

Shell utilization patterns of a tropical intertidal hermit crab assemblage

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The shell selection and utilization patterns of three sympatric hermit crab populations (*Clibanarius antillensis*, *C. scolopetarius*, and *C. vittatus*) and shell availability were studied in a tropical intertidal low energy area. Shell availability (except for *C. antillensis*) was low and the hermit crabs showed overlap in size (mainly *C. scolopetarius* and *C. vittatus*). The influence of shell availability and selection on shell use was dependent on crab species. *Clibanarius antillensis* used mainly shells of *Cerithium atratum*, the most available shell species, while *Clibanarius scolopetarius* and *C. vittatus* occupied shells with lower availability in the studied area such as *Chicoreus senegalensis*, *Stramonita haemastoma*, *Leucozonia nassa* and *Cymatium parthenoepum*. The three species selected different gastropod shells with only *Clibanarius antillensis* using almost exclusively its preferred shell species in nature. The relationship between shield length and the weight of the used shell was not dependent on crab species or shell species, indicating that the size (not species) of the shells defines what size (not species) of crabs will occupy them.

INTRODUCTION

Hermit crabs are anomuran crustaceans distributed worldwide and are particularly abundant in intertidal and shallow subtidal areas (Reese, 1969). These organisms have morphological adaptations that enable them to use gastropod shells. In consequence, shell availability may strongly influence crab growth (Fotheringham, 1976a; Bertness, 1981a; Blackstone, 1985) and reproduction (Fotheringham, 1976b; Bertness, 1981a). Shell availability is generally thought to be low (Reese, 1969; Vance, 1972; Spight, 1977) but empty shells may be especially abundant in some areas (Scully, 1979; Leite et al., 1998; Turra & Leite, 2001).

Shell availability may directly influence the abundance of hermit crab populations (Vance, 1972; Kellogg, 1976; Spight, 1977). Bertness (1980) suggested that shell availability is a function of the relative abundance of the different gastropod species living in a given area, of their death rates, of the causes of their mortality, and of the architecture and size of their shells. In addition, availability can be reduced when empty shells become buried or broken (Bertness, 1980), and when they are removed from the area by wave action (Bertness, 1980). The co-existence of species also influences the amount of empty shells available to the crabs, mainly to competitive subordinate species (Reese, 1969; Bertness, 1981a).

Intraspecific (Abrams, 1988; Imazu & Asakura, 1994; Asakura, 1995; Turra & Leite, 2001) and interspecific (Bach et al., 1976; Gherardi & Nardone, 1997; Barnes, 1999) shell partitioning is very common in hermit crab assemblages. Patterns of shell use in nature may be dependent on shell availability (Scully, 1979; Bertness, 1980; Leite et al., 1998; Turra & Leite, 2001) and on crab preferences (Bertness, 1980). Therefore, evaluation of shell preferences for coexisting hermit crab species may

elucidate shell utilization patterns in nature (Kellogg, 1976; Bertness, 1981b). Such differences in shell use among coexisting species may also be attributed to differences in the sizes of individuals (Mitchell, 1975; Bertness, 1980; Manjón-Cabeza & García-Raso, 1999; Turra & Leite, 2001), to microhabitat separation (Mitchell, 1975; Kellogg, 1977; Gherardi, 1990; Gherardi & Nardone, 1997; Floeter et al., 2000), and to particular abilities to obtain new shells in contests (interference competition) or through active searching (exploitation competition) (Bertness, 1981c).

This study evaluated the patterns of shell utilization and selection of three intertidal coexisting species of *Clibanarius* and their relationships with shell availability in a tropical intertidal area. Shell use was compared among reproductive (males, ovigerous females and non-ovigerous females) and size-classes.

MATERIALS AND METHODS

Field work

This study was conducted in the intertidal region of Pernambuco Islet (23°49'S 45°24'W), São Sebastião Channel, São Paulo, south-eastern Brazil. This is an organically enriched area that presents great microhabitat heterogeneity (Turra et al., 2000), where three species of *Clibanarius* coexist: *C. antillensis* Stimpson, 1859, *C. scolopetarius* (Herbst, 1796), and *C. vittatus* (Bosc, 1802).

Random samples of hermit crabs and living snails were taken monthly over one year from October 1995 to September 1996 during spring low tide periods (see Turra et al., 2000 for sampling details). Hermit crabs were sexed and measured (shield length). Living gastropods and the shells used by the crabs were identified. The shells used by the crabs had their total (apex to syphonal canal) and

aperture lengths measured with a caliper to the nearest 0.05 mm. Shell weight was obtained after drying at 120°C for 24 h to the nearest 0.1 mg.

The log-likelihood *G*-test (Zar, 1984) was employed to compare the patterns of shell occupation among the three populations, reproductive classes (males, ovigerous females and non-ovigerous females), and individuals of different populations of a single size-class. This test was also employed to compare shell use and availability (abundance of living gastropods). Per cent of similarity (Renkonen index; Krebs, 1989) was also calculated to compare shell use among the three species. Regression analyses were used to generate models between the crab size and dimensions of the shells used. Covariance analyses were performed to compare the slopes and elevations (*y*-intercept) of the models fitted by the regression analyses. Total and aperture lengths and the weight of the most used shells were compared among the three populations and among reproductive classes using analysis of variance (ANOVA) and post-hoc Scheffé's test (Zar, 1984). All tests were conducted at the

0.05 significance level. Standard error is presented through the text.

Shell selection

These experiments were performed in the marine laboratory of Centro de Biologia Marinha of Universidade de São Paulo (CEBIMar-USP). Forty individuals of each species of variable sizes were maintained in 500-l aquaria with running seawater (35 psu, 24–25°C) and subjected to an abundant supply of different species and sizes of shells (Wilber, 1993). The selected shells were recorded after 48 h. The crabs were removed from their shells and sized. Shells were identified, measured, and weighed. The relationship between crab size and the weight of the preferred shells were estimated using regression analyses (Zar, 1984). The log likelihood *G*-test was performed to compare the patterns of shell selection among the three hermit crabs species and to compare shell preferences with shell use in nature.

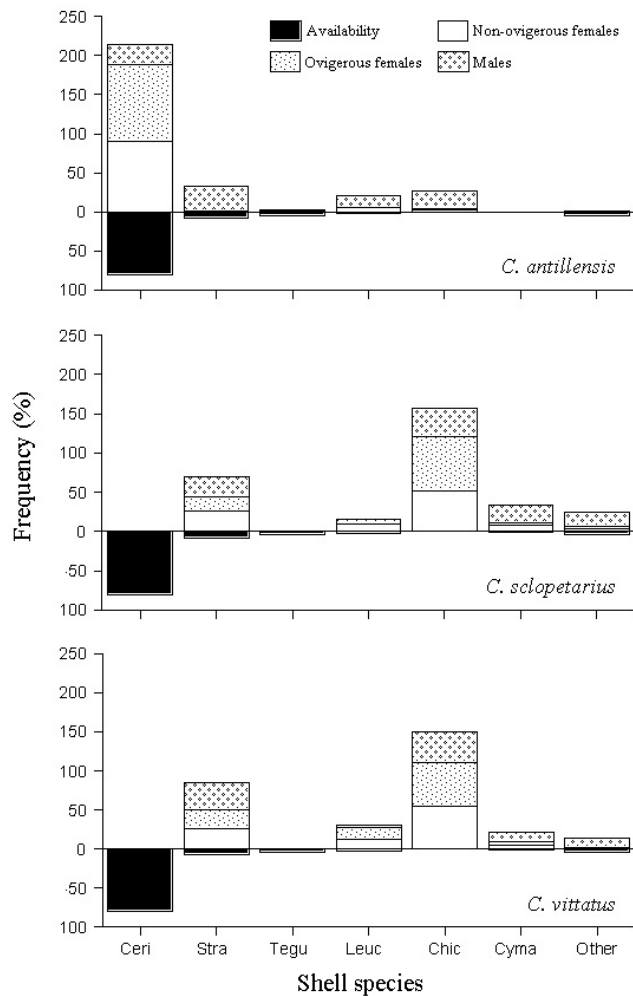


Figure 1. Shell availability (N=913) and use by males and ovigerous and non-ovigerous females of *Clibanarius antillensis* (N=724), *C. scolopetarius* (N=391) and *C. vittatus* (N=534). Ceri, *Cerithium atratum*; Stra, *Stramonita haemastoma*; Tegu, *Tegula viridula*; Leuc, *Leucozonia nassa*; Chic, *Chicoreus senegalensis*; Cyma, *Cymatium parthenopeum*.

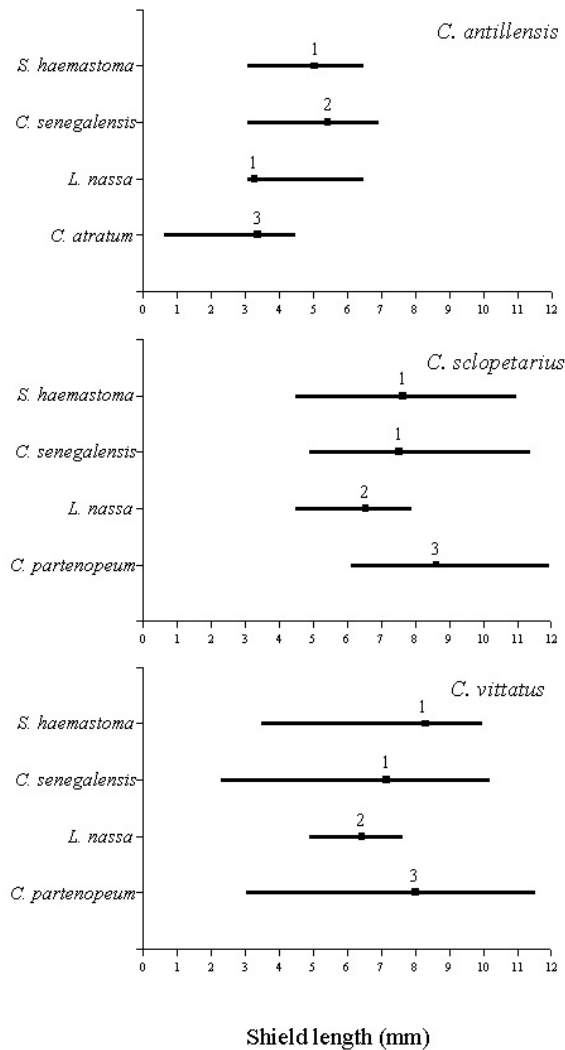


Figure 2. Mean (■) and range of shield length of *Clibanarius antillensis*, *C. scolopetarius* and *C. vittatus* in the most used shells in the field. Superscript figures indicate significant differences given by Scheffé's test at $\alpha=0.05$. *Stramonita haemastoma*; *Chicoreus senegalensis*; *Leucozonia nassa*; *Cerithium atratum*; *Cymatium parthenopeum*.

RESULTS

Shell utilization

Clibanarius antillensis occupied different shell species than *C. scolopetarius* ($G=581.90$; $df=6$; $P<0.001$) and *C. vittatus* ($G=887.74$; $df=5$; $P<0.001$), while these two latter species used the same shells in different proportions ($G=37.08$; $df=5$; $P<0.001$) (Figure 1). *Clibanarius antillensis* used mainly shells of *Cerithium atratum* (Born, 1778), while *Clibanarius scolopetarius* and *C. vittatus* were found frequently in shells of *Chicoreus senegalensis* (Gmelin, 1790), *Stramonita haemastoma* (Linnaeus, 1767), *Leucozonia nassa* (Gmelin, 1791) and *Cymatium parthenopeum* (von Salis, 1793). The overlap in shell use was higher between these two latter crab populations (per cent of similarity, 79.96%) than between them and *Clibanarius antillensis* (31.58% and 31.82%, respectively). This latter population used mainly the shells of the most abundant gastropod (*Cerithium*) but in different proportions than expected by the abundance of living gastropods ($G=185.19$; $df=7$; $P<0.001$). Shell utilization by *C. scolopetarius* and *C. vittatus* did not follow availability in this area ($G=1076.52$; $df=7$; $P<0.001$; $G=1301.99$; $df=7$; $P<0.001$, respectively) (Figure 1).

Ovigerous and non-ovigerous females of *Clibanarius antillensis* occupied mainly *Cerithium* while males used a wider variety of shells ($G=1665.72$; $df=8$; $P<0.001$) (Figure 1). The reproductive classes of *Clibanarius scolopetarius* and *C. vittatus* occupied shells of the same species but in different proportions ($G=64.92$; $df=8$; $P<0.001$; $G=58.54$; $df=8$; $P<0.001$, respectively). Ovigerous and non-ovigerous females used mainly shells of *Chicoreus* while males those of *Stramonita* and *Cymatium*. Differences in shell weight were also recorded among reproductive classes of *Clibanarius antillensis*, *C. scolopetarius* and *C. vittatus* (ANOVA, $F=207.075$, $df=2$, $P<0.001$; $F=31.856$, $df=2$, $P<0.001$; $F=28.983$, $df=2$, $P<0.001$, respectively). Ovigerous and non-ovigerous females used shells with similar weights (*C. antillensis*: 1.620 ± 0.549 g and 1.785 ± 0.108 g, respectively, Scheffé's test, $P=0.773$; *C. scolopetarius*: 13.185 ± 0.398 g and 12.426 ± 0.311 g, respectively, $P=0.437$; *C. vittatus*: 10.920 ± 0.342 g and 12.074 ± 0.283 g, respectively, $P=0.098$) but lighter than those occupied by males (*C. antillensis*: 5.378 ± 0.230 g; *C. scolopetarius*: 17.621 ± 0.700 g; *C. vittatus*: 14.885 ± 0.395 g, Scheffé's test, $P<0.001$ for all comparisons). About 75.67% of the individuals of *C. antillensis* collected in shells of *Cerithium* were ovigerous females. The four most used shells by *Clibanarius scolopetarius* and *C. vittatus* presented from 22 to 30% of ovigerous females, except by 43.21% of ovigerous females of *C. scolopetarius* in shells of *Chicoreus*.

Analyses of variance showed that the size of *Clibanarius antillensis*, *C. scolopetarius* and *C. vittatus* was related to the shell used (ANOVA, $F=382.795$; $df=3$; $P<0.001$, $F=14.833$; $df=3$; $P<0.001$, $F=15.705$; $df=3$; $P<0.001$, respectively). Shells of *Stramonita* and *Leucozonia* were used by individuals of *C. antillensis* of similar sizes, and, together with *Chicoreus*, were occupied by larger individuals than shells of *Cerithium* (Figure 2). Shells of *Cymatium* were occupied by larger individuals of *Clibanarius scolopetarius* and *C. vittatus* than those of *Leucozonia*, *Chicoreus* and *Stramonita*. Shells of *Stramonita* and *Chicoreus* sheltered

individuals of similar sizes of these two hermit crab populations but larger than those of *Leucozonia*.

Differences in shell use among size-classes were recorded for the three populations but were more evident for *Clibanarius antillensis* due to the extensive utilization of *Cerithium* in the smallest size-classes and of *Chicoreus* and *Stramonita* in the largest (Figure 3). *Clibanarius scolopetarius* and *C. vittatus* occupied shells of these two gastropods in almost all size-classes, although in lower frequencies by the largest individuals, which used mainly shells of *Cymatium*. Only small- and medium-sized individuals of these two hermit crabs utilized shells of *Leucozonia*. The individuals of *Clibanarius antillensis*, *C. scolopetarius*, and *C. vittatus* in the 5–6 mm size-class used proportionally more shells of *Stramonita*, *Chicoreus*, and *Leucozonia*, respectively ($G=9.931$, $df=4$, $P=0.042$) (Figure 3). Moreover,

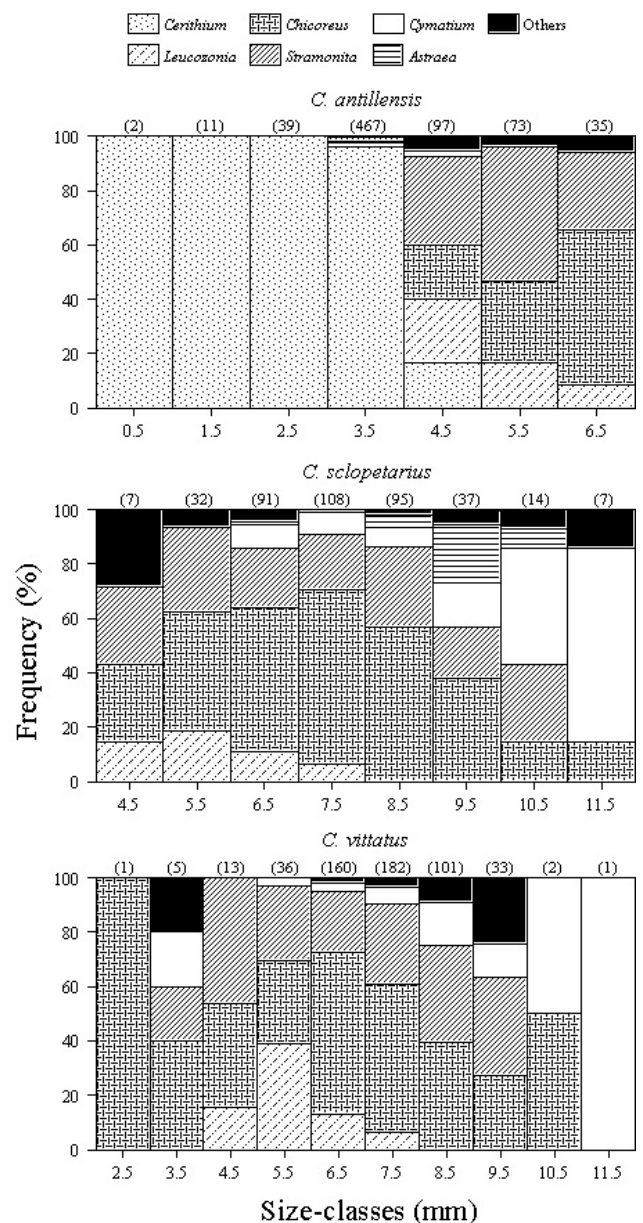


Figure 3. Shell use in relation to the size of *Clibanarius antillensis* ($N=724$), *C. scolopetarius* ($N=391$) and *C. vittatus* ($N=534$). Figures in parentheses indicate the number of individuals of each species in each size-class.

Table 1. Analysis of variance of total length (mm), aperture length (mm) and weight (g) of the most used shells by individuals in the 5–6 mm size-class of *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus*. Superscript figures indicate the result of the Scheffé's test for multiple pair-wise comparisons at $\alpha=0.05$.

Gastropod	<i>Clibanarius antillensis</i>			<i>Clibanarius sclopetarius</i>			<i>Clibanarius vittatus</i>			F	df	P
	N	\bar{x}	SE	N	\bar{x}	SE	N	\bar{x}	SE			
<i>Chicoreus senegalensis</i>												
Total length	18	45.625	1.151	9	47.628	1.627	9	49.011	1.627	1.551	2	0.227
Aperture length	18	13.769	0.343	9	14.683	0.485	9	14.211	0.485	1.213	2	0.310
<i>Stramonita haemastoma</i>												
Total length	30	37.118	0.656	4	40.700	1.796	9	39.617	1.197	2.944	2	0.064
Aperture length	30 ¹	24.535	0.359	4 ²	26.950	0.984	9 ²	26.433	0.656	5.048	2	0.011
<i>Leucozonia nassa</i>												
Total length	12	41.504	1.191	2	44.700	2.919	12	45.167	1.191	2.463	2	0.107
Aperture length	11	24.441	0.714	2	24.150	1.675	12	26.275	0.684	1.976	2	0.162
All shells												
Weight	60 ¹	7.276	0.300	26 ²	9.150	0.456	28 ³	9.616	0.459	12.053	2	<0.001

\bar{x} , mean; SE, standard error.

Table 2. Linear regressions between the shield length (\log_{10}) of males, ovigerous and non-ovigerous females (reproductive classes), and all individuals of *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus* and the weight of the shells (\log_{10}).

Reproductive class	N	r ²	P	Equation
<i>Clibanarius antillensis</i>				
Non-ovigerous females	104	0.364	<0.001	y=1.122+0.185x
Ovigerous females	266	0.329	<0.001	y=1.177+0.146x
Males	208	0.655	<0.001	y=1.036+0.321x
All individuals	597	0.639	<0.001	y=1.108+0.271x
<i>C. sclopetarius</i>				
Non-ovigerous females	149	0.371	<0.001	y=1.317+0.256x
Ovigerous females	90	0.353	<0.001	y=1.400+0.234x
Males	87	0.338	<0.001	y=1.477+0.246x
All individuals	328	0.476	<0.001	y=1.212+0.313x
<i>C. vittatus</i>				
Non-ovigerous females	200	0.306	<0.001	y=1.375+0.219x
Ovigerous females	71	0.213	<0.001	y=1.493+0.169x
Males	154	0.113	<0.001	y=1.655+0.159x
All individuals	439	0.284	<0.001	y=1.348+0.247x

Table 3. Covariance analyses of the linear regressions between the shell weight (\log_{10}) and the shield length (\log_{10}) of males, ovigerous and non-ovigerous females (reproductive classes), and all individuals of *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus*.

Model	N	df	F	P
Among reproductive classes				
<i>Clibanarius antillensis</i>	578			
Shield length		1	327.550	<0.001
Elevation (y-intercept)		2	2.575	0.077
Slope		2	0.380	0.684
<i>Clibanarius sclopetarius</i>	326			
Shield length		1	145.018	<0.001
Elevation (y-intercept)		2	0.162	0.850
Slope		2	0.104	0.901
<i>Clibanarius vittatus</i>	425			
Shield length		1	66.494	<0.001
Elevation (y-intercept)		2	5.838	0.003
Slope		2	5.212	0.006
Among hermit crab species	1366			
Shield length		1	853.775	<0.001
Elevation (y-intercept)		2	80.513	<0.001
Slope		2	56.383	<0.001

shells used by *Clibanarius antillensis* were lighter than those used by *C. scolopetarius* and *C. vittatus* while the total and aperture lengths of the shells did not vary among crab species (except aperture length of *Stramonita*) (Table 1).

Significant linear models were fitted between shell weight and the size of all individuals and of males and ovigerous and non-ovigerous females (Table 2). Covariance analysis showed that the linear models fitted for

males and ovigerous and non-ovigerous females of both *C. antillensis* and *C. scolopetarius* showed same slopes and elevation (y-intercept) (Table 3). This relationship was dependent on the reproductive status of *C. vittatus* and on crab species, as evidenced by the differences in the slopes and y-intercepts of the fitted models for this species (Table 3). Regression models between the size of the crabs and the parameters (total and aperture length and weight)

Table 4. Linear regressions between shield length of *Clibanarius antillensis*, *C. scolopetarius* and *C. vittatus* and shell parameters (shell weight and total and aperture length).

	N	r ²	P	Equation
Total length				
<i>Clibanarius antillensis</i>				
<i>Chicoreus senegalensis</i>	56	0.157	0.002	y=27.695+2.948x
<i>Stramonita haemastoma</i>	69	0.420	<0.001	y=13.286+4.395x
<i>Leucozonia nassa</i>	43	0.503	<0.001	y=12.119+5.357x
<i>Cerithium atratum</i>	439	0.242	<0.001	y=18.371+2.878x
<i>Clibanarius scolopetarius</i>				
<i>Chicoreus senegalensis</i>	163	0.507	<0.001	y=25.255+3.786x
<i>Stramonita haemastoma</i>	62	0.411	<0.001	y=27.578+2.485x
<i>Leucozonia nassa</i>	14	0.432	0.011	y=27.305+3.330x
<i>Cymatium parthenopeum</i>	30	0.619	<0.001	y=4.750+6.354x
<i>Clibanarius vittatus</i>				
<i>Chicoreus senegalensis</i>	208	0.399	<0.001	y=26.615+3.802x
<i>Stramonita haemastoma</i>	122	0.396	<0.001	y=22.584+2.931x
<i>Leucozonia nassa</i>	33	0.359	<0.001	y=25.129+3.679x
<i>Cymatium parthenopeum</i>	30	0.324	0.001	y=22.854+3.978x
Aperture length				
<i>Clibanarius antillensis</i>				
<i>Chicoreus senegalensis</i>	55	0.262	<0.001	y=6.481+1.338x
<i>Stramonita haemastoma</i>	69	0.431	<0.001	y=10.214+2.616x
<i>Leucozonia nassa</i>	42	0.408	<0.001	y=7.680+3.124x
<i>Cerithium atratum</i>	438	0.217	<0.001	y=6.998+1.244x
<i>Clibanarius scolopetarius</i>				
<i>Chicoreus senegalensis</i>	163	0.415	<0.001	y=5.312+1.482x
<i>Stramonita haemastoma</i>	65	0.496	<0.001	y=15.741+1.948x
<i>Leucozonia nassa</i>	14	0.599	0.001	y=11.710+2.516x
<i>Cymatium parthenopeum</i>	28	0.634	<0.001	y=-5.076+3.452x
<i>Clibanarius vittatus</i>				
<i>Chicoreus senegalensis</i>	207	0.358	<0.001	y=7.141+1.256x
<i>Stramonita haemastoma</i>	120	0.507	<0.001	y=14.726+2.000x
<i>Leucozonia nassa</i>	33	0.197	0.010	y=15.459+1.953x
<i>Cymatium parthenopeum</i>	27	0.579	<0.001	y=-0.300+2.718x
Weight (log₁₀)*				
<i>Clibanarius antillensis</i>				
<i>Chicoreus senegalensis</i>	52	0.198	0.001	y=1.341+0.173x
<i>Stramonita haemastoma</i>	77	0.333	<0.001	y=1.204+0.233x
<i>Leucozonia nassa</i>	41	0.238	0.001	y=1.278+0.170x
<i>Cerithium atratum</i>	415	0.213	<0.001	y=1.140+0.179x
<i>Clibanarius scolopetarius</i>				
<i>Chicoreus senegalensis</i>	166	0.491	<0.001	y=1.244+0.294x
<i>Stramonita haemastoma</i>	84	0.438	<0.001	y=1.101+0.360x
<i>Leucozonia nassa</i>	20	0.289	0.014	y=1.138+0.300x
<i>Cymatium parthenopeum</i>	32	0.425	<0.001	y=1.417+0.275x
<i>Clibanarius vittatus</i>				
<i>Chicoreus senegalensis</i>	225	0.394	<0.001	y=1.292+0.262x
<i>Stramonita haemastoma</i>	124	0.393	<0.001	y=1.157+0.343x
<i>Leucozonia nassa</i>	42	0.256	0.001	y=1.185+0.272x
<i>Cymatium parthenopeum</i>	29	0.036	ns	y=1.752+0.112x

*; shield length also transformed by log₁₀; ns, not significant.

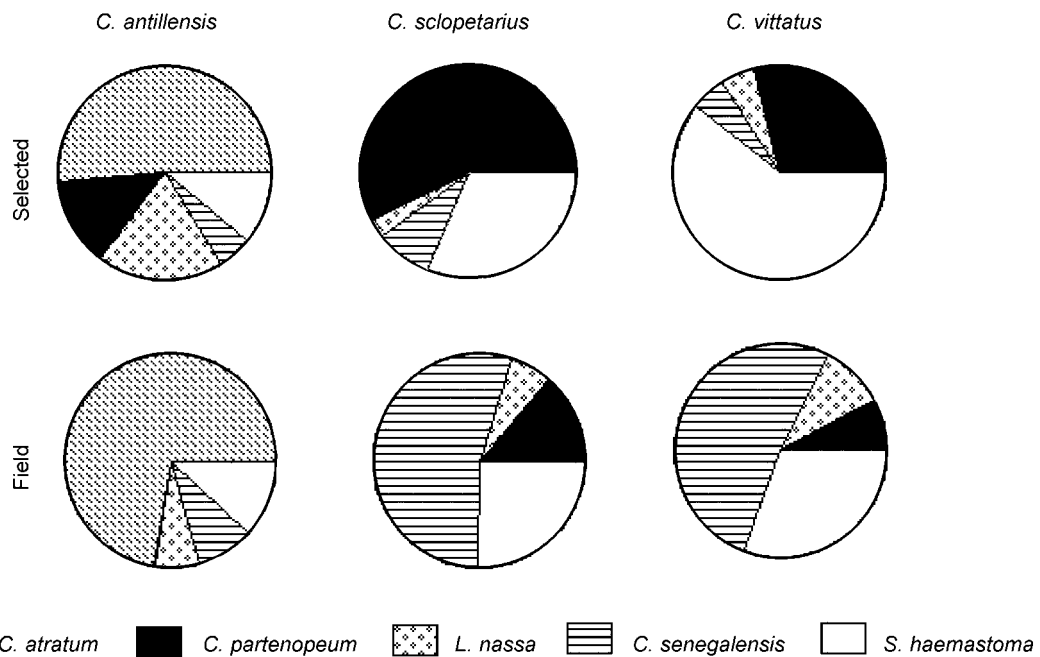
Table 5. Covariance analyses of the linear regressions between the shield length of *Clibanarius antillensis*, *C. scolopetarius* and *C. vittatus* and the total and aperture length of the most used shells.

Model	N	df	F	P
Shield length×shell total length				
Among hermit crab species				
<i>Chicoreus senegalensis</i>	427			
Shield length		1	132.299	<0.001
Elevation (y-intercept)		2	0.146	0.864
Slope		2	0.526	0.591
<i>Stramonita haemastoma</i>	253			
Shield length		1	137.117	<0.001
Elevation (y-intercept)		2	4.915	0.008
Slope		2	3.039	0.050
<i>Leucozonia nassa</i>	90			
Shield length		1	52.595	<0.001
Elevation (y-intercept)		2	2.558	0.083
Slope		2	1.430	0.245
<i>Cymatium parthenopeum</i>	60			
Shield length		1	37.707	<0.001
Elevation (y-intercept)		2	1.716	0.196
Slope		2	1.994	0.163
Among shell species				
<i>Clibanarius antillensis</i>	597			
Shield length		1	215.846	<0.001
Elevation (y-intercept)		3	5.478	0.001
Slope		3	4.949	0.002
<i>C. scolopetarius</i>	265			
Shield length		1	83.510	<0.001
Elevation (y-intercept)		3	6.272	<0.001
Slope		3	10.775	<0.001
<i>C. vittatus</i>	390			
Shield length		1	90.106	<0.001
Elevation (y-intercept)		3	0.506	0.678
Slope		3	1.228	0.299
Shield length×shell aperture length				
Among hermit crab species				
<i>Chicoreus senegalensis</i>	425			
Shield length		1	126.274	<0.001
Elevation (y-intercept)		2	0.924	0.398
Slope		2	0.791	0.454
<i>Stramonita haemastoma</i>	254			
Shield length		1	181.968	<0.001
Elevation (y-intercept)		2	2.449	0.088
Slope		2	1.195	0.304
<i>Leucozonia nassa</i>	89			
Shield length		1	37.789	<0.001
Elevation (y-intercept)		2	1.200	0.306
Slope		2	0.891	0.414
<i>Cymatium parthenopeum</i>	55			
Shield length		1	45.461	<0.001
Elevation (y-intercept)		2	0.400	0.530
Slope		2	0.644	0.426
Among shell species				
<i>Clibanarius antillensis</i>	594			
Shield length		1	247.731	<0.001
Elevation (y-intercept)		3	2.012	0.111
Slope		3	13.906	<0.001
<i>C. scolopetarius</i>	266			
Shield length		1	101.213	<0.001
Elevation (y-intercept)		3	15.678	<0.001
Slope		3	11.937	<0.001
<i>C. vittatus</i>	385			
Shield length		1	128.263	<0.001
Elevation (y-intercept)		3	11.922	<0.001
Slope		3	6.160	<0.001

Table 6. Covariance analyses of the linear regressions between the shield length (\log_{10}) of *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus* and the weight (\log_{10}) of the most used shells.

Model	N	df	F	P
Among hermit crab species				
<i>Chicoreus senegalensis</i>	435			
Shield length		1	208.605	<0.001
Elevation (y-intercept)		2	1.712	0.182
Slope		2	2.006	0.136
<i>Stramonita haemastoma</i>	281			
Shield length		1	160.955	<0.001
Elevation (y-intercept)		2	0.655	0.520
Slope		2	0.497	0.609
<i>Leucozonia nassa</i>	101			
Shield length		1	29.969	<0.001
Elevation (y-intercept)		2	0.899	0.410
Slope		2	0.262	0.770
Among shell species				
<i>Clibanarius antillensis</i>	585			
Shield length		1	89.402	<0.001
Elevation (y-intercept)		3	1.892	0.130
Slope		3	0.361	0.781
<i>C. sclopetarius</i>	302			
Shield length		1	89.994	<0.001
Elevation (y-intercept)		3	1.914	0.127
Slope		3	1.924	0.126
<i>C. vittatus</i> *	391			
Shield length		1	96.579	<0.001
Elevation (y-intercept)		2	2.104	0.123
Slope		2	2.830	0.060

*, *Cymathium parthenopeum* was not included due to non-significant regression.

**Figure 4.** Proportions of the selected shells by *Clibanarius antillensis* (N=37), *C. sclopetarius* (N=35) and *C. vittatus* (N=38) in laboratory experiments and of the most used gastropod shells in the field (N=713, 371 and 507, respectively).

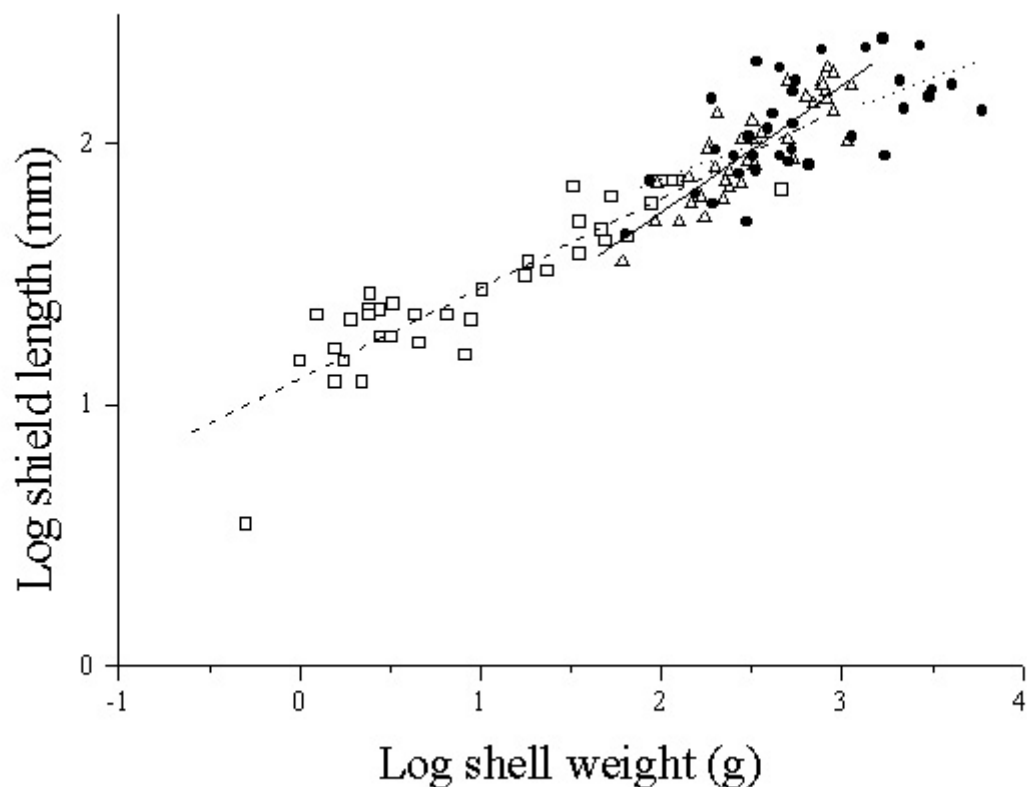


Figure 5. Linear regressions between shield length (\log_{10}) of *Clibanarius antillensis* (open squares, dotted line; $y=1.082+0.355x$, $N=36$, $r^2=0.817$, $P<0.001$); *C. sclopetarius* (filled circles, dashed line; $y=1.353+0.256x$, $N=35$, $r^2=0.389$, $P<0.001$) and *C. vittatus* (open triangles, solid line; $y=0.771+0.482x$, $N=37$, $r^2=0.733$, $P<0.001$) and the weight (\log_{10}) of the shells selected in shell selection experiments.

of each of the most used shells were generally significant (except between *C. vittatus* and *Cymatium*) but had low values of r^2 (less than 0.5) (Table 4).

The relationship between crab size and the parameters of each gastropod (see Table 4) was compared among hermit crab species (Tables 5 & 6, 'among hermit crab species' factor). The results revealed that these relationships were independent of the hermit crab species (except for *Stramonita*). The relationships between crab size and shell parameters (see Table 4) were compared among the shell species used by each hermit crab (Tables 5 & 6, 'among shell species' factor). The regressions between shield length and the total length of the shells did not enable generalization as can be done for aperture length and weight. All regressions using shell aperture revealed differences among shell species, i.e. each shell presented a particular match with the hermit crabs regarding shell aperture. In contrast, all regressions fitted between crab size and shell weight were independent of shell species, i.e. the relationship between the size of a given hermit crab and shell weight is the same for any shell species.

Shell selection

The three hermit crab populations selected different shell species ($G=72.72$, $df=4$, $P<0.001$). *Clibanarius antillensis* selected mainly shells of *Cerithium*, *Clibanarius sclopetarius* shells of *Cymatium*, and *Clibanarius vittatus* those

of *Stramonita* (Figure 4). Despite the fact that *C. antillensis* chose mainly the most used shell in the field, it also selected shells of *Leucozonia* and *Cymatium* more than expected by field surveys ($G=30.36$, $df=4$, $P<0.001$). The proportion of shells selected by *Clibanarius sclopetarius* and *C. vittatus* ($G=44.06$, $df=3$, $P<0.001$; $G=45.12$, $df=3$, $P<0.001$, respectively) diverged more from their patterns of shell use in nature than *C. antillensis*. These two populations selected shells of *Cymatium* and *Stramonita* more than expected and shells of *Leucozonia* and *Chicoreus* less than expected by the shell use pattern. The fitted models revealed significant and positive relationships between crab size and weight of the selected shells, which demonstrated a dependence on crab species (analysis of covariance, slope: $F=4.018$, $df=2$, $P=0.021$; elevation (y-intercept): $F=4.256$, $df=2$, $P=0.017$) (Figure 5).

DISCUSSION

The high overlap index in shell use, 80% among *Clibanarius sclopetarius*, *C. vittatus* and the largest individuals of *C. antillensis* (associated with the low availability of the shell species used by them), indicates that these crabs may undergo competitive interactions. In fact, as Gherardi (1990) pointed out, there is a contradiction between high rates of overlap in shell use and coexistence of hermit crabs. Despite *C. vittatus* and *C. sclopetarius* occupying the same shell species they used shells with different

dimensions (present study) as well as degrees of encrustation and physical damages (Turra, in press). *Clibanarius antillensis* used relatively lighter shells than individuals of the same size of the two other species, despite the similarities in aperture and total lengths. This difference in shell weight was probably due to the higher degree of physical damage to the shells used by *C. antillensis* in this area (Turra, in press). Consequently, a stronger competition would be expected between these two species than between them and *C. antillensis*. Coexistence of these two hermit crab species seems to be associated with small differences (partitioning) in their shell utilization and selection pattern (see below). Moreover, microhabitat segregation was recorded between *C. scopetarius* and *C. vittatus* (Turra et al., 2000) and may be of fundamental importance in enabling their coexistence at Pernambuco Islet as demonstrated in other hermit crab assemblages (Mitchell, 1975; Kellogg, 1977; Gherardi, 1990; Gherardi & Nardone, 1997).

Intraspecific shell partitioning was also recorded among the three studied populations regarding reproductive and size-classes. Males showed a strong tendency to utilize larger shells than females as also demonstrated by Imazu & Asakura (1994) and Asakura (1995) (but see Manjón-Cabeza & García-Raso, 1999). This can be explained by the competitive dominance of males over females (Bertness, 1981c; Abrams, 1988; Asakura, 1995), or by their particular patterns of shell selection (Abrams, 1988). Moreover, this situation at Pernambuco Islet may be a direct consequence of the larger size attained by the males of the studied species in relation to females (Turra & Leite, 2000). In addition, larger individuals of *C. scopetarius* and *C. vittatus* showed a tendency to use less shell species than the smaller ones as also recorded for other species (Reddy & Bisewar, 1993; Imazu & Asakura, 1994; Turra & Leite, 2001). In contrast, *C. antillensis* had the opposite pattern at Pernambuco Islet, i.e. larger individuals used more shell species than the smaller ones. This is not a species-specific characteristic because another population of *C. antillensis* presents the same pattern as *C. scopetarius* and *C. vittatus* (Turra & Leite, 2001), reinforcing the importance of the shell availability, which is quite different between the two areas, on shell utilization pattern.

The importance of resource partitioning in enabling species coexistence may be especially important at Pernambuco Islet given the low shell availability when compared to nearby areas (Leite et al., 1998; Turra & Leite, 2001). This suggests that *C. scopetarius* and *C. vittatus*, populations that do not use shells of *Cerithium*, are subjected to a stronger shell limitation. This shell limitation is enhanced given the large sizes of these two species because shell availability is generally low for the largest individuals in natural hermit crab populations (Reese, 1969; Spight, 1985). In addition, hermit crabs that show larger discrepancies between the patterns of shell utilization and selection, as shown for these two populations, are thought to be more affected by shell limitation (Mitchell, 1975).

Hermit crabs show a tendency to use the shells of the coexisting most abundant gastropods (Reese, 1969; Wilber & Herrnkind, 1982; Leite et al., 1998), thus evidencing the importance of shell availability in the utilization

patterns of hermit crabs. However, shell use can also be modulated by crab preferences (Kellogg, 1977; Bertness, 1980), by intra- and inter-specific competition (Bach et al., 1976; Bertness, 1981d; Abrams, 1988), and by desiccation (Lively, 1988; Gherardi, 1990; Hahn, 1998) and predation pressures (Lively, 1988). In turn, shell preferences may be influenced by past experience (Hazlett, 1996) and growth rate of the individuals (Wada et al., 1997).

Shell selection experiments revealed that the three hermit crabs showed preferences for different shell species. These differences may represent adaptations to reduce interspecific competition (Vance, 1972; Grant & Ulmer, 1974), reflecting selective pressures that act on each crab population (Bertness, 1981e). Although these preferences did not explain the patterns of shell use in nature (except for *C. antillensis*), the comparison between shell use and availability indicates that crabs were selecting the shells they occupied, i.e. the shells were not occupied at random as also demonstrated previously for other hermit crab assemblages (Leite et al., 1998; Turra & Leite, 2001). The preferences of the crabs are related to shell architecture (Bertness, 1981e) and can be influenced by the presence of predators (Bertness, 1981f). Thus, the extensive use of *Chicoreus* by both *Clibanarius scopetarius* and *C. vittatus* can be explained by its architecture. According to Vermeij (1978), shells such as those of *Chicoreus* are less susceptible to predation and are useful in areas with high abundance of shell crushing predators like *Callinectes danae* at Pernambuco Islet (A.T., personal observation). The shell utilization by the population of *Clibanarius antillensis* seems to be influenced by both shell availability and crab preference since the individuals selected and used almost exclusively the shells of the most abundant gastropod *Cerithium atratum*. Furthermore, the selection and frequent utilization of such shells by *Clibanarius antillensis* may be associated with the success of this species in the intertidal Pernambuco Islet. *Cerithium atratum* is a high-spined gastropod that, according to Lively (1988), enables retention of large amounts of water and hermit crab retraction, thus reducing the risks of desiccation and predation, respectively.

Shell variables showed weak relationships with crab size indicating shell inadequacy to the crabs (Turra, in press). Covariance analysis revealed that aperture and total length showed particular relationships with each hermit crab species while the relationships between crab size and shell weight were independent of shell species. This occurred probably because total and aperture lengths are more directly related to shell architecture than shell weight, indicating that hermit crabs discriminate shell species (architecture) but not shell weight. This enables comparisons among different kinds of shells using shell weight. The results of covariance analysis also suggested that the relationships between crab size and shell variables for a given shell species were independent of crab species, i.e. shell morphology and dimensions were dictating the size (not species) of crab that will occupy it. This reinforces the importance of shells in influencing crab size and morphology (Blackstone, 1985). The sizes of the crabs showed particular relationships with shell weight when all shells were analysed together (see Table 3). This occurred because each crab species

used shells with different architectures in different proportions. In general, the parameters of the selected shells are closely related to crab size (Bertness, 1980). In contrast, the weight of the selected shells was poorly related to the shield length of the three hermit crab species, suggesting that the crabs are using other parameters rather than only shell weight in shell assessment as shown by Floeter et al. (2000). In addition, the crab species selected shells in different ways given the species-specific regression lines between crab size and the weight of the selected shells.

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