

# Patterns of shell utilization and selection in two sympatric hermit crabs (Anomura: Diogenidae) in south-eastern Brazil

S.R. Floeter\*<sup>†</sup>, R.C. Nalesso<sup>‡</sup>, M.M.P. Rodrigues\* and A. Turra<sup>§</sup>

\*Programa de Pós-Graduação em Psicologia, Universidade Federal do Espírito Santo, Avenida Fernando Ferrari S/N, Vitória, ES, CEP 29060-900, Brazil. <sup>†</sup>E-mail: floeter.vix@zaz.com.br. <sup>‡</sup>Departamento de Ecologia e Recursos Naturais, Universidade Federal do Espírito Santo. <sup>§</sup>Programa de Pós-Graduação em Ecologia, Departamento de Zoologia, IB, Unicamp, CEP 13083-970, CP 6109, Campinas, SP, Brazil; e-mail: turra@unicamp.br

The present study evaluated shell utilization and preference of two sympatric hermit crab species, *Calcinus tibicen* and *Clibanarius antillensis*, from Ilha Galheta de Dentro, Vitória Bay, south-eastern Brazil. Distribution of individuals and use and availability of shells were estimated in the field, where microhabitat and shell partitioning were demonstrated between the two species of crabs. *Calcinus* occurred in higher numbers in the infralittoral fringe and shallow subtidal, while *Clibanarius* was found mainly in the midlittoral zone. The crabs used shells of different architectures and sizes. *Calcinus* used mainly globose and low spired shells (*Tegula viridula* and *Cymatium parthenopeum*), while *Clibanarius* utilized predominantly the elongated and high spired ones (mainly *Cerithium atratum*). *Clibanarius* used shells with smaller volume, weight, and aperture. Free access experiments were conducted in the laboratory and showed that *Calcinus* and *Clibanarius* had a high satisfaction rate, i.e. only 50% of the crabs exchanged their shells. From those that exchanged, they chose shells with higher internal volume than that used in the field, while shell weight did not present any increase. *Clibanarius* was found in shells closer to the preferred ones and in a very different proportion from shell availability, contrasting to *Calcinus*, which followed shell availability instead of their preferences. Shell internal volume was more important as a choice factor than the weight for both hermit crab species, showing that crabs optimized shell volume in relation to shell weight in the free access experiments.

## INTRODUCTION

Hermit crabs (Anomura: Diogenidae) are crustaceans adapted to use empty gastropod shells as shelter, which influences their life histories in many ways (Hazlett, 1981 for review). Populations subjected to different shell supplies present particular characteristics of abundance, size and reproduction (Bertness, 1981a). The shell resource may function as a limiting factor for some species or certain size-classes (Vance, 1972a; Fotheringham, 1976; Spight, 1977), thus influencing shell utilization patterns by hermit crabs (Bertness, 1980; Leite et al., 1998). In fact, empty shells are often scarce (e.g. Vance, 1972a; Bach et al., 1976), so that hermit crabs are forced to use small and inadequate shells (Conover, 1978). However, such empty shells can be unusually abundant in certain areas (Kellogg, 1976; Scully, 1979; Turra & Leite, in press), as is the case of the studied inlet in south-eastern Brazil.

Coexisting hermit crab species generally use different shells, present particular preferences for some shell types (e.g. Reese, 1962; Vance, 1972b; Bertness, 1980), and occur in different microhabitats (Kellogg, 1976; Gherardi, 1990). Shell selection behaviour seems to be based in a complex of simultaneous and interactive factors such as: shell weight, size, shape, internal volume, epibionts, resistance to predation, and desiccation. When the shell resource is scarce, the crabs may initiate a competitive interaction, through exploitation or interference (Busato et al., 1998).

The study of resource partitioning is of fundamental interest to understanding the patterns of species coexistence in ecological assemblages. In this way, several studies have examined shell utilization patterns in coexisting species to determine the factors responsible for minimizing interspecific competition (e.g. Vance, 1972a; Kellogg, 1977; Gherardi, 1990; Gherardi & Nardone, 1997; Floeter & Nalesso, 1998).

The aim of the present work was to evaluate: (1) shell use, availability, and preference of two sympatric hermit crab species: *Calcinus tibicen* (Herbst, 1791) and *Clibanarius antillensis* Stimpson, 1859, subjected to an uncommon high shell supply environment; and (2) the degree of importance of shell internal volume and shell weight as a choice factor in free access experiments.

## MATERIALS AND METHODS

### Study area

The present study was carried out in a small inlet in the Galheta Islands, Vitória Bay, State of Espírito Santo, in south-eastern Brazil (20°19'S 40°20'W), from July 1997 to March 1999. This area belongs to an Environmental Protection Zone that presents a high diversity of marine life. The inlet is surrounded by granite rocks and the bottom substrate comprises pebbles, cobbles, gravel, coarse sand, broken and empty shells, and coral and

urchin fragments. The average depth is about 1 m at high tide.

*Calcinus tibicen* and *Clibanarius antillensis*, the two most common species, coexist with four other species of hermit crabs in this area: *Dardanus venosus* (H. Milne-Edwards, 1848), *Pagurus provenzanoi* Forest & Saint Laurent, 1967, *Pagurus criniticornis* (Dana, 1852), and *Paguristes calliopsis* Forest & Saint Laurent, 1967. Hereafter, the two studied species will be referred as *Clibanarius* and *Calcinus*.

#### Field observations

To access the species composition and the basic aspects of the natural history of the hermit crabs, 27 h of underwater observations with snorkelling were made (including 2 h in nocturnal periods), encompassing all seasons, tides and temperature variations.

Hermit crabs, the empty shells (not extremely damaged and not filled by sand), and the living gastropods were counted and identified in eight samples (on different days) by 15 min of active search by two researchers, in total up to 4 h of underwater observations. The internal volume (ml) of the empty shells was measured by filling them with water from a graduated syringe. The shell weight (g) was registered to the nearest 0.01 g.

All shells were classified according to their general morphology regarding shape (globose or elongate), extent of spiralization (low spired: with four or less spires; high spired: more than four spires), and relative aperture size (large aperture—the aperture width and/or length was at least half of the shell width and/or length; small aperture—the opposite).

#### Laboratory experiments

Shell selection experiments were undertaken to verify shell preferences for *Clibanarius* and *Calcinus*. The crabs were collected and immediately placed in plastic trays (35×50×8 cm) with aerated seawater. Single crabs (with their original shell marked with a small stain of paint to avoid confusion with the offered shells) were placed in trays containing 50 gastropod shells (ten of the five most used types by the crabs in nature) of all sizes used by them. These shells were all free of damages and encrustation and randomly distributed inside the trays. The crabs remained in the tray for 24 h, time enough to investigate many shells (Conover, 1978; Scully, 1979). After that, the occupied shell was considered the preferred one, and its type and size registered. Each crab was removed from the selected shell, by heating the apex, and had its shield length (distance from the tip of the rostrum to the mid point of the cervical groove; Gherardi & Nardone, 1997) measured with vernier calliper to the nearest 0.5 mm. The preferred and the original shells were weighed (g) and had their internal volume (ml) calculated as described above.

#### Statistical analysis

Statistical analysis were based on Zar (1999) and performed at the 0.05 significance level. Data transformation was conducted when necessary (indicated through the text). The Student's *t*-test was used to compare crab size and shell weight and volume between crab species.

The weight of the different empty shells was compared through analysis of variance (ANOVA) followed by the Scheffé's test for multiple pairwise comparisons.

The log-likelihood *G*-test was employed to contrast shell availability with shell use and preference regarding shell type and morphology. Cluster analyses (UPGMA and squared Euclidean distance) (Krebs, 1989) was accomplished to explore the similarities among the relative abundance (percentages) of available shells and those used in the field and selected in the free access experiments. Paired *t*-tests were conducted to verify differences in shell volume and weight between shells used in the field and selected in the experiments by the two crab species. The relationships between crab size and shell variables were evaluated through regression analysis. Covariance analysis (ANCOVA) was used to compare the elevation (*y*-intercept) and the slopes of the linear models fitted for crab size and shell parameters.

## RESULTS

### *Species composition and behaviour*

The most abundant species in the Galheta Islands was *Clibanarius antillensis* (716 ind) followed by *Calcinus tibicen* (320 ind). Both hermit crabs were more active at night, as showed for *C. antillensis* in the field as well as in the laboratory (Hazlett, 1966; S.R.F. & A.T., personal observation). It was verified that all hermit crab species showed high activity at low tides, but at the incoming tides they looked for refuges in holes, crevices or under pebbles.

*Calcinus* was observed feeding mainly on algae, having also been seen moving (possible feeding) on colonies of *Palythoa* sp., zoanthid that produces a potent toxin (palytoxin) (Gleibs & Mebs, 1998). *Calcinus* was always found in the infralittoral fringe and shallow subtidal. Ovigerous females were all of small size (4–6 mm) and found in all seasons.

*Clibanarius* is an agile species and of smaller size than *Calcinus* (4.19 ±1.01 mm and 4.90 ±1.07 mm, respectively;  $t = -4.673$ ,  $df = 99$ ,  $P < 0.001$ ), that has gregarious behaviour, being commonly found in clusters of up to 30 individuals (Turra & Leite, 2000). They were frequently found in the midlittoral zone and supralittoral fringe, sometimes exposed to the air with their shell openings turned upward (Turra & Leite, 2000). This species was observed feeding mainly on detritus. Ovigerous females were found in all seasons in smaller numbers (12%) than *Calcinus* (40%), with shield length varying between 3.5 and 4 mm.

### *Patterns of shell use*

The main gastropod species found in the studied area and used by the hermit crabs were *Tegula viridula* (Gmelin, 1791); *Cerithium atratum* (Born, 1778); *Cymatium parthenopeum* (von Salis, 1793); *Leucozonia nassa* (Gmelin, 1791) and *Astraea latispina* (Philippi, 1844). Other shell types as *Siratus* (= *Chicoreus*) *senegalensis* (Gmelin, 1790), *Fusinus marmoratus* (Philippi, 1846), *Morula nodulosa* (C.D. Adams, 1845) and *Stramonita* (= *Thais*) sp. were used in lower frequencies by

the hermit crabs and were not computed in further analyses.

The amount of empty shells accumulated in the studied inlet was high (649 shells), overcoming in three times the number of living snails (208 ind), with *Tegula* and *Cymatium* being the most abundant ones (79.2%). Availability differed between empty shells and living gastropods ( $G=104.76$ ,  $df=4$ ,  $P<0.001$ ) (Table 1). Individuals of *Cerithium* were proportionally more frequent than their empty shells (4.3%), in opposition to empty shells of *Cymatium* that accumulated in the area in larger proportions (31.9%) than living snails (3.4%).

The two hermits used shells in different proportions ( $G=542.46$ ,  $df=4$ ,  $P<0.001$ ), with *Calcinus* occupying proportionally more shells of *Tegula*, *Astraea*, *Leucozonia* and *Cymatium*. On the other hand, *Clibanarius* occupied predominantly shells of *Cerithium* (~70%) (Table 1). The pattern of shell utilization of *Calcinus* was more similar to the pool of empty shells than to the pattern of *Clibanarius* ( $G=9.80$ ,  $df=4$ ,  $P<0.05$  and  $G=817.78$ ,  $df=4$ ,  $P<0.001$ , respectively). The patterns of shell use of both species also differed markedly from the living snails (*Calcinus*,  $G=77.74$ ,  $df=4$ ,  $P<0.001$ ; *Clibanarius*,  $G=236.54$ ,  $df=4$ ,  $P<0.001$ ).

The difference between hermit crab species in shell utilization was also evident when shells were analysed regarding their general architecture. *Clibanarius* occupied elongated, high spired and small aperture shells more frequently than *Calcinus* ( $G=123.02$ ,  $df=1$ ,  $P<0.001$ ;  $G=491.26$ ,  $df=1$ ,  $P<0.001$ ; and  $G=176.06$ ,  $df=1$ ,  $P<0.001$ , respectively) (Figure 1). *Cerithium* was the only shell that presented at the same time high spiralization, elongated and small aperture shells. *Cymatium* and *Leucozonia* present similar morphological characteristics to each other (elongated, low spiralization and proportionally large aperture shells), differing from both *Tegula* and *Astraea* (globose, low spiralization and small aperture shells).

Shell use regarding architecture was also compared between hermit crabs and empty shells (Figure 1). *Clibanarius* used proportionally more elongate, high spired and small aperture shells than available in the field ( $G=101.96$ ,  $df=1$ ,  $P<0.001$ ;  $G=713.92$ ,  $df=1$ ,  $P<0.001$ ; and  $G=337.12$ ,  $df=1$ ,  $P<0.001$ , respectively). In contrast, shell utilization by *Calcinus* was more similar to empty shells than *Clibanarius* regarding shell shape, spiralization, and relative aperture width ( $G=8.48$ ,  $df=1$ ,  $P<0.005$ ;

**Table 1.** Shell utilization pattern of *Calcinus tibicen* and *Clibanarius antillensis* and frequency of available empty shells and living snails.

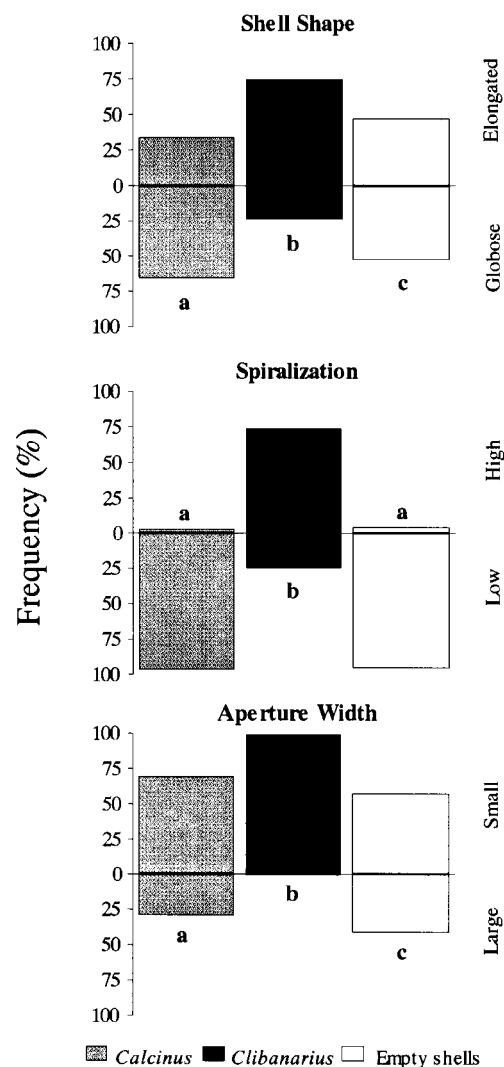
	<i>Calcinus tibicen</i>	<i>Clibanarius antillensis</i>	Empty shells	Living snails
Shell types	Frequency (%)			
<i>Astraea latispina</i>	7.0	1.0	6.0	10.6
<i>Cerithium atratum</i>	2.0	70.5	4.3	14.4
<i>Cymatium parthenopeum</i>	27.0	2.5	31.9	3.4
<i>Leucozonia nassa</i>	8.0	1.0	10.5	9.1
<i>Tegula viridula</i>	56.0	25.0	47.3	62.5

$G=3.02$ ,  $df=1$ , ns and  $G=5.34$ ,  $df=1$ ,  $P<0.025$ , respectively).

The most abundant empty shells in the studied inlet were of different mean weights (ANOVA,  $F=8.604$ ,  $df=4$ ,  $P<0.001$ ). Shells of *Leucozonia* and *Cymatium* were the heaviest and *Cerithium* the lightest ones. *Clibanarius* occupied lighter shells ( $4.17 \pm 0.92$  g,  $N=50$ ) and shells with lower internal volumes ( $0.41 \pm 0.29$  ml,  $N=50$ ) than *Calcinus* ( $5.22 \pm 1.22$  g,  $N=51$  and  $0.93 \pm 1.03$  ml,  $N=51$ , respectively;  $t=-4.866$ ,  $df=99$ ,  $P<0.001$  and  $t=-3.425$ ,  $df=99$ ,  $P=0.001$ , respectively). An overlap in shell use between the two crab species was registered for individuals ranging from 3 to 6 mm (Figure 2).

#### Free access experiments

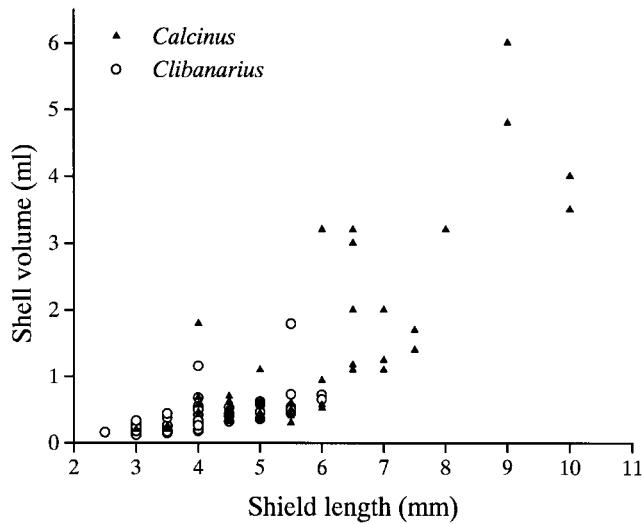
The results showed that almost half of the crabs (48% for both species) selected their original shells at the end of the experiments, i.e. these shells were considered to be preferred sizes and types. *Calcinus* and *Clibanarius* selected



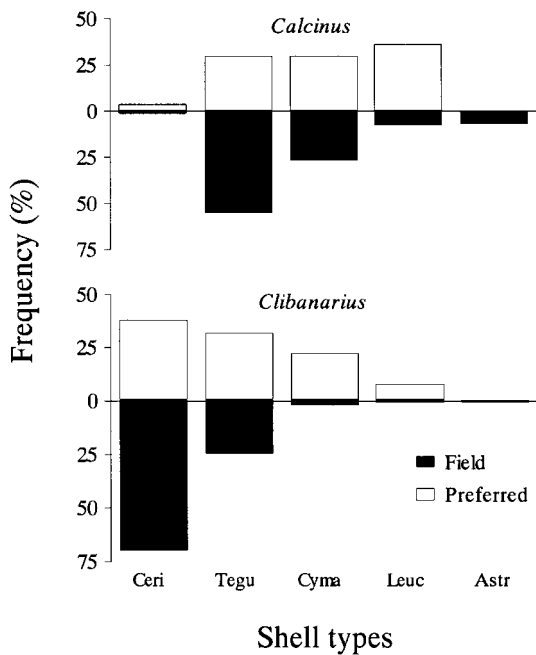
**Figure 1.** Architecture of the shell types (shell shape; spiralization; and aperture width) occupied by hermit crabs: *Calcinus tibicen* ( $N=320$ ) and *Clibanarius antillensis* ( $N=716$ ), and of the empty shells ( $N=649$ ). Labels (a, b and c) indicate the comparisons ( $G$ -test,  $P<0.05$ ) of the proportions of shells with a given shell feature.

different types of shells ( $G=26.24$ ,  $df=3$ ,  $P<0.001$ ), with the former showing a preference order for *Leucozonia*, *Tegula* and *Cymatium*. *Clibanarius* selected shells of *Cerithium*, *Tegula* and *Cymatium*, showing a slightly preference for the former ones (Figure 3).

Crabs selected shells in different proportions from those used in the field (*Calcinus*,  $G=33.00$ ,  $df=4$ ,  $P<0.001$ ; and *Clibanarius*,  $G=42.04$ ,  $df=4$ ,  $P<0.001$ , respectively) (Figure 3). Cluster analysis revealed that there was a greater similarity between shell use and preference for *Clibanarius* than for *Calcinus*, whose utiliza-



**Figure 2.** Relationship between shield length (mm) and shell internal volume (ml) for shell types used by *Calcinus tibicen* and *Clibanarius antillensis*.

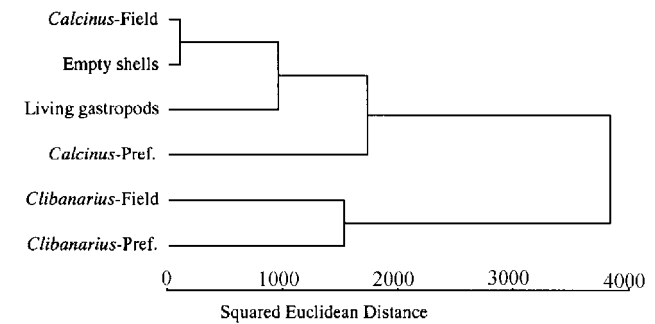


**Figure 3.** Frequency of shells occupied by *Calcinus tibicen* and *Clibanarius antillensis* in the field and after the free access experiments. Ceri, *Cerithium atratum*; Tegula, *Tegula viridula*; Cyma, *Cymatium parthenopeum*; Leuc, *Leucozonia nassa*; Astr, *Astraea latispina*.

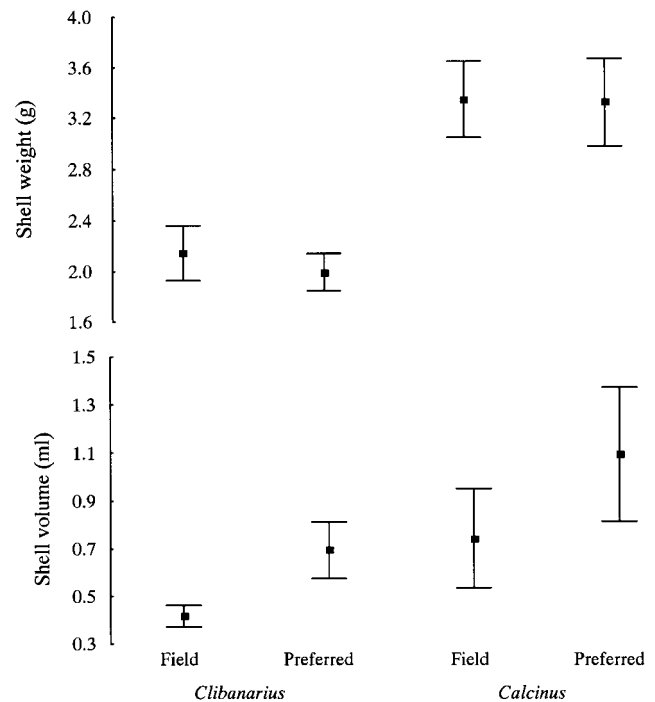
tion pattern was more similar to the pool of empty shells and living gastropods (Figure 4).

Individuals of *Calcinus* and *Clibanarius* that had changed to a new shell in the free access experiments, selected shells with higher internal volumes than those used in the field (Figure 5) (paired  $t$ -test,  $t=-3.345$ ,  $df=26$ ,  $P<0.005$  and  $t=-2.868$ ,  $df=26$ ,  $P<0.05$ , respectively). In contrast, no significant differences were registered for shell weight (paired  $t$ -test,  $t=0.063$ ,  $df=26$ , ns and  $t=0.561$ ,  $df=26$ , ns, respectively).

Linear regression models were fitted between the shield length of the two hermit crabs and shell volume and weight in the field and in the free access experiments (Table 2). Low values of the determination coefficient ( $r^2$ )



**Figure 4.** Cluster analysis comparing shell availability as empty gastropod shells and living gastropods with shell use in the field and after the free access experiments (preferred) by *Calcinus tibicen* and *Clibanarius antillensis* using UPGMA method and squared Euclidean distance. (Original data were transformed in percentages to standardize abundance in all situations). Pref., preferred.



**Figure 5.** Internal volume (Mean  $\pm$ SE) and weight of shells occupied by *Calcinus tibicen* and *Clibanarius antillensis* in the field and after the free access experiments.

**Table 2.** Linear regression models between shield length (SL) of the hermit crabs and shell dimensions (SW, shell weight; SV, shell volume) in the field and after the free access experiments.

Models	N	$r^2$	F-values	P	Regression equation
<i>Calcinus</i>					
SL vs SW					
Field*	51	0.467	42.916	<0.001	SW=0.108+0.265SL
Free access experiments	26	0.552	26.172	<0.001	SW=-1.864+0.971SL
SL vs SV					
Field*	51	0.569	64.591	<0.001	SV=-0.641+0.232SL
Free access experiments*	27	0.811	107.109	<0.001	SV=-0.870+0.296SL
<i>Clibanarius</i>					
SL vs SW					
Field*	49	0.605	71.887	<0.001	SW=-0.177+0.283SL
Free access experiments	27	0.348	13.335	0.001	SW=-0.567+0.612SL
SL vs SV					
Field*	48	0.574	61.903	<0.001	SV=-0.124+0.103SL
Free access experiments*	27	0.746	73.548	<0.001	SV=-0.673+0.274SL

\*, Shell dimensions were transformed by  $\text{Log}_{10}(x+1)$ .

**Table 3.** Covariance analysis (ANCOVA) for the regression lines between shield length and shell weight and volume for *Calcinus tibicen* and *Clibanarius antillensis* in the field and in the free access experiments ( $df=1$  for all tests).

Parameters	N	F-values	P
<i>Calcinus</i>			
Weight	78		
Elevation (Y-intercept)		0.189	0.665
Slope		0.439	0.509
Volume	78		
Elevation (Y-intercept)		3.910	0.052
Slope		5.956	0.017
<i>Clibanarius</i>			
Weight	77		
Elevation (Y-intercept)		0.618	0.434
Slope		0.709	0.402
Volume	77		
Elevation (Y-intercept)		11.839	0.001
Slope		19.819	<0.001

were registered for all models in the field and between shield length and shell weight in the experiments. High values of  $r^2$  were only observed between crab size and the volume of the preferred shells, indicating higher accuracy in estimating shell volume from crab size. Comparisons of these regression lines through covariance analysis (ANCOVA) are presented in Table 3. The linear models fitted for shells used in the field and selected after the experiments regarding shell weight presented equal elevation (y-intercept) and slopes. In contrast, the fitted lines for internal volume between these two situations varied significantly.

## DISCUSSION

### *Patterns of shell utilization and resource partitioning*

The crabs used shells of contrasting architectures and sizes. Upper intertidal species such as *Clibanarius antillensis*

need to minimize dehydration during the low tides. This species occupied preferentially elongated, high spired and small aperture shells (e.g. *Cerithium*), which could function as an efficient water reservoir, thus reducing thermal stress (Bertness, 1981b, 1982; Lively, 1988). On the other hand, *Calcinus*, that occurred near the infralittoral fringe and was found frequently submerged, used mainly globose, low spired and large aperture shells (e.g. *Tegula* and *Cymatium*). Gherardi (1990) pointed out that the genus *Clibanarius* survives dehydration longer than *Calcinus*.

*Calcinus* occupied five shell types in the field, with *Tegula* and *Cymatium* representing more than 80%. However, in the laboratory they selected mainly *Leucozonia* shells that were scarce in the field. *Clibanarius* used shells of few gastropod species with *Cerithium* and *Tegula* comprising more than 95%. In the laboratory, they chose these two shell types but also selected shells of *Cymatium* and *Leucozonia*. The latter two shell types were seldom found in adequate size for *Clibanarius* in nature. Although the two species presented high satisfaction rates in shell selection experiments, *Clibanarius* occupied relatively better shells in the field than *Calcinus* (i.e. *Clibanarius* in the field showed higher similarities with the preferred shells than those verified by *Calcinus*).

*Clibanarius* used shells in markedly different proportions from those available, showing that they are actively selecting their shells. However, shell use was shown to be influenced by shell availability, as also suggested by Bertness (1982) and Wilber & Herrnkind (1982) for other areas. This becomes evident because the most abundant gastropod and empty shell (*Tegula*) was frequently used by both *Calcinus* and *Clibanarius*. Shell availability can also be influenced by the utilization pattern of the crabs as evidenced by the use of *Cerithium* shells by *Clibanarius*. Empty shells of *Cerithium* were rare in the field, but were highly utilized by this species. These shells are preferred by this crab species so that they would have a quick flow into crab population due to exploitation ability of this crab in obtaining these shells. The same situation was also registered by shells of *Leucozonia* used by *Calcinus*.

Preferred shells were frequently scarce while the less preferred ones, as *Tegula* and *Cymatium*, were more abundant.

Therefore, this hermit crab assemblage does not seem to be restricted by shell supply and is able to grow and reproduce normally, as evidenced by the large number of crabs in this relatively small area. The high availability of shells in the studied area may be due to the complex structure of this inlet that presents low hydrodynamism, which prevents shell erosion and burrowing. Plenty of empty shells occur, at least for certain size-classes of crabs. This explains the high satisfaction rate (nearly half of the crabs did not exchange shells) when compared with other areas where shells were considered a limiting resource (Vance, 1972a; Bach et al., 1976; Spight, 1977). A. Turra (unpublished data), working in another south-eastern Brazilian area (São Sebastião, SP), where empty shells were not as abundant as in this study area, obtained satisfaction rates around 15–25% for *Clibanarius* species.

However, shell availability may not directly correspond to new shells to all crabs of all populations coexisting in a given site. More competitive species may use this new resource first, leaving the worst shells for the other species (Bertness, 1980). Therefore, it is possible to find crabs in low adequacy shells even in sites with high shell availability. The studied populations seemed to occupy low adequacy shells in the field due to the low  $r^2$  values (Scully, 1983) between shield length and shell weight and volume.

*Calcinus* used larger shells with larger volume and weight than *Clibanarius*, reflecting the size differences between these two species. However, there was an overlap in the sizes of the individuals (shield length, 3–6 mm), so that competition for shells may occur. Nevertheless, competition for shells can be minimized due to the high availability of empty shells of *Tegula* that are frequently used by both species in this size range. Some differences in the size of the shells of *Tegula* used by the two species should also have an important role in reducing the competition for shells between crabs of similar sizes.

Coexistence of these two hermit crabs may be enabled by: (1) shell partitioning between regarding shell morphology, type, and size, probably associated with microhabitat separation; (2) differences in the ability to locate and use new shells; (3) particular shell preferences; and (4) high availability of empty shells.

#### *The importance of the various shell characteristics: volume vs weight*

*Clibanarius* is also active at low tides and have to carry their shells when exposed to the air, it would be advantageous to this species to use a relatively light shell as *Cerithium*. *Calcinus*, which is much more frequent near the infralittoral fringe, will benefit from carrying heavier shells that are generally more resistant to predation as *Cymatium* and *Leucozonia*. This later shell (*Leucozonia*) belongs to the family Fasciolaridae, which (like Thaididae, referred by Gherardi & Nardone, 1997) offers good defence against predators. Shells of *Astraea* were less frequent as living snails and empty shells and were seldom used by the crabs, a fact that can be a consequence of their high weight in relation to internal volume, making them extremely costly to be carried by the crabs.

The degree of importance of several morphologic shell characteristics was always debatable. However, there are agreements about the advantages of shell volume to offspring and mating (cf. Gherardi & Nardone, 1997). Significant differences in the internal volume were found between the preferred shells and that used in nature. The volume increased after shell selection experiments, indicating that crabs were optimising the internal volume, without increasing shell weight.

It can be inferred that the internal volume is more important as a choice factor than the weight for both hermit crab species. In the aquatic hermit crabs the effect of the weight of the shell is less important than for the terrestrial hermits (genus *Coenobita*) (Elwood & Neil, 1992). Therefore, the importance of these shell characteristics to intertidal hermit crabs depends on the degree of exposure experienced by each individual during low tides. In general, it is important for a hermit crab to obtain a larger and a more resistant shell, but it is also necessary to minimise the energetic costs of carrying it (Osorno et al., 1998).

We would like to thank Maria Saete G. Floeter, Jean-Christophe Joyeux, Celso Azevedo, Carlos Ruiz Miranda, and Silvia M. Gandolfi for reviewing the paper. Professor Gustavo S. Melo and Ricardo Absalão for helping in the identification of the crabs and the gastropods, respectively. Aldicea G.V. Floeter, João Luiz Gasparini, Alexandre Fontana, Alexandre Arantes and Fábio Lyrio for the help in the field. The first author is indebted to CNPq and CAPES for grant funding.

## REFERENCES

- Bach, C.B., Hazlett, B. & Rittschof, D., 1976. Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. *Ecology*, **57**, 579–586.
- Bertness, M.D., 1980. Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama. *Journal of Experimental Marine Biology and Ecology*, **48**, 1–16.
- Bertness, M.D., 1981a. Pattern and plasticity in tropical hermit crab growth and reproduction. *American Naturalist*, **117**, 754–773.
- Bertness, M.D., 1981b. Conflicting advantages in resource utilization: the hermit crab housing dilemma. *American Naturalist*, **118**, 432–437.
- Bertness, M.D., 1982. Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. *Journal of Experimental Marine Biology and Ecology*, **64**, 159–187.
- Busato, P., Benvenuto, C. & Gherardi, F., 1998. Competitive dynamics of a Mediterranean hermit crab assemblage: the role of interference and exploitative competition for shells. *Journal of Natural History*, **32**, 1447–1451.
- Conover, M.R., 1978. The importance of various shell characteristics to the shell-selection behaviour of hermit crabs. *Journal of Experimental Marine Biology and Ecology*, **32**, 131–142.
- Elwood, R.W. & Neil, S.J., 1992. *Assessments and decisions: a study of information gathering by hermit crabs*. London: Chapman & Hall.
- Floeter, S.R. & Nalesso, R.C., 1998. Padrões de utilização de conchas e distribuição espacial em duas espécies simpátricas de caranguejos-ermitões (Crustacea, Anomura) na Ilha Galheta de Dentro—Baía de Vitória, ES. *Anais do IV Simpósio de Ecossistemas Brasileiros, ACIESP Publicações*, **104**, 349–355.
- Fotheringham, N., 1976. Population consequences of shell utilization by hermit crabs. *Ecology*, **57**, 570–578.

- Gherardi, F., 1990. Competition and coexistence in two Mediterranean hermit crabs, *Calcinus ornatus* (Roux) and *Clibanarius erythropus* (Latreille) (Decapoda, Anomura). *Journal of Experimental Marine Biology and Ecology*, **143**, 221–238.
- Gherardi, F. & Nardone, F., 1997. The question of coexistence in hermit crabs: population ecology of a tropical intertidal assemblage. *Crustaceana*, **70**, 608–629.
- Gleibs, S. & Mebs, D., 1998. Sequestration of a marine toxin. *Coral Reefs*, **17**, 338.
- Hazlett, B.A., 1966. Social behavior of the Paguridae and Diogenidae of Curaçao. *Studies on Fauna of Curaçao*, **88**, 1–143.
- Hazlett, B.A., 1981. The behaviour ecology of hermit crabs. *Annual Review of Ecology and Systematics*, **12**, 1–22.
- Kellogg, C.W., 1976. Gastropod shells: a potentially limiting resource for hermit crabs. *Journal of Experimental Marine Biology and Ecology*, **22**, 101–111.
- Kellogg, C.W., 1977. Coexistence in a hermit crab ensemble. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **153**, 133–144.
- Krebs, C.J., 1989. *Ecological methodology*. New York: Harper Collins Publishers.
- Leite, F.P.P., Turra, A. & Gandolfi, S.M., 1998. Hermit crabs (Crustacea: Decapoda: Anomura), gastropod shells and environmental structure: their relationship in south-eastern Brazil. *Journal of Natural History*, **32**, 1599–1608.
- Lively, C.M., 1988. A graphical model for shell-species selection by hermit crabs. *Ecology*, **69**, 1233–1238.
- Osorno, J.L., Fernandez-Casillas, L. & Rodriguez-Juarez, C., 1998. Are hermit crabs looking for light and large shells? Evidence from natural and field induced shell exchanges. *Journal of Experimental Marine Biology and Ecology*, **222**, 163–173.
- Reese, E.S., 1962. Shell selection behaviour of hermit crabs. *Animal Behaviour*, **10**, 347–360.
- Scully, E.P., 1979. The effect of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. *Journal of Experimental Marine Biology and Ecology*, **37**, 139–152.
- Scully, E.P., 1983. The effects of shell availability on intraspecific competition in experimental populations of the hermit crab, *Pagurus longicarpus* Say. *Journal of Experimental Marine Biology and Ecology*, **71**, 221–236.
- Spight, T.M., 1977. Availability and use of shells by intertidal hermit crabs. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **152**, 120–133.
- Turra, A. & Leite, F.P.P., 2000. Clustering behaviour of hermit crabs (Decapoda, Anomura) in an intertidal rocky shore at São Sebastião, southeastern Brazil. *Revista Brasileira de Biologia*, **60**, 1–6.
- Turra, A. & Leite, F.P.P., in press. Shell utilization patterns of tropical intertidal hermit crabs. I. The case of Grande Beach. *Journal of Crustacean Biology*.
- Vance, R.R., 1972a. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. *Ecology*, **53**, 1062–1074.
- Vance, R.R., 1972b. The role of shell adequacy in behavioral interactions involving hermit crabs. *Ecology*, **53**, 1076–1083.
- Wilber, T.P. & Herrnkind, W., 1982. Rate of new shell acquisition by hermit crabs in a salt marsh habitat. *Journal of Crustacean Biology*, **2**, 588–592.
- Zar, J.H., 1999. *Biostatistical analysis*, 4th ed. New Jersey: Prentice-Hall.

Submitted 25 April 2000. Accepted 12 June 2000.