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Shell occupancy of the intertidal hermit crab *Clibanarius erythropus* (Decapoda, Diogenidae) on São Miguel (Azores)

Andrea Z. Botelho & Ana C. Costa*
*Universidade dos Açores, Departamento de Biologia, Rua Mãe de Deus, 58, P-9500 Ponta Delgada, Portugal. Tel: +351-296653044. Fax: +351-296653455. E-mail: costa@alf.uac.pt (*Author for correspondence)*

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Abstract

The intertidal hermit crab *Clibanarius erythropus* was collected at three sites on São Miguel (Azores) during low spring tides. Shells occupied were identified and measured. Crab sizes ranged from 1.78 to 13.67 mm (cephalothoracic shield length), with an average size of 4.40 ± 1.44 mm. Of the 19 different shells utilised, the most frequent were *Littorina striata* (23.8%), *Nassarius incrassatus* (22.5%) and *Mitra* sp. (22.0%). At Fenais da Luz, *L. striata* was most frequently occupied, while at Água de Alto it was *N. incrassatus* and, at Caloura, *Mitra* sp. shells were most frequently used. Shell selection appears to be determined by respective sizes of hermit crab and shell species. Small size-class crabs occupy more shell species than larger crabs. The smallest crab was found at Fenais da Luz occupying a small *Bittium* sp., whereas the largest crab was found at Caloura inhabiting *Stramonita haemastoma*.

Introduction

Hermit crabs occupy empty gastropod shells for protection against predators (Vance, 1972) and physical stress (Reese, 1969). The strong association between hermit crabs and their adopted shelters has influenced greatly almost all aspects of their biology (Hazlett, 1981). Occupied shells, a limiting resource to most populations (Fotheringham, 1976; Kellog, 1976), may vary in size, shape and condition. Hermit crabs have preferences for shells of particular size, weight, aperture width, volume and condition; also important for selection are the presence of epibionts and the shell species (Hazlett, 1981). In natural populations, shell selection is determined primarily by shell availability and, to a lesser extent, by preference, despite the active choice of shells shown in laboratory experiments (Kellogg, 1976; Bertness, 1980, 1981; Reddy & Biseswar, 1993).

The intertidal hermit crab *Clibanarius erythropus* (Latreille, 1818) is a common species of Mediterranean shores and is also present along the Atlantic coasts from Brittany to the Azores (Zariquiey Alvarez, 1968; Ingle, 1993). However, references to the general biology and ecology of this species are scarce (Gherardi, 1991). In the Azores, *C. erythropus* (known since the early naturalists' studies in the 19th C, e.g. Barrois, 1888) is abundant in low-shore pools on the rocky shores of São Miguel. The aim of this study was to examine the shell utilisation by *C. erythropus*, in S. Miguel.

Description of sites

The Azores archipelago (37° 40' N and 25° 31′ W) consists of nine volcanic islands (Fig. 1). São Miguel is the largest island located in the oriental group of the archipelago. The coastline of this island is irregular and the shoreline consists mainly of high cliffs falling directly to the sea, or rocky platforms. Boulder and cobble beaches, resulting from erosion of volcanic rocks, are also common. Most shores are subject to swell and semi-diurnal tides with a range of less than 2 m. Three populations of *Clibanarius erythropus* were studied for shell occupancy (Fig. 1). Fenais da Luz is a wave-exposed site on the north shore; Cerco da Caloura is a sheltered, gently sloping bay on the

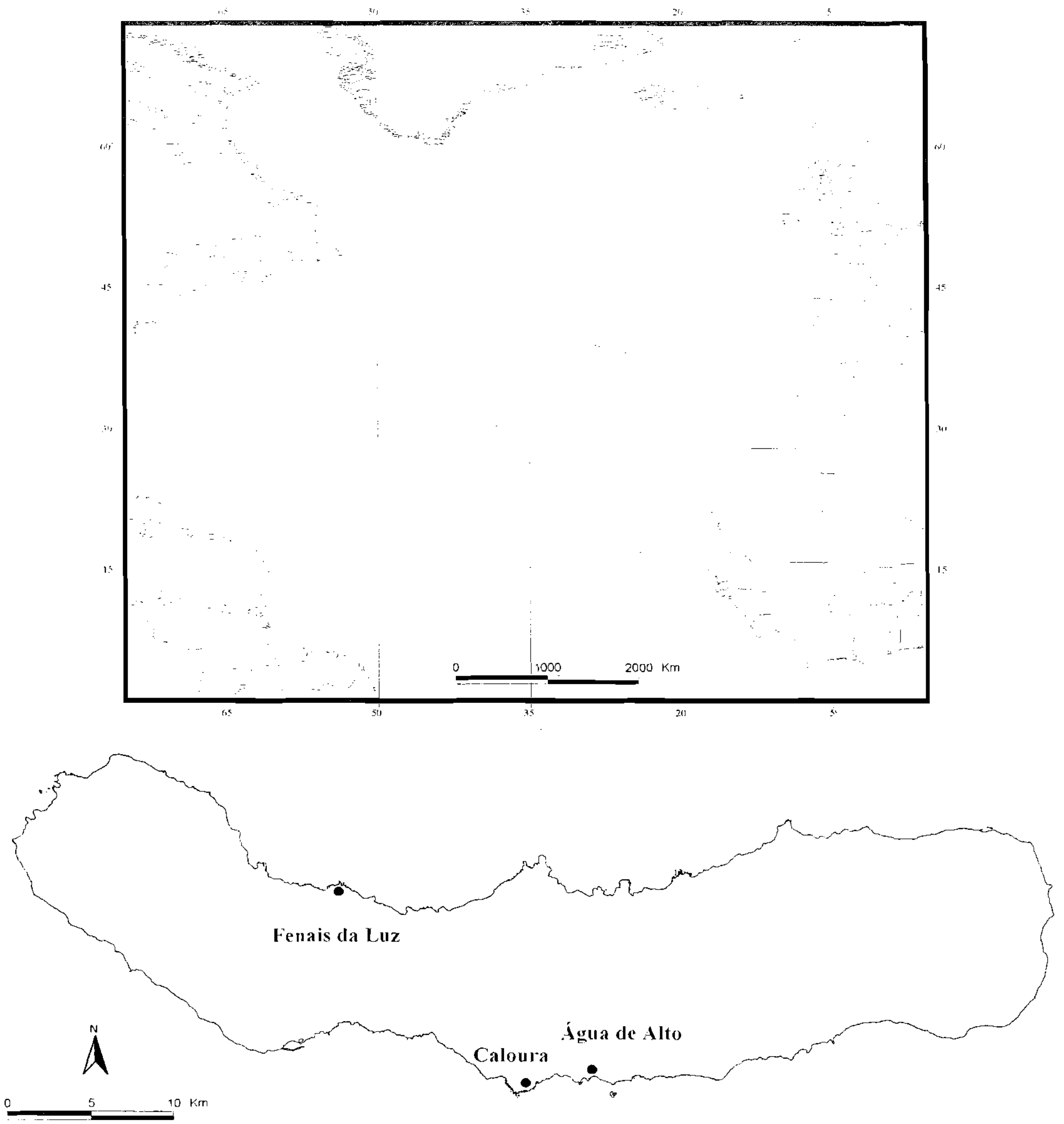

Figure 1. Location of the Azores and of the sampling sites in São Miguel island.

south coast, and Água de Alto is a rocky platform with boulders and rock pools backed by a sheer cliff, on the south coast.

Materials and methods

From each site, crabs were hand sampled during the low spring tides between November 1998 and June 1999. Eight hundred and forty nine crabs were examined. During crab collection, qualitative observations of living gastropods and of the availability of empty shells on each shore were made. In the laboratory, occupied shells were identified, measured (aperture length, shell length and shell width) with callipers (precision 0.01 mm) and weighed after removal of the crab. Cephalothoracic shield length (CL) of each crab was measured and specimens were grouped into 0.85 mm size classes calculated according to the highest and lowest sizes (e.g. 1.78–13.67 mm), following the method used by Manjón-Cabeza & García-Raso (1998).

Species composition of occupied shells at the three sites was compared with a Chi square (χ^2) test per-

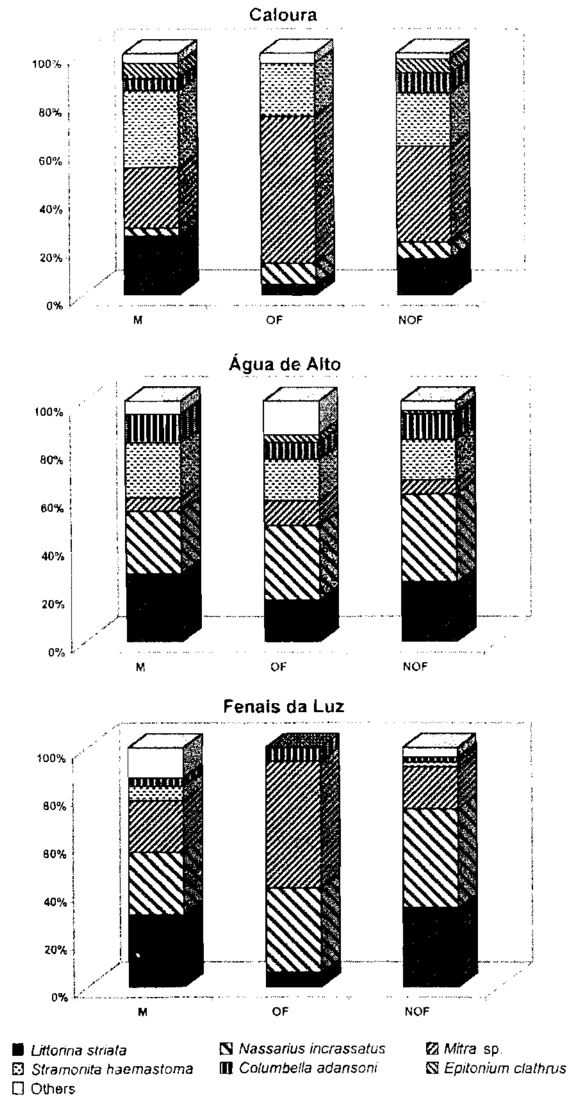

Figure 2. Frequency of the shell species occupied by each sex and ovigerous females, on the sites under study. M – male; OF – ovigerous females; NOF – non ovigerous females. Others – shell species present in low percentage (<1%).

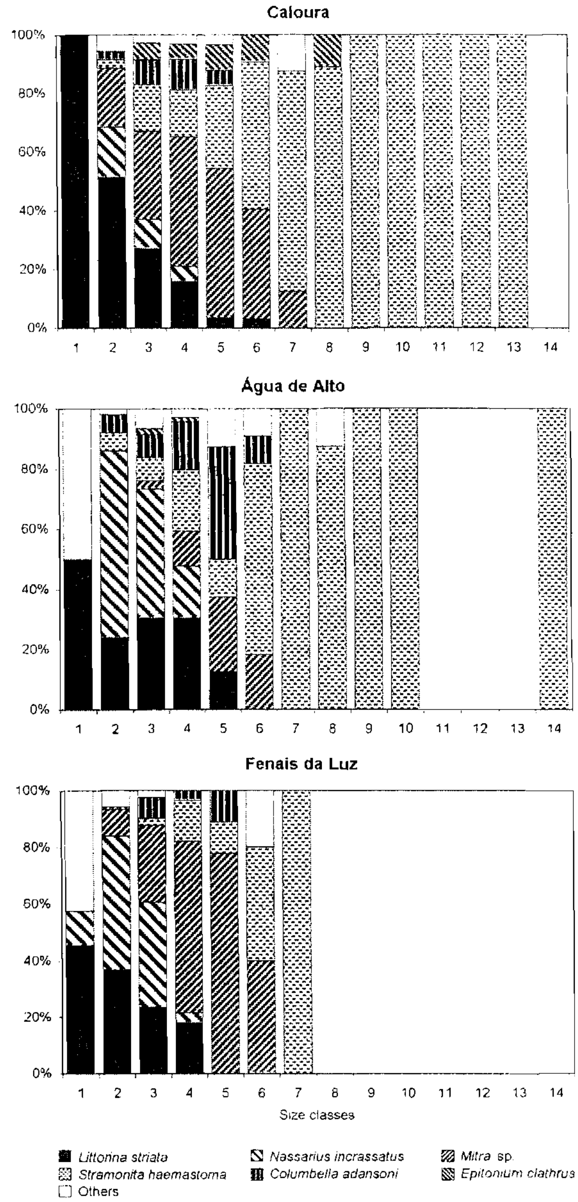

Figure 3. Shell species related to crab size classes.

formed on the seven most common shell species and an 8th category representing a pooled count for the remaining species. Differences in shell occupancy between the sexes, and between ovigerous and non ovigerous females, were tested by Spearman rank correlation (Zar, 1996).

To identify relationships between crab sizes and shell size variables, data were plotted, and correlation coefficients and linear regressions were calculated. Correlation between brood size of ovigerous females and size of the shell was determined. The relationship between shell species and hermit crab length (CL) was also subjected to statistical analysis (analysis of variance – ANOVA, Fry, 1996; Zar, 1996) against the null hypothesis that equal sizes of crabs would occupy different shell species. Twenty one individuals, occupying each of the six of the more common shell species, were chosen randomly for the ANOVA test, equal sample size, minimises type one error due to heterogeneity of variances (Green, 1979). Assumptions of ANOVA were checked applying Bartlett's test

Table 1. Frequencies of occupancy of shell species by *Clibanarius erythropus*

Species	Caloura	Água de Alto	Fenais da Luz	Total
Bittium sp.	0	0	1.5	0.5
Calliostoma sp.	0.3	1.1	0.4	0.6
Columbella adansoni	6.3	10.7	3.0	6.7
Epitonium clathrus	5.7	1.1	0	2.5
Fossarus ambiguus	0	0	1.5	0.5
Gibbula magus	0.6	0	0	0.2
Jujubinus sp.	0.3	0.7	0.4	0.5
Littorina striata	17.8	25.1	29.7	23.8
Melarhaphe neritoides	0.3	0	0	0.1
Mitra sp.	35.6	6.3	22.1	22.0
Natica sp	0.3	0	0	0.1
Nassarius incrassatus	5.7	32.5	32.3	22.5
Ocinebrina aciculata	0.6	2.6	0.8	1.3
Pedipes pedipes	0	0	0.8	0.2
Raphitoma sp.	0	0	0.4	0.1
Stramonita haemastoma	25.7	18.8	4.2	16.8
Tricolia pullus azorica	0	0	0.8	0.2
Vermetus sp.	0.3	1.1	0.4	0.6
None identified	0.3	0	0	0.1

for homogeneity of variance (Green, 1979; Fry, 1996; Zar, 1996). Raw data were transformed by $\log(x+1)$ to achieve normality and equal variance (Green, 1979; Zar, 1996). *Post hoc* multiple comparison was made using the Tukey's test. The significance level for all tests was $P<0.05$.

Results

Sizes of *Clibanarius erythropus* ranged from 1.78 to 13.67 mm (cephalothoracic shield length), with an average size of 4.40 ± 1.44 mm. Crabs occupied 19 species of gastropod shells; those most commonly occupied were *Littorina striata*, *Nassarius incrassatus*, *Mitra* sp. and *Stramonita haemastoma* (Table 1). Rare shell species (not present in Água de Alto) were usually occupied by males and never by ovigerous females.

Crabs occupied the same shells, but in significantly different proportions at each of the study sites (χ^2= 218.9, $P<0.05$). At Fenais da Luz, *L. striata* was the most common shell used while *N. incrassatus* was the most commonly inhabited shell at Água de Alto. At Caloura, *Mitra* sp. was the dominant shell used (Fig. 2). No empty shells utilised by *C. erythropus* was found at any shore.

The two sexes showed no significant difference in shell occupancy (Spearman rank correlation test: r_S=0.714, $P<0.05$). Although there was no significant difference between shells occupied by ovigerous and non ovigerous females (Spearman rank correlation test: r_S=0.855, $P<0.05$), 39% of ovigerous females were found in *Mitra* sp.

A direct relationship between size of hermit crab and host shell species was found (Fig. 3). While *S. haemastoma* was occupied by large crabs, smaller animals occupied a wide range of shell species. Significant differences were found in the size of crabs inhabiting different shell species (ANOVA, F=19.98; df=125; $P<0.05$). Crabs under 8.58 mm were found in 18 shell species, whereas those over 8.58 mm were found only in *S. haemastoma*. An *a posteriori* mean comparison test revealed that the bigger average size of crabs occupying *S. haemastoma* was responsible for the differences observed in the ANOVA results. The majority of small crabs occupied *L. striata* and *N. incrassatus* (Fig. 3). The largest crab was found at Caloura in a *S. haemastoma* shell, while the smallest was collected at Fenais da Luz occupying a small *Bittium* sp.

Shell sizes (both length and weight) occupied by hermit crabs were correlated with crab size. For the most commonly occupied shell species, the strongest relationship was found for *S. haemastoma* and *L. striata* (Fig. 4; Table 2). Brood size was also correlated with shell length for the shell species inhabited by ovigerous females (Pearson, r = 0.58).

Discussion

Present data are consistent with the observations made by Reddy & Biseswar (1993) on a congener species *Clibanarius virescens*, from South Africa. These authors reported that *C. virescens* occupied a similar number of shell species (23) and there was a close relationship between the crab size and the size of the occupied shell. In S. Miguel, *C. erythropus*, and its counterpart in Natal, displayed a shift in the shell species utilised during growth. Both species seem to occupy a wider variety of shell species in the size range of 3–4 mm than seen for larger individuals.

The availability of certain gastropod species influences the shell utilisation by hermit crabs in the natural habitat as they tend to be opportunistic with

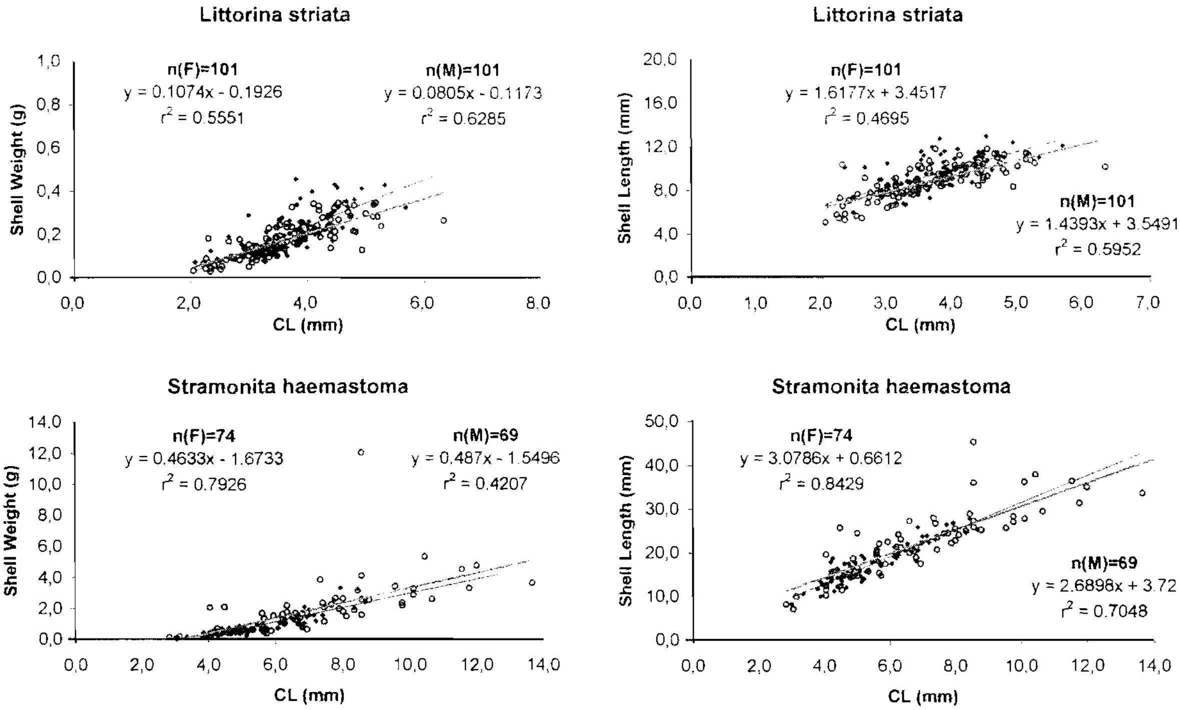

Figure 4. Morphometric relations between *C. erythropus* and two of the most common inhabited shells species, *Littorina striata* and *Stramonita haemastoma* (♦ Females; ○ Males), thicker line illustrates regression calculated for ♂.

regards to the shells they inhabit. Nevertheless, it is interesting to note that *C. virescens*, in contrast to *C. erythropus*, did not occupy *Littorina* sp. and *Mitra* sp., probably because of the availability of more suitable tropical gastropod shells. In southwest Britain, Southward & Southward (1977) found *C. erythropus* occupying mainly *Nucella lapillus*, whereas *Littorina littorea* and other species of shells accounted for a very small proportion of occupancy. Gherardi (1991) reported that a high number of shell species were occupied by this hermit species in Sardinia, where, amongst the most occupied shells, only two genera, *Columbella* and *Gibbula*, were common in our study.

Differences in shell occupation between the sampled populations can be related to the availability of empty shells at the specific site but can also be explained by the different sizes of crabs found in each location. For example, at Fenais da Luz, crab size was probably limited by the lack of large shells, and the abundance of *L. striata* and other small shell species (Fig. 3). It is known that crab growth is slowed by occupation of a small shell (Hazlett, 1981; Lancaster, 1988).

Availability of suitable empty shells in the intertidal is not only dependent on the mortality rate of gastropods but also on the type of mortality as this influences condition of the shells. Empty gastropod shells are usually very rare or absent in the intertidal (Fotheringham, 1976; Kellog, 1976; Bertness, 1980). This absence was also noted for the sites under study on the Azores, where crabs probably find shells subtidally. Physical processes (e.g. wave action) also remove or destroy shells and also influence availability (Gherardi, 1991).

Wilber (1990) reported that the hermit crab *Pagurus longicarpus* changed its preferences for shell species with size. The same probably happens with *C. erythropus*, as sizes of crabs inhabiting different shell species were different. It is, therefore, possible that larger animals choose *Stramonita haemastoma* shells, whereas smaller ones would occupy several shell species.

Differences in shell occupancy between sexes in *C. erythropus* were found by Gherardi (1991) who gave some behavioural explanations for this. Advantage of certain types of shells for females can be related to energy saving for reproductive process, whereas for males more importance might be giving to protection against predation (e.g. heavy *S. haemastoma* occupied by large males). Unbalanced sex ratio at certain size

Table 2. Pearson correlation test (r) and determination coefficients (r^2) obtained for linear regressions between shell parameters (length – SL (mm) and weight – SW (g)) and CL (mm) of the hermit crab (F – female; M – male), for the most abundant shell species

	Shell species	n		r^2		r	
		M	F	M	F	M	F
	Stramonita haemastoma	69	74	0.42	0.79	0.65	0.89
SW/CL	*Littorina striata*	101	101	0.63	0.56	0.79	0.75
	Mitra sp.	68	119	0.33	0.29	0.57	0.54
	Nassarius incrassatus	67	124	0.35	0.20	0.59	0.45
	Stramonita haemastoma	69	74	0.71	0.84	0.84	0.92
SL/CL	*Littorina striata*	101	101	0.60	0.47	0.77	0.69
	Mitra sp.	68	119	0.37	0.37	0.60	0.61
	Nassarius incrassatus	67	124	0.41	0.48	0.64	0.69

classes could also influence results (Gherardi, 1991). The narrow shell aperture of *Mitra* sp. might cause it to be a suitable shell for an ovigerous female as it not only provides enough space to accommodate a clutch, but also confers protection against desiccation.

For the most commonly occupied shell species, a good correlation was found between the sizes of shells occupied by hermit crabs and crab size as predicted by Hazlett (1981). However, linear regressions between shell measurements and crab size were not significant for most shell species; a well-fitted linear regression was found for *L. striata* and *S. haemastoma* (Fig. 4). Other host species are probably sub-optimal as there is a wide range of hermit size occupying the same shell size. Features of the shell, namely its architecture, could be responsible for this. The criteria by which hermit crabs select shells are not well understood, but it has been shown that shell configuration, aperture size, weight index (shell weight/crab weight) and volume index (shell volume/shell weight) are important for selection (Hazlett, 1981; Lancaster, 1988). Nevertheless, laboratory experiments are necessary to test differences in shell preferences of this species.

Crab size (CL) was better correlated with shell length than with shell weight. This latter relationship may be influenced by the frequent incrustation and damage of the shells.

From the correlation results of this study, it can be seen that ovigerous females in larger shells had bigger clutches. *Mitra* sp. seems to be preferred by ovigerous females and some of them will have larger broods than the size of the shell would predict. The measure chosen (length) as a descriptor of size may not be a good predictor for available internal space for clutch accommodation. The type of gastropod shell inhabited by a hermit crab influences both growth rate and clutch size (Bertness, 1981). Shell occupation affords egg protection, but the volume of eggs that can be protected is limited by shell volume. Shell volume is correlated with female size but a female hermit crab that obtains a larger shell may be able to carry a larger volume of well-protected eggs (Fotheringham, 1976; Hazlett, 1981; Lancaster, 1988).

More detailed studies to determine gastropod abundances and availability of shells at both intertidal and subtidal, and choice experiments in the laboratory, will elucidate the role of biotic/abiotic factors and behaviour shell occupancy by *Clibanarius erythropus*.

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