.00	0	0.00
Stramonita brasiliensis Claremont & Reid, 2011	2	0.64	0	0.00	0	0.00	2	0.4	13	6.02	2	3.38	0	0.00	15	4.36
Strombus pugilis Linnaeus, 1758	0	0.00	0	0.00	0	0.00	0	0.00	4	1.85	0	0.00	0	0.00	4	1.17
Tegula viridula (Gmelin, 1791)	135	43.41	8	13.79	0	0.00	143	28.2	19	8.81	0	0.00	0	0.00	19	5.52
Number of occupied species	6	4	1	6	7	2	1	8								

N, number of occupied shells; NOVF, non-ovigerous females; OVF, ovigerous females.

Males occupied six species in the north-east and eight species in the south-east, while non-ovigerous females occupied respectively four and two species in the two areas (Table 1).

There were significant differences in the proportion of shells occupied by males and females (non-ovigerous and ovigerous) in the north-east (G = 154.8244, df = 10, $P < 0.0001$) and south-east (G = 35.7942, df = 14, $P < 0.001$).

The relationships between the shell dimensions (SAL and SAW) and shield length (SL) were positive, and most were significant for the shells that were most occupied (Table 2).

Calcinus tibicen

In total, 377 hermit crabs were sampled: 247 (65.5%) in the north-eastern region, occupying nine species of gastropod shells, with *T. viridula* being the shell most occupied; and 130 (34.5%) in the south-eastern region, occupying five species of gastropod shells, with *Stramonita brasiliensis* being the shell most occupied (Table 3). Ovigerous females occupied four species of gastropod shells in the northeast, most frequently *T. viridula*. In the south-east, only three species of gastropod shells were occupied by ovigerous females, of which *S. brasiliensis* was the most frequent. Males occupied nine shell species in the north-east and four in the south-east. Non-ovigerous females occupied seven and five species in the north-east and south-east respectively (Table 3).

The proportions of shells occupied by males and females (non-ovigerous and ovigerous) differed significantly in the north-east (G = 33.9098; df = 16; $P < 0.005$), but not in the south-east (G = 12.6322; df = 8; $P = 0.1251$).

The relationships between the shell dimensions (SAL and SAW) and shield length (SL) were positive, and most were significant for the most-occupied shell species (Table 4).

Shell damage

Clibanarius antillensis

The percentage of damaged shells occupied was not significant in the north-east (N = 283; 55.82%; $\chi^2 = 2.899$, $P = 0.1058$) and the south-east (N = 344; 49.42%; $\chi^2 = 0.8715$, $P = 0.8715$). Most of the damage was to the shell aperture; damage to the body whorl, protoconch and spire was less frequent (Table 5).

Calcinus tibicen

In this species, the percentage of damaged shells was not significant in the north-east (N = 247; 45.35%; $\chi^2 = 2.142$; $P = 0.1616$), while in the south-east the percentage was significantly high (N = 130; 70%; $\chi^2 = 20.80$; $P < 0.0001$). Damage to the shell aperture was the most common in both areas (Table 5).

Characterization of ectosymbionts

Clibanarius antillensis

In the north-east, 91.91% (N = 466) of the shells were incrusted by ectosymbionts, while in the south-east, the percentage was 52.27% (N = 197). In both regions, some shells

Table 2. *Clibanarius antillensis*. Correlation analysis between SL × SAL and SAW for shells most occupied in north-eastern and south-eastern Brazil.

Brazilian region	Most occupied shells	Relation	Linear equation	*r*	*t*	*P*
North-eastern	*Cerithium atratum*	SL × SAL	SAL = 1.33SL + 4.44	0.51	8.2088	<0.0001
		SL × SAW	SAW = 0.45SL + 3.15	0.30	4.3602	<0.0001
	Tegula viridula	SL × SAL	SAL = 0.19SL + 6.70	0.18	1.8256	0.0708^{ns}
		SL × SAW	SAW = 0.65SL + 5.37	0.14	1.4427	0.1521^{ns}
South-eastern	*Cerithium atratum*	SL × SAL	SAL = 1.55SL + 4.88	0.52	8.4151	<0.0001
		SL × SAW	SAW = 0.81SL + 2.92	0.51	8.2543	<0.0001

-SL, shield length; SAL, shell aperture length; SAW, shell aperture width; R, correlation coefficient; *t*, value of Student's *t* test.
ns, not statistically significant.

Table 3. Gastropod shell species occupied by the hermit crab *Calcinus tibicen* in the two study areas in north-eastern and south-eastern Brazil.

Shell species	Northeastern								Southeastern							
	Males		NOVF		OVF		Total		Males		NOVF		OVF		Total	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	
Astralium latispina (Philippi, 1844)	2	1.69	1	1.11	0	0.00	3	1.21	0	0.00	0	0.00	0	0.00	0	0.00
Cerithium atratum (Born, 1778)	5	4.2	12	13.34	1	2.65	18	7.29	0	0.00	0	0.00	0	0.00	0	0.00
Monoplex parthenopeus (Salis-Marschlins, 1793)	0	0.00	1	1.11	0	0.00	1	0.4	0	0.00	0	0.00	0	0.00	0	0.00
Leucozonia nassa (Gmelin, 1791)	7	5.89	9	10	7	18.41	23	9.31	10	12.82	4	18.19	7	23.33	21	16.15
Olivancillaria deshayesiana (Ducros de Saint Germain, 1857)	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	4.54	0	0.00	1	0.77
Pisania pusio (Linnaeus, 1758)	16	13.44	11	12.22	4	10.52	31	12.55	1	0.13	1	4.54	0	0.00	2	1.54
Pleuroploca aurantiaca (Lamarck, 1816)	8	6,72	0	0.00	0	0.00	8	3.25	0	0.00	0	0.00	0	0.00	0	0.00
Stramonita brasiliensis Claremont & Reid, 2011	8	6,72	2	2.22	0	0.00	10	4.05	63	80.77	12	54.54	19	63.33	94	72.31
Tegula viridula (Gmelin, 1791)	72	60.5	54	60	26	68.42	152	61.54	4	6.28	4	18.19	4	13.34	12	9.23
Turbinella laevigata Anto, 1839	1	0.84	0	0.00	0	0.00	1	0.4	0	0.00	0	0.00	0	0.00	0	0.00
Number of occupied species	8	7	4	9	4	5	3	5								

N, number of occupied shells; NOVF, non-ovigerous females; OVF, ovigerous females.

Table 4. *Calcinus tibicen*. Correlation between SL × SAL and SAW for the most-occupied shell species in north-eastern and south-eastern Brazil.

Brazilian region	Most occupied shells	Relation	Linear equation	*r*	*t*	*P*
North-eastern	*Tegula viridula*	SL × SAL	SAL = 0.4796SL + 5.4556	0.41	4.4970	<0.0001
		SL × SAW	SAW = 1.0045SL + 3.9273	0.45	5.0310	<0.0001
	Pisania pusio	SL × SAL	SAL = 1.7034SL + 6.9615	0.58	3.1515	<0.05
		SL × SAW	SAW = 1.0479SL + 1.4134	0.44	2.1705	<0.05
Southeastern	*Stramonita brasiliensis*	SL × SAL	SAL = 1.34SL + 1.0714	0.67	7.1484	<0.0001
		SL × SAW	SAW = 1.7034SL + 6.961	0.61	6.0261	<0.0001

N, number of individuals; SL, shield length; SAL, shell aperture length; SAW, shell aperture width; R, correlation coefficient; *t*, value of Student's *t* test.

Table 5. Relative frequencies of shell damage in different areas of shells occupied by the hermit crabs *Clibanarius antillensis* and *Calcinus tibicen* in the two study areas in north-eastern and south-eastern Brazil.

	% Occurrence of damage			
Hermit crab species	*Clibanarius antillensis*		*Calcinus tibicen*	
Brazilian Region	North-eastern	South-eastern	North-eastern	South-eastern
Shell zone				
Aperture	86.24	70.25	84.95	84.61
Body whorl	6.69	13.92	7.96	1.28
Protoconch	2.6	8.86	0.88	10.25
Spire	4.47	6.97	6.21	3.86

bore one or more groups of ectosymbiont organisms, but in the south-east the number of ectosymbionts found per shell was higher (Table 6). Fouling organisms most frequently found and with higher prevalence on shells in the north-east were calcareous algae (order Corallinales) and bryozoans (Figure 2A; Table 6). Other organisms occasionally found were tubes of spirorbid and serpulid polychaetes, filamentous algae of the genus *Ulva* Linnaeus, 1753 and the exotic invader bivalve *Isognomon bicolor* C. B. Adams, 1845, which was always located cryptically in the umbilical region of shells of *T. viridula*. Calcareous algae and bryozoans were the most common fouling organisms found on the two shell species that were most occupied (Figure 2B). In the south-east, the most frequent ectosymbionts and with higher prevalence were coralline algae and the oyster *Crassostrea brasiliana* (Lamarck, 1819) (Figure 2A; Table 6). Although less frequently, the following ectosymbionts were also observed: the bivalve genus *Chama* Linnaeus, 1758; egg capsules of gastropods of the family Neritidae; the slipper snail *Crepidula plana* Say, 1822; and the barnacle *Amphibalanus amphitrite* (Darwin, 1854). For the most occupied shells, calcareous algae and ostreid bivalves were the most frequent ectosymbionts (Figure 2B, C).

Calcinus tibicen

In the north-east, 89.47% (N = 247) of shells were incrusted by ectosymbionts, while in the south-east, the percentage was 94.31% (N = 130). In both regions, some shells bore

Table 6. Prevalence and range in number of ectosymbionts on shells occupied by the hermit crabs *Clibanarius antillensis* and *Calcinus tibicen* in the two study areas in north-eastern and south-eastern Brazil.

Hermit crab species	*Clibanarius antillensis*				*Calcinus tibicen*			
Fouling character	N colonized shells		% Colonized Shells		N colonized shells		% Colonized shells	
Brazilian Region	NE	SE	NE	SE	NE	SE	NE	SE
Ectosymbionts								
Calcareous algae	397	111	78.30	32.26	201	91	81.37	70
Filamentous algae	60	14	11.83	4.07	22	4	8.9	3.07
Bryozoa	150	13	29.58	3.78	52	66	21.05	50.7
Polychaeta	33	9	6.51	2.61	8	13	3.23	10
Mollusca	1	73	0.20	21.22	50	56	2.02	43.07
Crustacea (Cirripedia)	0	2	0	0.58	1	2	0.40	1.54
Brazilian Region	NE	SE				NE	SE	
Range in number of ectosymbiont groups per shell	1–3	1–4				1–3	1–4	

N, number of shells; NE, north-east region; SE, south-east region.

one or more groups of ectosymbiont organisms, but in the south-east, the number of ectosymbionts found per shell was higher (Table 6). In the north-east, calcareous algae, bryozoans and polychaete worm tubes were the most frequently found and with higher prevalence on shells (Figure 3; Table 6). Occasionally, the slipper snail *Crepidula plana* Say, 1822, was observed in the umbilical region of *T. viridula* shells and inside a shell of *P. aurantiaca*. In the south-east, the occurrence of ectosymbionts was similar, and the bivalve *Sphenia antillensis* Dall & Stimpson, 1901 was occasionally found associated with *S. brasiliensis* shells.

Calcareous algae and bryozoans were the most frequent ectosymbionts on the four most-occupied shell species in the north-east. In the south-east, this pattern was the same for the two most-occupied shell species, followed by polychaete worm tubes (Figure 3B, C).

DISCUSSION

Shell occupation

The two sympatric hermit crab species showed different patterns of shell occupation. In both areas, *C. antillensis* occupied mainly *C. atratum*, and *Calcinus tibicen* occupied mainly *T. viridula* in the north-eastern area and *S. brasiliensis* in the south-east. These shell species are widely distributed along the Brazilian coast (Rios, 2009). The shell of *O. deshayesiana* was occupied only in the south-east, but this species has only been recorded in the south and south-east of Brazil (Rios, 2009). The observed differences in shell occupation between the two species of hermit crabs may be directly influenced by the diversity of gastropod populations in the two areas and to the geographic distributions of these molluscs (Mantelatto *et al.*, 2010). However, studies concerning the diversity of gastropod molluscs in rocky beaches are scarce in Brazil (Veras *et al.*, 2013); such studies could help to characterize the potential source of shells used as shelters by hermit crabs. In addition, according to Martinelli & Mantelatto (1999), hermit crabs do not necessarily occupy the shells of all existent gastropod species in a given area, due to shell characteristics and conditions.

Shell utilization in the field by hermit crabs changes according to each species, but it is limited by shell availability (Reese, 1969). As hermit crabs are attracted by chemoreceptors to sites where gastropods are predated (McLean, 1974; Rittschof *et al.*, 1995), these crustaceans can obtain the shells quickly after their death, before they are damaged or destroyed (Hazlett, 1981). Shells may also be obtained directly from another hermit crab, by moving between adjacent zones where these crabs may share shells (Spight, 1977).

Other factors influencing shell occupation by hermit crabs are sex and reproductive status (Neil & Elwood, 1985). Male and female hermit crabs exhibit different behaviours in shell occupation. Because of their larger size, males are able to outcompete females when in agonistic conflicts for shell occupation (Hazlett, 1966; Bertness, 1981; Neil & Elwood, 1985). In this study, the sexes showed significant differences in patterns of shell occupation for *C. antillensis* in both areas and only in the north-east for *C. tibicen*. Other hermit crab species such as the pagurid *Pagurus brevidactylus* (Stimpson, 1859) in the sublittoral area of Anchieta Island (Ubatuba, São Paulo) also showed differences in shell occupation between the sexes, with males occupying predominantly shells of *C. atratum* and ovigerous females occupying *Morula nodulosa* (C. B. Adams, 1845) (Mantelatto & Meireles, 2004). In the diogenid *Isocheles sawayai* Forest & Saint Laurent, 1968, a study on Margarita Island (Venezuela) also found differences in shell occupation, with males occupying mainly shells of *L. nassa* and females occupying *Engoniophos unicinctus* (Say, 1826) (Galindo *et al.*, 2008). In the present study, for *C. antillensis*, shells of *C. atratum* were more occupied in both areas, while for *C. tibicen* three species of shells were mainly occupied, two of which are found in both areas. In the present study, ovigerous females showed a specific pattern of shell occupation: *C. antillensis* occupied only *C. atratum* shells in both areas, while *C. tibicen* ovigerous females occupied three species of shells, two of which are found in both areas. The high frequency of ovigerous females in a specific gastropod shell species is well documented (Bach *et al.*, 1976; Fotheringham, 1976). The limited occupation of shell species by ovigerous females suggests that the choice is restricted by the need for space to accommodate the egg mass (Mantelatto & Garcia, 2000) and therefore shell features such as internal volume and aperture width are very important (Mantelatto & Garcia, 2000; Frameschi *et al.*, 2013).

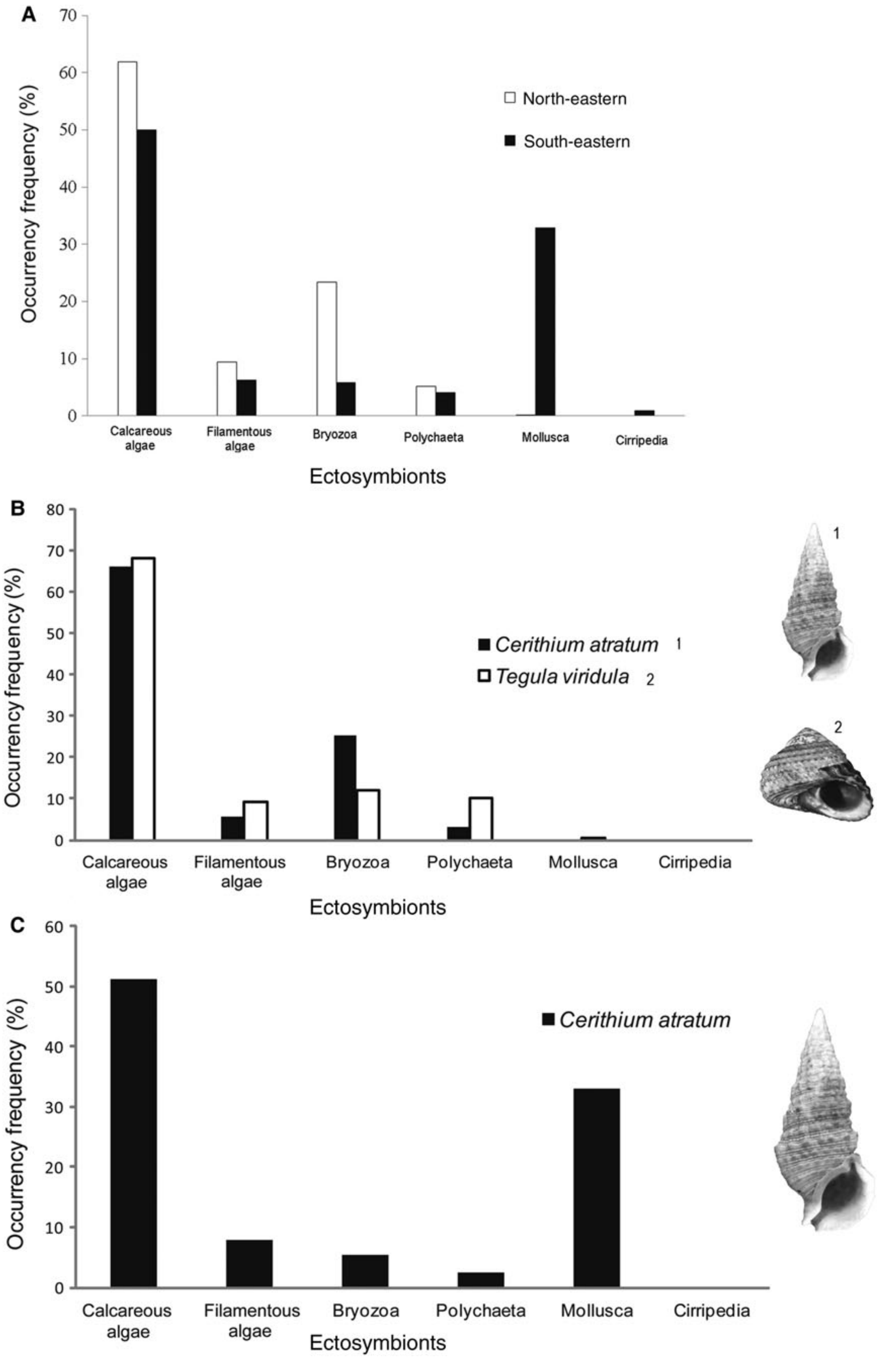

Fig. 2. *Clibanarius antillensis* ectosymbiont groups: (A) found on gastropod shells occupied in the north-eastern and south-eastern regions; (B) found on gastropod shells most often occupied in the two study areas in the north-eastern region and (C) south-eastern region.

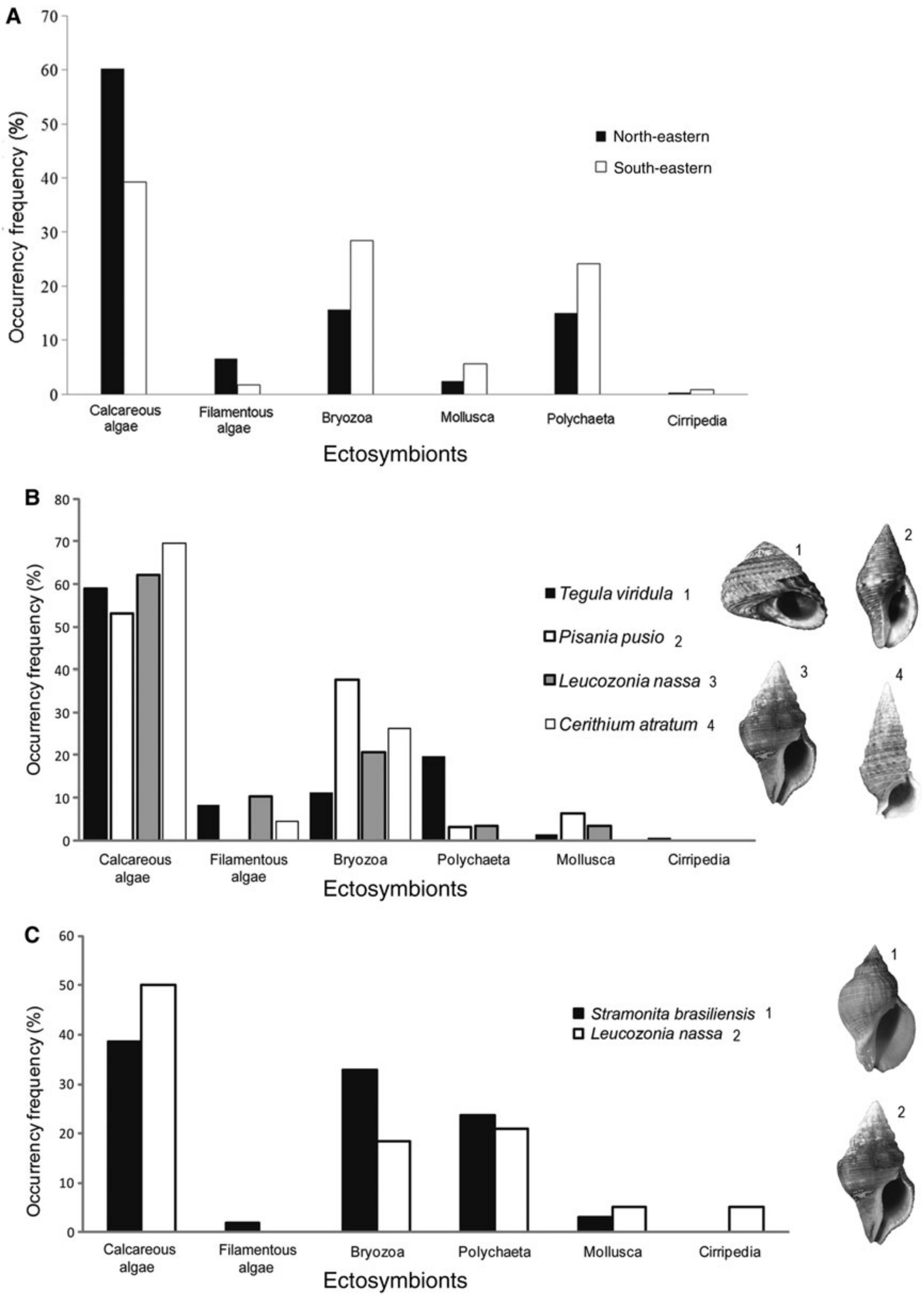

Fig. 3. *Calcinus tibicen* ectosymbiont groups: (A) found on gastropod shells occupied in the north-eastern and south-eastern regions; (B) found on gastropod shells most often occupied in the two study areas in the north-eastern region and (C) south-eastern region.

In addition, taking into account that these species are located in different types of environments according to the region, the spatial heterogeneity and physical and biological properties of these habitats can influence the occupation of different shells by each population (Dominciano *et al*., 2009; Teoh *et al*., 2014). In this study, we observed that the north-eastern locality is spatially more heterogeneous than the south-eastern localities. Although, we observed that only for non-ovigerous females of *C. antillensis* and for both sexes of *C. tibicen* there was a greater number of species of occupied shells in the north-east. A more heterogeneous habitat can provide a wider choice of shells, minimizing interspecific competition for the available shells (Teoh *et al.*, 2014). Some studies have shown differences in the shell occupation by hermit crabs between populations of the same species in different habitats (Leite *et al.*, 1998; Garcia & Mantelatto, 2000; Mantelatto *et al.*, 2007, 2010; Ayres-Peres *et al.*, 2012).

The positive relationships observed between hermit crabs and shell sizes indicates that larger individuals occupy larger shells, as observed by Turra & Leite (2001) for sympatric species of the genus *Clibanarius* in an intertidal zone. The coexistence of hermit crab species is closely related to shell occupation, and it is influenced by differences in the shell species presence and on a finer scale associated with shell selection and shell occupation patterns (Turra & Leite, 2001). Habitat segregation by hermit crabs in the intertidal zone is related to differences in the supply of shells (Spight, 1977), and can generate a sharing of resources, reducing interspecific competition.

Shell damage

Shells occupied by hermit crabs can be damaged by physical factors such as wave hydrodynamics, chemical degradation and biological action caused by ectosymbionts and even predators (Turra *et al.*, 2005). In this study, we suggest that predation and wave hydrodynamics could be important factors causing damage to the shells.

The damage to the shells was mostly located at or near the shell aperture. According to Bertness & Cunningham (1981), this type of damage can indicate high gastropod predation rates by brachyuran crabs (Turra *et al.*, 2005). These crustaceans are very common in Brazilian rock shores (Melo, 1996), especially the families Eriphiidae and Menippidae, represented respectively by two abundant species, *Eriphia gonagra* (Fabricius, 1781) and *Menippe nodifrons* Stimpson, 1859. These crabs are important predators of gastropods and hermit crabs in the intertidal zone (Rossi & Parisi, 1973) and frequently found in the study area in the north-east (Coelho *et al.*, 2008) and south-east regions (Bertini *et al.*, 2007; Amaral *et al.*, 2010). Claws of the crab *M. nodifrons* are well designed for breaking mollusc shells (Vermeij, 1977; Santana *et al.*, 2009). Turra (2003) reported similar damage for shells occupied by sympatric species of the genus *Clibanarius*, including *C. antillensis*, at Pernambuco Island, São Sebastião, São Paulo. Damaged shells could make hermit crabs more susceptible to predation by brachyuran crabs and increase exposure to the parasites (Reese, 1969) and osmotic stress (Shumway, 1978). In addition to predation by crabs, the high frequency of damage found in hermit crabs collected on Grande Beach (especially around the shell aperture) may be due to the strong waves and currents in this area (Fransozo & Mantelatto, 1998).

Other types of damage such as perforations along the spire or cracks in the protoconch were found in low percentages. Shells with this type of damage may be unfavourable for use, because damage to the upper shell prevents water retention during low tide, making the hermit crabs more susceptible to desiccation (Reese, 1969), especially in intertidal species.

In this study, we did not assess the presence of damage in unoccupied shells. Empty shells normally used by hermit crabs are rare in the rocky intertidal zone (Childress, 1972; Vance, 1972) and availability is directly related to environmental characteristics and the presence of live gastropods (Bollay, 1964; Mantelatto & Garcia, 2000). Shells in good condition (with no cracks or perforations) are ideal for hermit crabs and can be the result of non-destructive gastropod death due to desiccation, parasitism or diseases (Bertness, 1980). Pechenik & Lewis (2000) found that in *Pagurus longicarpus* Say, 1817, damage was more common in empty gastropod shells than in occupied shells, suggesting that individuals of this species avoid damaged shells. Hermit crabs seem to be able to discriminate between intact and damaged shells based on tactile cues, once broken shelters can increase the vulnerability of crabs under osmotic stress, predation and eviction by conspecifics (Pechenik & Lewis, 2000).

Characterization of ectosymbionts

Marine animals, especially crustaceans, are commonly associated with ectosymbiont organisms. In hermit crabs, these organisms are mainly associated on the surface of occupied gastropod shells. The few studies on the occurrence of ectosymbiont organisms on shells occupied by hermit crabs include those of Turra & Leite (2001) and Turra (2003), who investigated the ectosymbionts and adequacy of shells used by sympatric hermit crabs of the genus *Clibanarius* Dana, 1852 on the Island of Pernambuco, São Sebastião, São Paulo; and Ayres-Peres & Mantelatto (2010), who analysed the occurrence of ectosymbionts on shells used by *Loxopagurus loxochelis* Moreira, 1901 in two areas of the north-east coast of São Paulo. These studies were restricted to the southern region of Brazil. In the two hermit crab species studied in both areas, most of the shells were covered by ectosymbionts, mainly incrusting calcareous algae, bryozoans, polychaete worm tubes and ostreid bivalves.

Organisms that compose the macrophytobenthos, such as filamentous and coralline algae, are often found covering the shells, providing substrates for other species (Hazlett, 1984). Filamentous algae were found in shells of all populations. Hermit crabs can eventually decorate shells with algae to provide a food resource or camouflage. Some crustaceans such as spider crabs exhibit a curious behaviour in which they decorate themselves with materials from their environment, including algae, to provide camouflage against predators (Wicksten, 1993). Calcareous algae were the most frequent ectosymbionts and with higher prevalence, found on all parts of the shells and usually entirely covering them, leaving no space for the settlement of other organisms. The paucity of studies of epiphytes on shells occupied by hermit crabs does not allow comparisons, but the shells are important substrates for calcareous algae in the marine environment (Tendal & Dinesen, 2005).

Bryozoans were present in high percentages and prevalences, as also found by Ayres-Peres & Mantelatto (2010) for *L. loxochelis*. The high rate of occurrence of these organisms may stem from their high abundance in the surrounding environment and to the susceptibility of shells for settlement. Bryozoans produce calcareous colonies that can grow large enough to alter the morphology of the shells and may provide greater protection for the hermit crabs against predators, by strengthening the shell or by providing camouflage (Taylor, 1994; Sandford, 2003; Ayres-Peres & Mantelatto, 2010). The high incidence of bryozoan species indicates that these organisms may depend extensively on these crustaceans for settlement substrate (Taylor, 1994). In this contribution, bryozoan colonies were found mainly near the shell aperture, the inner lip or the siphonal canal. Taylor (1994) suggests that bryozoans settle near the shell aperture, often in grooves among the whorls. Some colonies can develop at the apex of the shells, as also observed in this study. In addition, bryozoan colonies may also be found on the surface of other marine organisms such as horse-shoe crabs and sea snakes (Key *et al.*, 1996) and even on other crustaceans such as the giant isopod *Glyptonotus antarticus* Eights, 1852 (Key & Barnes, 1999).

Polychaete worms of the families Spirorbidae and Serpulidae were also frequent on the shells. Bick (2006) studying populations of *Clibanarius erythropus* (Latreille, 1818) and *Calcinus tubularis* (Linnaeus, 1767) in Ibiza, Mediterranean Sea, found that shells occupied by hermit crabs supported polychaete communities dominated by Spirorbidae in the case of *C. erythropus* and by small Sabellidae in *C. tubularis*. These annelids produce calcareous tubes of variable morphology, are prevalent on occupied shells (Williams & McDermott, 2004), and may attach to the outer or inner surface of the shells. Their occurrence is usually facultative or accidental, and only a few species are obligate associates (Al-Ogily & Knight-Jones, 1981).

With respect to molluscs, the occurrence of ostreid bivalves on the shells is mostly accidental. The oysters attach to the outer surface by the left valve (Williams & McDermott, 2004). The high prevalence of oyster *Crassostrea brasiliana* in shells of *C. antillensis* in the Araçá beach can be related to the extensive cultivation of these molluscs in the southern region. The gastropod *Crepidula plana* is a commensal and shows a preference for occupied shells, mainly in the lumen region (McDermott, 2001). The occurrence of egg capsules of gastropods of the family Neritidae is common on the surface of live gastropods (Kano & Fukumori, 2010), but can be eventually found in shells utilized by hermit crabs.

Barnacles can attach to a variety of live substrates, including gastropod shells (McDermott, 2001), shrimp and crab carapaces (Key *et al.*, 1997; Farrapeira & Calado, 2010) and vertebrate skin (Caine, 1986; Ribeiro *et al.*, 2010) among others. In the present study, barnacles occurred sporadically, differing somewhat from observations by Ayres-Peres & Mantelatto (2010), who found larger numbers of barnacles attached to shells occupied by *L. loxochelis*.

The presence of ectosymbionts can influence shell selection and also provide advantages and disadvantages for hermit crabs. Incrusted shells can provide camouflage, protecting the crabs against predation. On the other hand, fouling organisms can reduce the resistance and the internal volume of shells, as well as increase shell weight (Partridge, 1980; Gherardi, 1990, 1991). Ectosymbionts receive some benefits beyond just the availability of substrates for colonization. For example, sessile filter-feeding organisms can be transported to locations with better feeding conditions and higher concentrations of dissolved oxygen (Wahl, 1989).

Final considerations

The differences in shell occupation, shell damage and ectosymbiont coverage in shelters between populations of the hermit crabs *C. antillensis* and *C. tibicen* in this study are probably attributed to habitat characteristics of each area and shell availability in the environment, as well as reproductive condition and sex of hermit crabs. This can reflect the adaptive capability of these crustaceans to exploit different shelter resources and niches in different areas. These factors interact together and should be considered in biological studies of hermit crabs in the field. The results of this contribution should encourage future comparative studies in order to comprehend the plasticity of biological traits of hermit crabs in different environments.

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