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Characterization of the occupied shells by the hermit crab *Clibanarius vittatus* (Decapoda, Diogenidae) at Baixio Mirim tideflat, Guaratuba Bay, southern Brazil

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ABSTRACT

A characterization of the occupied shells by the hermit crab *Clibanarius vittatus* was carried out. Hermit crabs we collected in the intertidal zone, during the low spring tide monthly from April 2005 to March 2006. They were sex and their cephalothoracic shield length (CL) was measured. Shells were identified, dried, weighed and the apertu length (AL) and width (AW) were measured. 1187 crabs were collected (949 males, 216 females and 22 intersexe which occupied 12 species of gastropod shells. *Stramonita haemastoma*, *Olivancillaria urceus* and *Dorsanum mo liferum* made up 96.55% of the total shell species. Male hermit crabs attained significantly larger sizes than femal therefore, males occupied a wider spectrum of shells in size and weight. A stronger correlation ratio was obtain between CL and AW of *S. haemastoma*. Last whorl with a rounded shape and a spacious inner area is a comm feature of all shell species most frequently occupied by this hermit crab where it occurs. The successful establishme of *C. vittatus* at Baixio Mirim is mainly due to the appropriately shaped and wide range of size of *S. haemastoma* she that were most often occupied by the hermit crabs of the studied population.

Key words: Guaratuba Bay, shell availability, shell occupation, shell size and shape.

INTRODUCTION

Hermit crabs are anomuran crustaceans that use empty shells of gastropods as a shelter. These shells can be acquired from the habitat if empty and available; if not, by removing dead or dying mollusks, once hermit crabs are unable to dislodge alive gastropods from their shells (Rittschof 1980, Bertness 1981, Tricarico and Gherardi 2006). The gastropod shells perform several important roles in the life of these crabs, mainly the protection of their uncalcified abdomen against eventual mechanical shocks and dryness.

The use of the specific shell species by a hermit crab is firstly related to the availability of these shells and Leite 2001, Meireles et al. 2003). When thi ability is restricted in the habitat, hermit crabs ar pelled to occupy shells that are not always approp size, form or integrity, and this restriction affects duction (Childress 1972, Bertness 1981, Hazlet Bertini and Fransozo 2000, Hazlett et al. 2005 2005), growth (Markham 1968, Bertness 1981, et al. 1998, Bertini and Fransozo 2000) and bod phology (Turra and Leite 2002).

Secondly, the occupation of a specific shel fluenced either by the interactions among hermi such as intra-specific competition for the shell other resources (Bertness 1980, 1981, Gherardi a

1997, Floeter et al. 2000, Turra 2003, Sant'Anna et al. 2006b), predation (Bertness 1982, Rotjan et al. 2004), presence of gastropods in the community (Bertness 1980, Turra and Leite 2001, Sant'Anna et al. 2006a), previous experience (Hazlett 1993, Hahn 1998, Meireles et al. 2008, Alcaraz and Kruesi 2009) and formation of aggregations (Hazlett 1981, Turra and Leite 2000a). The hermit crab ability in detecting odours of died or dying gastropods was also reported (Kratt and Rittschof 1991, Chiussi et al. 2001).

Likewise, morphometric characteristics of shells influence their occupation by hermit crabs. Among these characteristics are weight (Hahn 1998, Dominciano and Mantelatto 2004, Turra and Leite 2004), size (Bertini and Fransozo 2000, Turra and Leite 2004), opening size (Botelho and Costa 2000, Bertini and Fransozo 2000, Sant'Anna et al. 2006a) and architecture and volume (Gherardi and Nardone 1997, Floeter et al. 2000, Shih and Mok 2000).

Clibanarius vittatus (Bosc, 1802) has a wide geographical distribution in western Atlantic, from the eastern of the United States to West Indies, including Gulf of Mexico, and from Venezuela to southern Brazil, in Santa Catarina State (Melo 1999). In spite of the wide distribution, the ecological aspects of this species were only reported in the USA in North and South Carolina, Florida and Gulf of Mexico, and in Brazil these aspects are restricted to the São Paulo State coast (Turra 2003, 2005, Turra and Leite 2001, 2002, 2004, Sant'Anna et al. 2006a, b). The present study is the first research about the relationships of the hermit crab *C. vittatus* and its occupied shell from the Guaratuba Bay, Paraná State, southern Brazil.

MATERIALS AND METHODS

Baixio Mirim is a 6.300m^2 tideflat located within Guaratuba Bay and isolated from the continent by a narrow channel of 15-20m width. Most of its substrate is covered by the smooth cordgrass *Spartina alterniflora* Loisel, but it is also provided with sandy and muddy surface especially in the bordering areas. In spite of urban influence, this tideflat is inhabited by hundreds of

Hermit crabs occur individually or in groups of 5-10 crabs either in the vegetated areas or in non-vegetated ones in Baixio Mirim tideflat, from where they were collected during low spring tides, monthly from April/2005 to March/2006. Each monthly sample consisted of nearly a hundred crabs collected with the following shell size frequency distribution: 25% of individuals occupying small shells, 50% medium and 25% big ones. This procedure aimed to avoid collections biased towards more visible shells because hermit crabs have a gregarious habit, and a sampling based on the area or CPUE would be improper. Furthermore, such number was sufficient or more than sufficient to represent populations of hermit crabs in other studies in the Brazilian coast (Fransozo and Mantelatto 1998, Floeter et al. 2000, Turra and Leite 2000b, 2001, Sant'Anna et al. 2006a).

Hermit crabs were packed in plastic bags and kept in a thermal box; at the laboratory, they were preserved in freezer until their handling. They were extracted by hand from the occupied shells but, when necessary, it was done with the help of a small vice. After this, the crabs were preserved in alcohol 70% while shells were dried up indoors for 24h. Hermit crabs were identified, sexed, and the length (CL) of the cephalothoracic shield was obtained with a 0.01mm precision digital caliper. Sexes were identified according to the position of genital openings; intersex individuals had both male and female genital openings. Empty shells were identified and weighted (SWE) with an electronic scale of 0.01g precision, and their aperture length (AL) and width (AW) were measured with the same caliper. Only the most occupied shells were used for comparative analysis and, therefore, those having less than 5% occupation were excluded.

Krukal-Wallis was used for statistical comparison of the dimensions among the different shell species, and for comparison of these dimensions in the occupied shells by different sexes (these dimensions had not a normal distribution), the Dunn's test was used to locate the source of variations. The χ^2 was used to compare the shell occupation frequencies between males and females. Correlation Indices of Spearman were calculated for all

RESULTS

A total of 1187 hermit crabs *Clibanarius vittatus* were collected, out of which 949 were males, 204 non-ovigerous females, 12 ovigerous females and 22 intersexes. They occupied 12 species of gastropod shells, with the highest frequency of occupation in *Stramonita haemastoma* (Linnaeus, 1767) with 64.61%, followed by *Olivancillaria urceus* (Röding, 1798) with 26.47%, and *Dorsanum moniliferum* (Valenciennes, 1834) with 5.48%. The remainder shells were occupied with less than 1% each one, and altogether they did not sum up 4% – *Achatina fulica* (Bowdich, 1822), *Buccinanops lamarckii* (Kiener, 1834), *Cymatium parthenopeum* (Von Salis, 1793), *Chicoreus (Siratus) senegalensis* (Gmelin, 1791), *Olivancillaria steeriae* (Reeve, 1850), *Olivancillaria uretai* Klappenbach, 1965, *Semicassis granulatum* (Born, 1778), *Polinices hepaticus* (Röding, 1798) and *Zidona dufresnei* (Donovan, 1823) (Table I). Only *S. haemastoma*, *O. urceus* and *D. moniliferum* (more than 95% of occupation) were used for comparative analysis.

The shell species differed significantly in their weight (H = 116.37, $p < 0.0001$) and dimensions (AL: H = 314.85; $p < 0.0001$. AW: H = 59.96; $p < 0.0001$) (Fig. 1), showing that each one has its own characteristics. In this context, *D. moniliferum* had the smallest dimensions (SWE = 3.74 ± 1.24g; AL = 16.04 ± 2.33 mm; AW = 8.32 ± 1.11 mm), while *O. urceus* the largest weight and length (SWE = 8.16 ± 4.05g; AL = 25.82 ± 3,99 mm; AW = 8.51 ± 1.42 mm), and *S. haemastoma* the largest aperture width (SWE = 6.62 ± 4.14g; AL = 18.77 ± 5.91 mm; AW = 9.88 ± 2.67 mm) (Table II).

Male hermit crabs ranged from 2.97 to 11.56 mm CL, females from 2.97 to 8.24 mm, and intersexes from 3.76 to 9.45 mm. The hermit crabs' CL average ranged according to the shell species occupied by them (H = 54.91; $p < 0.0001$): those living inside the shells of *S. haemastoma* (CL = 6.11 ± 1.39) had highest CL, while those of *O. urceus* (CL = 5.54 ± 0.90 mm) and *D. moniliferum* (CL = 5.17 ± 0.90 mm) had close CL average without statistical difference (Fig. 2). Dimensions of the shells occupied by males were statistically

non-ovigerous and ovigerous females. AL and
the shells occupied by the latter ones had no sig
difference from those occupied by intersexes (K
Wallis, $p < 0.05$) (Table III).

The three most frequently occupied shell
were common among these sexes. Furthermore
tern in the shell use was observed: *S. haemastom*
were occupied by almost all hermit crab sizes, *O.*
by medium-sized crabs and *D. moniliferum* by
ones. However, each sex occupied these shells w
tinct frequencies: 29.29% males used *O. urceus*
15.58% females and 18.18% intersexes did it.
trast, only 4.52% males, 8.33% females and
intersexes occupied *D. moniliferum* (Fig. 3).

In the correlation analyses between hermi
CL and the shell species dimensions, *S. haem*
showed the higher correlation indices, followed
urceus and *D. moniliferum*. Shell SWE was the
sion with the highest correlation indices with
crab CL. Among the hermit crabs occupying *O.*
and *S. haemastoma* shells, males presented high
relation indices than females, but the opposi
found for *D. moniliferum* shell users (Table IV).

DISCUSSION

The total number of shell species occupied by *C*
tus (=12) in the present study is similar to that
ulations living in shallow waters of the southeas
of Brazil (Negreiros-Fransozo et al. 1991, Reiga
Santos 1997, Sant'Anna et al. 2006a). Howev
number can increase up to 16 in tropical areas
Florida, USA (Lowery and Nelson 1988).

The dominant occupation of the gastropo
S. haemastoma by *C. vittatus* observed in Baix
rim tideflat was also reported in previous stu
populations coming from Galveston Island, US
theringham 1975), and from São Paulo State (
ros-Fransozo et al. 1991, Reigada and Santos
Sant'Anna et al. 2006a), excepting in Turra an
(2002), who found *Chicoreus senegalensis* (
1791) as the most frequently occupied shell
hermit crab

TABLE I
***Clibanarius vittatus*. Absolute and relative frequencies of occupation of 12 shell species by male, female and intersex hermit crabs.**

Shell species	Male hermit crabs		Female hermit crabs		Intersex hermit crabs		Total		χ^2
	N	%	N	%	N	%	N	%	
Stramonita haemastoma	591	62.29	161	74.54	15	68.18	767	64.61	n.s.
Olivancillaria urceus	278	29.29	33	15.58	3	13.64	314	26.47	*
Dorsanum moniliferum	43	4.53	18	8.33	4	18.18	65	5.48	n.s.
Semicassis granulatum	9	0.94	1	0.46			10	0.84	n.s.
Buccinanops lamarckii	7	0.74	2	0.93			9	0.76	n.s.
Polinices hepaticus	7	0.74					7	0.59	n.s.
Chicoreus senegalensis	5	0.53					5	0.42	n.s.
Cymatium parthenopeum	5	0.53					5	0.42	n.s.
Zidona dufresnei	2	0.21					2	0.17	n.s.
Achatina fulica	1	0.10					1	0.08	n.s.
Olivancillaria steeriae			1	0.46			1	0.08	n.s.
Olivancillaria uretai	1	0.10					1	0.08	n.s.
TOTAL	949	100.0	216	100.00	22	100.00	1187	100.00	

N = absolute number; * = significant; n.s. = not significant.

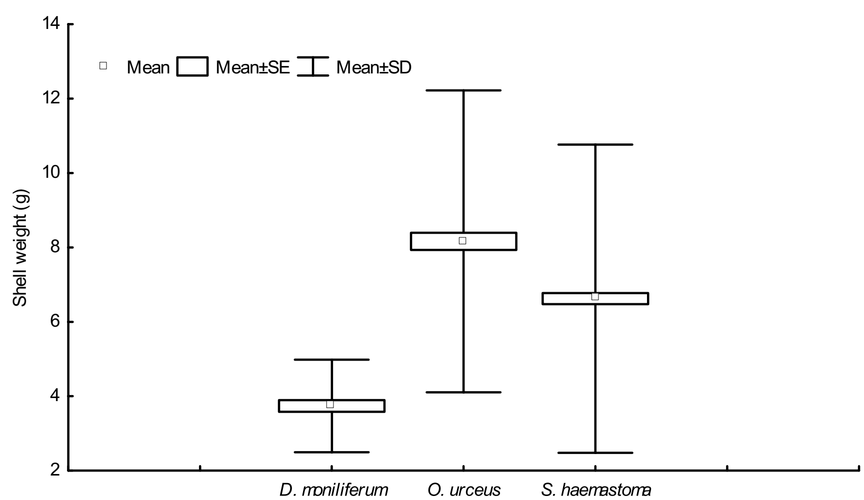

Fig. 1 – *Clibanarius vittatus*. Mean, standard deviation and standard error of the shell weight of the gastropod species more occupied by hermit crabs.

pation. Turra and Leite (2002), studying *C. vittatus*, demonstrated that the shell dimension was more important than its volume. Furthermore, in the study carried by Floeter et al. (2000) with *Calcinus tibicen* (Herbst, 1971) and *Clibanarius antillensis* Stimpson, 1859, the *Calcinus latens* (Randall, 1839), respectively, considered that the shell was the most important feature for occupation, and more recently Masunari et al. (2008) observed that *Isocheles sawayai* (Forest and Saint Laurent, 1968), living in infralittoral waters of southern

TABLE II

***Clibanarius vittatus* and shell species most often occupied by the hermit crabs. Dunn's multiple comparisons test (P<0.05) with significant differences in the comparison of morphometric variables between pairs of shell species and average CL of the hermit crabs that occupied these shells.**

Shell species pairs compared	SWE (g)	AL (mm)	AW (mm)	CL (mm)
D. moniliferum × *O. urceus*	***	***	n.s.	n.s.
D. moniliferum × *S. haemastoma*	***	**	***	***
O. urceus × *S. haemastoma*	***	***	***	***

SWE = shell weight; AL = aperture length; AW = aperture width; CL = cephalothoracic shield length. ** = p<0.01; *** = p<0.001; n.s. = not significant.

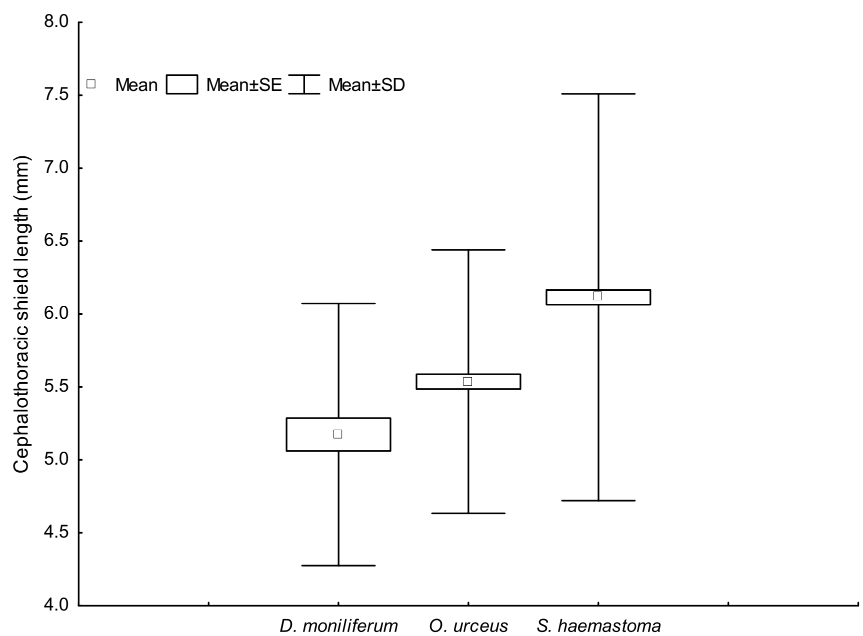

Fig. 2 – *Clibanarius vittatus*. Mean, standard deviation and standard error of the hermit crabs' cephalothoracic shield that occupied three more frequent shell species.

TABLE III

Shell species occupied by the hermit crab *Clibanarius vittatus*. Dunn's multiple comparisons (p<0.05) between the hermit crab sexes in the morphometric variables of occupied shells (H=157.53).

	SWE (g)	AL (mm)	AW (mm)
Females × Ovigerous females	n.s.	n.s.	n.s.
Females × Intersexes	***	**	***
Females × Males	***	***	***
Ovigerous females × Intersexes	*	n.s.	n.s.
Ovigerous females × Males	***	**	*

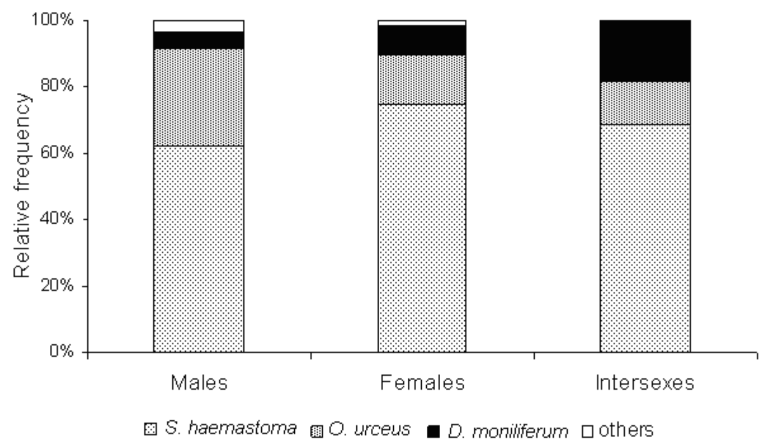

Fig. 3 – *Clibanarius vittatus*. Relative frequencies of occupied shells by males, females and intersexes.

There is a common architectural feature among the shell species occupied mainly by populations of *C. vittatus* living along the western Atlantic Ocean coast: the last whorl is globe-shaped and spacious, with shell aperture measuring 50-70% of the total length (Table V; see figures in Rios 1975 and Abbott and Dance 1998). According to Floeter et al. (2000), the preference for shells with enlarged last whorl and higher internal volume by hermit crabs of the genus *Clibanarius* is related to the maintenance of a humid microhabitat, especially during the exposed condition due to the low tide.

Stramonita haemastoma occurs in the western Atlantic Ocean coast from North Carolina, USA, to southern Brazil (Rios 1975). The almost complete overlapping in the geographical distribution of *S. haemastoma* and *C. vittatus* (compare to Melo 1999) can indicate that the shell availability is the main reason for occupying in higher frequency this shell species. Moreover, Turra and Leite (2002) demonstrated through laboratory experiment that *S. haemastoma* had been chosen among other shell species, which means that *C. vittatus* has a specific preference. The most frequently occupied shell *Chicoreus senegalensis* observed by these authors in the environment could be due to competition with other sympatric hermit crab species. Alongside the western Atlantic Ocean coast, where *S. haemastoma* is present, this hermit crab can occupy preferably another species, such as *Littorina irrorata* (Say, 1822) in North (Lowery and Nelson 1988) (Table V). The significant occupation of other shell species with similar morphology to *S. haemastoma* (last whorl relatively enlarged than others) may indicate that the shell architecture is more important than shell species in the selection by *C. vittatus*.

Another indication that *S. haemastoma* is the suitable shell due to its shell architecture and/or general shape, is the highest correlation indices obtained between the shell dimensions and its occupier. Turra and Leite (2002) and Sant'Anna et al. (2006a) reported a strong correlation in the relationships of CL × SL (shell length) and CL × AL.

The dissimilar frequencies in the occupation of the shell species among males, females and intersexes are difficult to explain. As *C. vittatus* males attain larger sizes than females (Lowery and Nelson 1988, Sant'Anna et al. 2006a), an eventual intra-specific competition for the best shells would result in a large proportion of males occupying *S. haemastoma* shells. However, the opposite was observed: about 62% males occupied this shell species, while about 75% females did it. It is possible to conjecture that females' requirement in occupying *S. haemastoma* is the need to accommodate their eggs inside the spacious whorl of this shell species. The dominance of males in the occupation of *O. urceus* shell, the second most occupied one, supports this assumption (see Table I).

TABLE IV

***Clibanarius vittatus*. Statistics for morphometric relationships ($p<0.05$) between the hermit crab sexes and the three most frequently occupied shell species.**

Shell species	Relation	Equation	r
S. haemastoma	CL×SWE	LnSWE = –0.92+2.16LnCL	0.8119
Males	CL×AL	LnAL = 0.39+1.11LnCL	0.7849
n = 591	CL×AW	LnAW = 0.23+0.97LnCL	0.8311
Females	CL×SWE	LnSWE = –0.6+1.62LnCL	0.6849
n = 151	CL×AL	LnAL = 0.58+0.82LnCL	0.6068
	CL×AW	LnAW = 0.41+0.68LnCL	0.6677
O. urceus	CL×SWE	LnSWE = –0.63+2.04LnCL	0.7338
Males	CL×AL	LnAL = 0.88+0.72LnCL	0.7739
n = 278	CL×AW	LnAW = 0.37+0.75LnCL	0.7475
Females	CL×SWE	LnSWE = –0.50+1.73LnCL	0.6751
n = 33	CL×AL	LnAL = 0.94+0.61LnCL	0.7462
	CL×AW	LnAW = 0.41+0.66LnCL	0.6491
D. moniliferum	CL×SWE	LnSWE =–0.08+0.89LnCL	0.4985
Males	CL×AL	LnAL =1.03+0.26LnCL	0.3752
n = 43	CL×AW	LnAW = Ln0.76+0.24LnCL	0.4052
Females	CL×SWE	LnSWE = Ln(-0.60)+1.65LnCL	0.6851
n = 17	CL×AL	LnAL = Ln(0.80)+0.56LnCL	0.4796
	CL×AW	LnAW = Ln0.42+0.68LnCL	0.7187

CL = cephalothoracic shield length; SWE = shell weight; SL = shell length; SW = shell weight; AL = aperture length; AW = aperture width; r = correlation indices of Spearman.

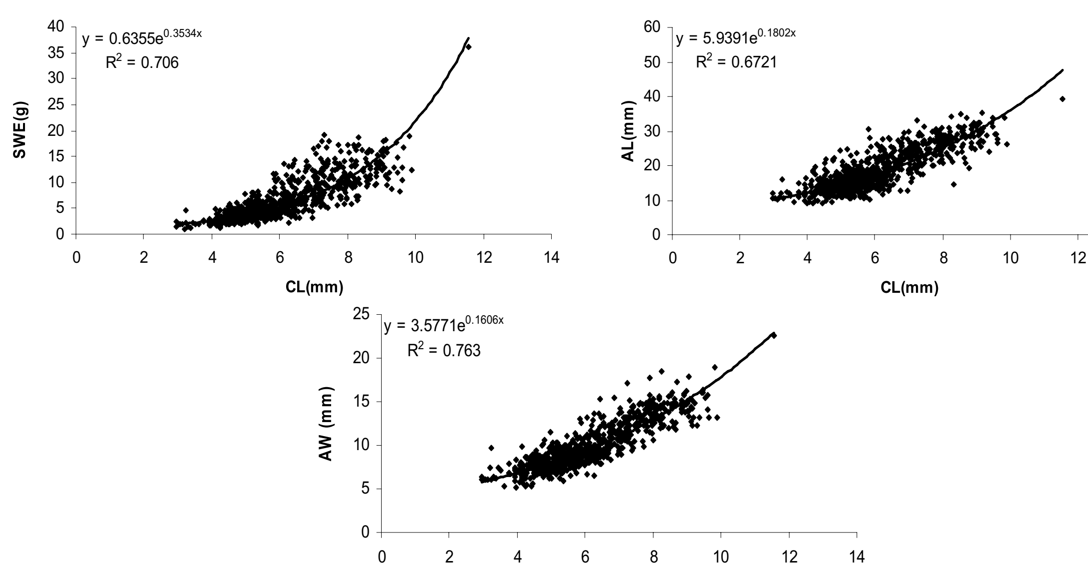

TABLE V

***Clibanarius vittatus*. Localities where the hermit crabs was reported, total number and most frequently occupied shell species.**

Locality	Most frequently occupied shell species by the hermit crab	No. of occupied shell species	Reference
North Carolina, USA	*Littorina irrorata*	5	Mitchell (1975)
South Carolina, USA	*Littorina irrorata*	6	Young (1979)
Gulf Coast, USA	*Stramonita haemastoma*	8	Fotheringham (1975)
Florida, USA	*Melongena corona*	16	Lowery and Nelson (1988)
São Sebastião, Brazil	*Chicoreus senegalensis*	9	Turra (personal communication)
Ubatuba, Brazil	*Stramonita haemastoma*	2	Negreiros-Fransozo et al. (1991)
São Vicente, Brazil	*Stramonita haemastoma*	13	Sant'Anna et al. (2006a)
Guaratuba, Brazil	*Stramonita haemastoma*	12	Present study

empty shells, it is possible to infer that this hermit crab can find plenty of shelters at Baixio Mirim tideflat, either in abundance or in size spectrum. The morphometric dimensions of the three mostly occupied shells – *S. haemastoma*, *O. urceus* and *D. moniliferum* – that showed positive correlation with hermit crab size support this assumption.

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RESUMO

A caracterização das conchas ocupadas pelo ermitão *Clibanarius vittatus* (Bosc, 1802) foi realizada. Os ermitões foram coletados de abril/2005 a março/2006, na zona intertidal, durante a maré baixa de sizígia. Os ermitões tiveram o sexo reconhecido e foram medidos no comprimento do escudo cefalotorácico. As conchas foram identificadas, pesadas depois de secas e medidas no comprimento e na largura da abertura. *Dorsanum moniliferum* perfizeram 96,55% do total das conchas ocupadas. Ermitões machos atingiram tamanhos significativamente maiores do que as fêmeas; entretanto ocuparam um maior espectro de conchas em tamanho e peso. Fortes índices de correlação foram obtidos para a relação entre o escudo cefalotorácico dos ermitões e a largura da abertura de *S. haemastoma*. A última espira espaçosa e de formato globoso é um aspecto comum das conchas mais frequentemente ocupadas pelo presente ermitão em todos os locais de sua ocorrência. O sucesso no estabelecimento de *C. vittaus* no Baixio Mirim é devido principalmente ao formato e à amplitude de tamanhos das conchas de *S. haemastoma*, as quais são mais frequentemente ocupadas pelos ermitões da população estudada.

Palavras-chave: Baía de Guaratuba, disponibilidade de conchas, ocupação de conchas, tamanho e formato da concha.

REFERENCES

Abbott RT and Dance SP. 1998. Compendium of seashells. El Cajon: Odyssey, 411 p.

Alcaraz G and Kruesi K. 2009. The role of previous shell occupancy in the wild on laboratory shell choice by hermit crab *Calcinus californiensis*. Mar Fresh Behav Physiol 42: 55–62.

Bertini G and Fransozo A. 2000. Patterns of shell utilization in *Petrochirus diogenes* (Decapoda, Anomura, Diogenidae) in the Ubatuba region, São Paulo, Brazil. J Crust Biol 20(3): 468–473.

BERTNESS MD. 1981. Interference, exploitation, and sexual components of competition in a tropical hermit crab assemblage. J Exp Mar Biol Ecol 49: 189–202.

BERTNESS MD. 1982. Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. J Exp Mar Biol Ecol 64: 159–187.

BOTELHO AZ AND COSTA AC. 2000. Shell occupancy of the intertidal hermit crab *Clibanarius erythropus* (Decapoda, Diogenidae) on São Miguel (Azores). Hydrobiologia 440: 111–117.

CHILDRESS JR. 1972. Behavioral ecology and fitness theory in a tropical hermit crab. Ecology 53(3): 960–964.

CHIUSSI R, DIAS H, RITTSCHOF D AND FORWARD JR RB. 2001. Orientation of the hermit crab *Clibanarius antillensis*: effects of visual and chemical cues. J Crust Biol 21(3): 593–605.

DOMINCIANO LCC AND MANTELATTO FLM. 2004. The influence of Shell species and size in the shell selection pattern of *Paguristes tortugae* (Decapoda, Diogenidae) from Anchieta Island (Ubatuba, Brazil). Iheringia, Ser Zool 94(4): 425–428.

FLOETER SR, NALESSO RC, RODRIGUES MMP AND TURRA A. 2000. Patterns of shell utilization and selection in two sympatric hermit crabs (Anomura, Diogenidae) in south-eastern Brazil. J Mar Biol Ass UK 80: 1053–1059.

FOTHERINGHAM N. 1975. Structure of seasonal migrations of the littoral hermit crab *Clibanarius vittatus*. J Exp Mar Biol Ecol 18: 47–53.

FRANSOZO A AND MANTELATTO FLM. 1998. Populations structure and reproductive period of the tropical hermit crab *Calcinus tibicen* (Decapoda: Diogenidae) in the region of Ubatuba, São Paulo, Brazil. J Crust Biol 18(4): 738–745.

GHERARDI F AND NARDONE F. 1997. The question of coexistence in hermit crabs: population ecology of a tropical intertidal assemblage. Crustaceana 70: 608–629.

HAHN DR. 1998. Hermit crab shell use pattern: response to previous Shell experience and to water flow. J Exp Mar Biol Ecol 184: 35–51.

HAZLETT BA. 1981. The behavior ecology of hermit crabs. Ann Rev Ecol Syst 12: 1–22.

HAZLETT BA. 1989. Mating success of male hermit crabs in shell generalist and shell specialist species. Behav Ecol Sociobiol 25: 119–128.

HAZLETT BA, RITTSCHOF D AND BACH CE. 200
effects of shell size and coil orientation on reprodu
female hermit crabs, *Clibanarius vittatus*. J Exp M
Ecol 323(2): 93–99.

KELLOG CW. 1977. Coexistence in a hermit crab
ensemble. Biol Bull 153: 133–144.

KRATT CM AND RITTSCHOF D. 1991. Peptide attra
hermit crabs *Clibanarius vittatus* Bosc: roles of e
and substrates. J Chem Ecol 17(12): 2347–2366.

LOWERY WA AND NELSON WG. 1988. Population
of the hermit crab *Clibanarius vittatus* (Decapod
genidae) at Sebastian Inlet, Florida. J Crust Bio
548–556.

MARKHAM BA. 1968. Notes on growth-patterns a
utilization of the hermit crab *Pagurus bernhard*
Ophelia 5: 189–205.

MASUNARI S, DISSENHA N AND FALCÃO RC. 200
cimento relativo e destreza dos quelípodos de *Uc*
coani (Latreille) (Crustacea, Decapoda, Ocypodi
Baixio Mirim, Baía de Guaratuba, Paraná, Bras
Bras Zool 22(4): 974–983.

MASUNARI S, FONTANELLI AM AND SAMPAIO S
Morphometric relationships between the hermit c
cheles sawayai (Forest and Saint Laurent) (Cr
Anomura, Diogenidae) and its shell from southern
The open Mar Biol J 2: 13–20.

MEIRELES AL, BIAGI R AND MANTELATTO FL
Gastropod Shell availability as a potential resou
the hermit crab infralittoral fauna of Anchieta
(SP), Brazil. Nauplius 11(2): 99–105.

MEIRELES AL, BIAGI R AND MANTELATTO FL. 2
fluence of prior experience on shell selection by th
spotwrist hermit crab *Pagurus criniticornis* (Cr
Paguridae). Hydrobiologia 605: 259–263.

MELO GAS. 1999. Manual de identificação dos C
Decapoda do litoral brasileiro: Anomura, Thalas
Palinuridea, Astacidea. São Paulo: Plêiade, 551 p

MITCHELL KA. 1975. An analysis of shell occupatio
sympatric species of hermit crab. I. Ecological
Biol Bull 149: 205–213.

NEGREIROS-FRANSOZO ML, FRANSOZO A AND H
NJ. 1991. Estrutura populacional e determinaçã
manho da concha em 4 espécies de ermitões (Cr
Decapoda, Anomura) do litoral paulista. Biotem

large shell? Evidence from natural and field induced shell exchanges. J Exp Mar Biol Ecol 222: 163–173.

REIGADA AL AND SANTOS S. 1997. Biologia e relação com a concha em *Clibanarius vittatus* (Bosc, 1802) (Crustacea, Diogenidae) em São Vicente, SP, Brasil. Arq Biol Tecnol 40(4): 941–952.

RIOS EC. 1975. Brazilian marine mollusks iconography. Rio Grande: Fundação Universidade do Rio Grande, 330 p.

RITTSCHOF D. 1980. Chemical attraction of hermit crabs and other attendants to simulated gastropod predation sites. J Chem Ecol 6(3): 665–676.

ROTJAN RD, BLUM J AND LEWIS SM. 2004. Shell choice in *Pagurus longicarpus* hermit crabs: does predation threat influence shell selection behavior? Behav Ecol Sociobiol 56: 171–176.

SANT'ANNA BS, ZANGRANDE CM, REIGADA ALD AND PINHEIRO MAA. 2006a. Shell utilization pattern of the hermit crab *Clibanarius vittatus* (Crustacea, Anomura) in a estuary at São Vicente, State of São Paulo, Brazil. Iheringia, Ser Zool 96(2): 261–266.

SANT'ANNA BS, ZANGRANDE CM, REIGADA ALD AND SEVERINO-RODRIGUES E. 2006b. Spatial distribution and shell utilization in three sympatric hermit crabs at non-consolidated sublittoral of estuarine-bay complex in São Vicente, São Paulo, Brazil. Rev Biol Mar Oceanogr 41(2): 141–146.

SHIH H AND MOK H. 2000. Utilization of shell resources by the hermit crabs *Calcinus latens* and *Calcinus gaimardii* at Kenting, southern Taiwan. J Crust Biol 20(4): 786–795.

TRICARICO E AND GHERARDI F. 2006. Shell acquisition by hermit crabs: which tactic is more efficient? Behav Ecol Sociobiol 60: 492–500.

TURRA A. 2003. Shell condition and adequacy of three sympatric intertidal hermit crab populations. J Nat Hist 37: 1781–1795.

TURRA A. 2005. Reproductive behavior of intertidal hermit crabs (Decapoda, Anomura) in southeastern Brazil. Rev Bras Zool 22(2): 313–319.

TURRA A AND LEITE FPP. 2000a. Clustering behavior of hermit crabs (Decapoda, Anomura) in an intertidal rocky shore at São Sebastião, southeastern Brazil. Rev Bras Biol 60: 39–44.

TURRA A AND LEITE FPP. 2000b. Population biology and growth of three sympatric species of intertidal hermit crabs in south eastern Brazil. J Mar Biol Ass UK 80: 1061–1069.

TURRA A AND LEITE FPP. 2001. Shell utilization patterns of a tropical rock intertidal hermit crab assemblage: I. The case of Grande Beach. J Crust Biol 21(2): 393–406.

TURRA A AND LEITE FPP. 2002. Shell utilization patterns of a tropical intertidal hermit crab assemblage. J Mar Biol Ass UK 82: 97–107.

TURRA A AND LEITE FPP. 2004. Shell-size selection by the intertidal sympatric hermit crabs. Mar Biol 145: 251–257.

VANCE RR. 1972. Competition and mechanisms of coexistence in three sympatric species of intertidal hermit crabs. Ecology 53: 1062–1074.

YOUNG AM. 1979. Differential utilization of gastropod shells by three hermit crab species in North Inlet, South Carolina, USA. Crustaceana 5(suppl): 101–104.