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Influence of Human Exploitation of Intertidal Mollusk Resources on the Selection and Utilisation of Gastropod Shells by the Hermit Crab *Clibanarius longitarsus* (de Haan) in Costa do Sol Mangrove, Maputo

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ABSTRACT
The use of gastropod shells by the hermit crab *Clibanarius longitarsus* at Costa do Sol Mangrove was investigated. Particular attention was paid to the influence of human collection of intertidal gastropod resources on the availability and utilization of shells by *C. longitarsus*. Three main methods were used in this study: crab field collections, shell selection laboratory experiments and interviews with local women who collect intertidal mollusk resources. A total of 23 shell types were used by *C. longitarsus* at the Costa do Sol mangrove, the most common being *Volema pyrum*, *Murex brevispina* and *Terebralia palustris*. Gastropod shells were a limiting resource for hermit crabs. Although shell availability could not be explained by human exploitation, which represent less than 3% of the total collection. In laboratory experiments, *C. longitarsus* significantly preferred *V.* pyrum over all other shell species. Comparing the morphological characteristics of the shell species studied, *V. pyrum* always showed intermediate characteristics and was present in large numbers, which could explain its preference by *C. longitarsus*.

RESUMO
O uso de conchas de gastrópodes pelo caranguejo eremita *Clibanarius longitarsus* foi investigado no mangal da Costa do Sol. Particular atenção foi dada à influência da colecta de gastrópodes da zona inter-marés, pela população humana, na disponibilidade e utilização de conchas por *C. longitarsus*. Três métodos principais foram usados neste estudo: colectas no campo, experiências de selecção de conchas em laboratório e entrevistas às mulheres colectoras de recursos da zona entre-marés. Um total de 23 espécies de conchas são usados por *C. longitarsus*, sendo *Volema pyrum*, *Murex brevispina* e *Terebralia palustris* as mais comuns e simultaneamente as mais utilizadas no campo pelos caranguejos ermita. Observou-se uma limitação da disponibilidade de conchas para utilização pelos caranguejos ermita. No entanto, esta limitação não poderá ser atribuída à colecta humana, já que esta representa menos de 3 % dos recursos colectados. Em experiências de laboratório, verificou-se uma significativa preferência de *C. longitarsus* por *V. pyrum* sobre todas as outras conchas. Da comparação das várias características morfológicas das espécies de conchas estudas, *V. pyrum* apresentou-se sempre numa posição intermédia, que aliada à sua grande abundância, poderia explicar a preferência desta por parte de *C. longitarsus*.

INTRODUCTION

Hermit crabs are very common marine organisms that have adapted to live in empty gastropod shells that serve as portable shelters and provide protection for their otherwise vulnerable abdomens (Hahn, 1998).

Despite the fact that hermit crabs actively select the shells they inhabit (Macia, 1995; Borjesson & Szelistowski, 1989), it has been demonstrated that the occurrence of certain sizes, or even species, is limited by the availability of shells (Vance, 1972a; Abrams, 1978; Emmerson & Alexander, 1986; Borjesson & Szelistowski, 1989). Shell availability may depend upon various factors, including: (i) occurrence of hard-shelled mollusks in sufficient quantity and species, in order to provide the available shell pool with diverse and enough shells; (ii) durability of empty shells in the environment (Emmerson & Alexander, 1986); and (iii) behavioral interactions, such as intra- and interspecific competition (Vance, 1972ab; Abrams, 1980; Bertness, 1980; Shaw & Hoggarth, 1981; Abrams *et al*., 1986; Gherardi, 1990), predation (Borjesson & Szelistowski, 1989) and symbiotic relationships (Brooks & Mariscal, 1986).

The collection by humans of intertidal mollusk resources is another factor that may influence the availability of shells in intertidal areas (Barnes, 1997a), especially if this collection is intensive and systematic. At Inhaca Island (Longamane, 1995; de Boer & Longamane, 1996; Pereira, 1998) and Praia da Costa do Sol (Oliveira, 1972; Bandeira, 1995 and pers. obs.), intertidal mollusk resources (especially bivalves and gastropods) are collected on a daily basis by local populations, either for self consumption or for sale. This activity may influence the availability and utilization of shells by hermit crabs therefore, this study aims to investigate the following: (1) What gastropod shell species do hermit crabs use; (2) what gastropod species do the human population collect and (3) what are the effects of the human collection of intertidal gastropods on the shell availability, selection and utilization by the hermit crab *Clibanarius longitarsus* (de Haan) in Costa do Sol mangrove and surrounding area.

MATERIALS AND METHODS

Study Area and Species

C. longitarsus (de Haan) is a pan-tropical species, very common in southern Africa, occurring from Transkei to Zanzibar, mainly on the pneumathophores of mangroves (Day, 1974; Branch *et al*., 1995).

This study was done in Costa do Sol mangrove, located 6 km north of Maputo City (Figure 1). This small mangrove forest is dominated by the white mangrove *Avicennia marina* and has been considered as almost lost, due to coastal development (Hatton, 1995). High levels of urban pollution and timber exploitation (pers. obs.), also affect the area. *C. longitarsus* is the only hermit crab species recorded in this area. Various fiddler crab species (*Uca* spp.) and the soldier crab *Dottila fenestrata* (in sandy areas), dominate the crustacean fauna.

Transect Sampling

Field sampling was conducted in July 2000, along the seaward edge of a 500 m section of mangroves, following an adaptation of the methodology described in Borjesson & Szelistowski (1989). At the border of the mangroves, we established a 5 m transect line perpendicular to the root edge, extending 5 m into the root system and 5 m outside the root edge. We collected all hermit crabs, gastropods, and empty shells within 1 m of each side of an imaginary vertical extension of this line. Four transects were completed. All collections were returned to the laboratory for analysis. Gastropods and empty shells were identified and counted. *C. longitarsus* were sorted by the species of gastropod shell they occupied and were similarly counted. To increase our sample size, we also collected crabs within the study area but outside of specific transects.

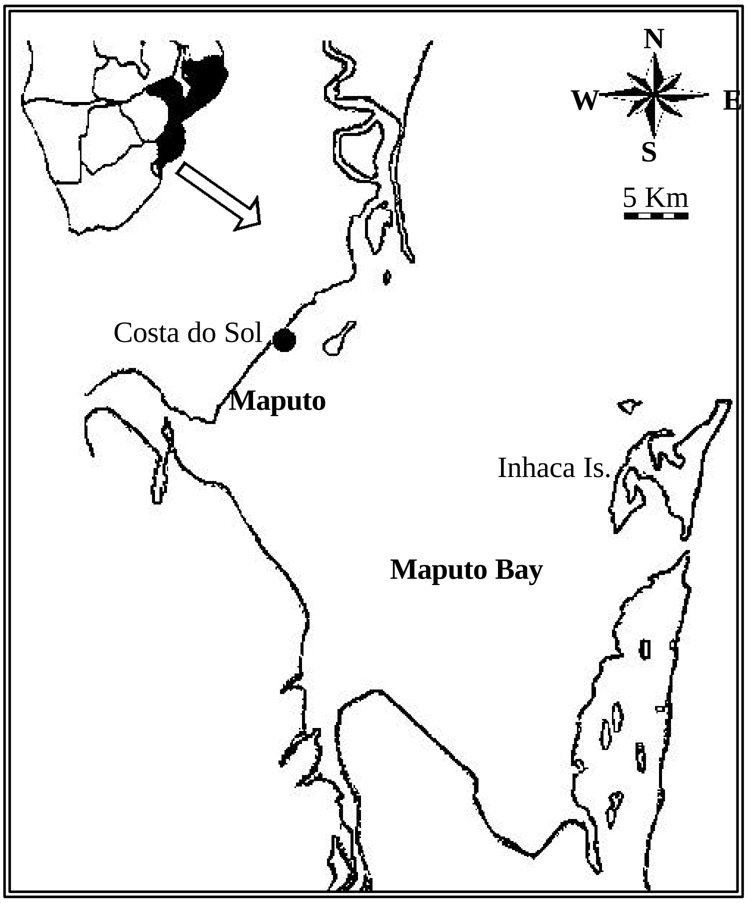

Figure 1. Location of study site (dark circle).

Human Exploitation

The human exploitation of intertidal mollusc resources was assessed at the end of the tidal exposure period. Ten individuals were interviewed regarding locality, resource preferences and whether they collected to sell or to consume.

Shell Morphology

Shell morphology was examined to compare specific characteristics of the five shell types used in the selection experiments. Shells were cleaned of encrusting organisms and dried. We measured length, diameter (defined as the maximum width of the shell, perpendicular to the axis of coiling), aperture width (maximum aperture width of the shell, perpendicular to the axis of coiling) of each shell with calipers to the nearest 0.5 mm, and weighted each to the nearest 0.1 g. Internal shell volume was measured to the nearest 0.1 ml by filling shells with water from a syringe. The shell with water was then weighted and the difference between the dried empty shell and the filled one was the weight of water, which was converted to water volume, using a water density of 1 g/ml.

Shell Selection Experiments

Shell selection experiments followed the experimental design proposed by Liszka & Underwood (1990). Only *C. longitarsus* originally found in *Volema pyrum* shells were used in the experiments. In many studies, hermit crabs have been removed from their shells and then presented with a range of empty shells into which they might move (e.g. Macia, 1995;

Borjesson & Szelistowski, 1989). Being out of shell is a very unnatural situation for hermit crabs; they choose new shells while still in their old shell. Thus, any apparent preference inferred from experiments with naked hermit crabs is likely to be biased by these unnatural circumstances (Liszka & Underwood, 1990). *C. longitarsus* in *V. pyrum* shells were used because these were the most abundant shells occupied and therefore most convenient for collecting crabs.

Prior to experiments crabs were not held in the laboratory for more than 1 day. Experiments were done in glass aquariums (at least 20 × 20 × 20 cm deep) with 5 cm of water taken daily from the crab mangrove collection site. Particular types of shells were arbitrarily considered to be used relatively often if they constituted 12 % or more of those used by *C. longitarsus* in the field. Three types of rarely used (< 12%) and two types of often used shells were compared to determine whether this distinction was due to preference. We also estimated the rate at which crabs changed into shells of each type when presented on its own.

Shells placed in each aquarium had approximately the same size distribution as found occupied by *C. longitarsus* in the field and the sizes were chosen to match those used by crabs of similar sizes to those used in each experiment. The different types of shells presented to the crabs were also of the same sizes, to reduce confounding influences due to different sizes of shells (Liszka & Underwood, 1990). Five *C. longitarsus* in *V. pyrum* shells were chosen and placed into each aquarium. Shells were cleaned of barnacles and other encrusting organisms and placed at random inside the aquariums. After 24 h, the aquariums were drained of seawater and the number of *C. longitarsus* in each type of shell was recorded in each aquarium. The numbers of shells used were always in excess of the number of crabs. *V. pyrum* shells occupied by crabs at the start of the experiment were marked with a small dot of correction fluid prior to being placed in aquariums whenever *V. pyrum* shells were to be selected. Reese (1963 cited in Liszka & Underwood, 1990) found that a dot of paint on the shell did not affect the selection of shells by hermit crabs.

C. longitarsus were removed from their shells and discarded at the end of each experiment. Appropriate shells were then rinsed in “Javel” water (sodium hipochlorite 3.5 % v/m solution), in freshwater, then in seawater and finally returned to experimental aquariums. It was assumed that occupancy of a shell by a crab would not affect any subsequent selection of that shell by other crab (Vance 1972b; Liszka & Underwood, 1990).

Table 1 presents the experimental designs followed. In all treatments 2 aquarium replicates were used. Treatments were made up of aquariums with either one or two types of shell. The total number of shells in each aquarium was always 10; thus, when an aquarium had two types of shell, there were 5 of each type. The number of crabs was always 5 in each aquarium.

Statistical Analysis

χ^2 tests (Zar, 1999) were used to test the null hypothesis of no preference of shell types used by hermit crabs in the laboratory experiments. Observed values were compared to expected values that were calculated using a powerful test described in Liszka & Underwood (1990).

Simple linear regression was used to study the relationship between shell characteristics and analysis of covariance (ANCOVA) (Zar, 1999) tested the significance of linear regression equation slopes between shell species. Whenever ANCOVA revealed that all regression slopes were not equal, a multiple comparison procedure (Turkey test) (Zar, 1999) was employed to test the difference between the first two higher *b* values. In all tests, differences were considered significant at $P < 0.05$.

Table 1. Experimental designs to determine shell preference (*n* = 2 replicates for each combination; 5 crabs in each aquarium).

Treatment 1	Treatment 2	Treatment 3	Treatment 4	Treatment 5
10 *Polinices mamilla*	10 *Thais carinfera*	10 *Murex brevispina*	10 *Terebralia palustris*	10 *Volema pyrum*
Treatment 6	**Treatment 7**	**Treatment 8**	**Treatment 9**	**Treatment 10**
5 *P. mamilla* + 5 *T. carinfera*	5 *P. mamilla* + 5 *M. brevispina*	5 *P. mamilla* + 5 *T. palustris*	5 *P. mamilla* + 5 *V. pyrum*	5 *T. carinfera* + 5 *M. brevispina*
Treatment 11	**Treatment 12**	**Treatment 13**	**Treatment 14**	**Treatment 15**
5 *T. carinfera* + 5 *T. palustris*	5 *T. carinfera* + 5 *V. pyrum*	5 *M. brevispina* + 5 *T. palustris*	5 *M. brevispina* + 5 *V. pyrum*	5 *T. palustris* + 5 *V. pyrum*

RESULTS

Shell Availability and Utilization in the Field

Results are summarized in Table 2. A total of 23 shell identities were used by *C. longitarsus* in Costa do Sol mangrove. *Volema pyrum* was the most common shell type in the field (43.6 %) and the most used by the hermit crabs (42.4 %). Other shells fairly common in the field and used by crabs were those of *Murex brevispina* and *Terebralia palustris*. These three types were considered as commonly used by crabs (>12 %). All others shell identities were considered rarely used (< 12%).

Crabs used the great majority of the shells collected (90%) and those not occupied (7.9%) were greatly damaged or filled with sand, i.e. unavailable, suggesting a great unavailability of shells in this area and that gastropod shells may be a limiting factor for hermit crabs. Gastropod shells with live gastropods inside were also in low numbers (2.1 %) and those collected were of small-sized species or individuals (such as *Littoraria scabra* and *Nerita albicila*).

Human Exploitation

Bivalves constitute the most important resource exploited by humans in Costa do Sol intertidal areas, especially the asiatic hard clam *Meretrix meretrix* which constituted 97 to 100% of the catches of all individuals interviewed. In general terms, gastropods were poorly represented in the mollusc collections and the species collected were those immediately available in the field.

In terms of availability in the field, “chidela” (*Natica* spp.), “mbawana” (*Volema pyrum*), “fumane” (*Polinices mamilla*), “búzio” (*T. carinfera*) and “ntsanga” (*Murex brevispina*) were, in descending order, the most important gastropod species. The collection of a particular species was, however, not only dependent on the availability of gastropods (as in the case of *V. pyrum*), but on abundance of preferred species (*P. mamilla* and *T. carinfera*) as well.

Table 2. Field sampling results. Gastropod shells are ranked in decreasing order of use; the first six types were considered to be used commonly (> 12 %), the others rarely (<12 %).

Species	Shells found in sample		Occupation by crabs			N° shells found with live gastropods			N° gastropod shells found empty		
	n	% of total	n	% of total	% of occupation	n	% of total	% within species	N	% of total	% within species
Volema pyrum	144	43.6	140	42.4	97.2	1	0.3	0.7	3	0.9	2.1
Murex brevispina	52	15.8	50	15.2	96.2	0	0.0	0.0	2	0.6	3.9
Terebralia pallustris	40	12.1	39	11.8	97.5	0	0.0	0.0	1	0.3	2.5
Polinices mamilla	35	10.6	29	8.8	82.9	0	0.0	0.0	6	1.8	17.1
Polinices didyma	18	5.5	14	4.2	77.8	1	0.3	5.6	3	0.9	16.7
Thais carinfera	11	3.3	11	3.3	100.0	0	0.0	0.0	0	0.0	0.0
Terrestrial snail sp. 1	4	1.2	2	0.6	50.0	0	0.0	0.0	2	0.6	50.0
Nerita albicilla	3	0.9	0	0.0	0.0	2	0.6	66.7	1	0.3	33.3
Chicoreus ramosus	2	0.6	2	0.6	100.0	0	0.0	0.0	0	0.0	0.0
Littoraria scabra	2	0.6	0	0.0	0.0	2	0.6	100.0	0	0.0	0.0
Natica gualteriana	2	0.6	1	0.3	50.0	0	0.0	0.0	1	0.3	50.0
Nassarius arcularia plicatus	2	0.6	2	0.6	100.0	0	0.0	0.0	0	0.0	0.0
Oliva sp.	2	0.6	0	0.0	0.0	0	0.0	0.0	2	0.6	100.0
Unidentified sp. 1	2	0.6	2	0.6	100.0	0	0.0	0.0	0	0.0	0.0
Unidentified sp. 2	2	0.6	0	0.0	0.0	0	0.0	0.0	2	0.6	100.0
Unidentified sp. 3	2	0.6	2	0.6	100.0	0	0.0	0.0	0	0.0	0.0
Cerithium sp.	1	0.3	0	0.0	0.0	0	0.0	0.0	1	0.3	100.0
Fusinus colus	1	0.3	0	0.0	0.0	0	0.0	0.0	1	0.3	100.0
Natica taeniata	1	0.3	0	0.0	0.0	1	0.3	100.0	0	0.0	0.0
Nassarius coronatus	1	0.3	1	0.3	100.0	0	0.0	0.0	0	0.0	0.0
Terrestrial snail sp. 2	1	0.3	0	0.0	0.0	0	0.0	0.0	1	0.3	100.0
Volema paradisica	1	0.3	1	0.3	100.0	0	0.0	0.0	0	0.0	0.0
Unidentified sp. 4	1	0.3	1	0.3	100.0	0	0.0	0.0	0	0.0	0.0
Total	**330**	**100**	**297**	**90.00**		7	**2.1**		26	**7.9**	

Human Exploitation

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In terms of availability in the field, “chidela” (*Natica* spp.), “mbawana” (*Volema pyrum*), “fumane” (*Polinices mamilla*), “búzio” (*T. carinfera*) and “ntsanga” (*Murex brevispina*) were, in descending order, the most important gastropod species. The collection of a particular species was, however, not only dependent on the availability of gastropods (as in the case of *V. pyrum*), but on abundance of preferred species (*P. mamilla* and *T. carinfera*) as well.

Shell Morphology

Table 3 summarizes all shell morphology results. Significant regression coefficients were found in all species for all shell characteristics except for *P. mamilla* (internal volume x length and internal volume x aperture width) and *T. palustris* (internal volume x weight). The ANCOVA test revealed that the regression equation slopes of all shell characteristics as function of internal volume were significantly different ($P < 0.0005$).

Table 3. Shell morphology results. Species marked with (*) were compared for differences in regression slopes using the Turkey test.

Shell characteristics	Shell species	n	Regression equation	R^2	Significance		
					ANOVA	ANCOVA	TURKEY
Internal volume X Length	***Murex****	46	Y = 0.3912X + 3.3729	0.5877	***P* < 0.0005**	***P* < 0.0005**	***P* < 0.025**
	Polinices	33	Y = 0.1579X + 3.7847	0.0268	*P* > 0.25		
	Terebralia	31	Y = 0.1296X + 3.8616	0.1856	***P* < 0.025**		
	Thais	31	Y = 0.2652X + 3.1226	0.7806	***P* < 0.0005**		
	*Volema**	110	Y = 0.2674X + 3.3256	0.4067	***P* < 0.0005**		
Internal volume X Width	***Murex****	46	Y = 2.2419X + 0.1607	0.7161	***P* < 0.0005**	***P* < 0.0005**	***P* < 0.001**
	Polinices	33	Y = 0.1513X + 1.8152	0.3559	***P* < 0.0005**		
	Terebralia	31	Y = 0.0917X + 2.4262	0.4544	***P* < 0.0005**		
	*Thais**	31	Y = 0.1952X + 1.7331	0.8835	***P* < 0.0005**		
	Volema	110	Y = 0.1919X + 1.8087	0.7244	***P* < 0.0005**		
Internal volume X Aperture width	*Murex*	46	Y = 0.0807X + 0.9486	0.7191	***P* < 0.0005**	***P* < 0.0005**	*P* > 0.2
	Polinices*	33	Y = 0.1046X + 0.8214	0.1415	P > 0.05		
	Terebralia	31	Y = 0.0399X + 1.0441	0.2848	***P* < 0.01**		
	Thais	31	Y = 0.0803X + 0.7031	0.8005	***P* < 0.0005**		
	*Volema**	110	Y = 0.0685X + 0.8321	0.4275	***P* < 0.0005**		
Internal volume X Weight	*Murex*	46	Y = 0.7776X + 3.6034	0.3608	***P* < 0.0005**	***P* < 0.0005**	***P* < 0.025**
	Polinices	33	Y = 1.3707X + 4.5081	0.2770	***P* < 0.01**		
	Terebralia	31	Y = 0.6520X + 7.6446	0.1198	*P* > 0.05		
	Thais*	31	Y = 2.0550X + 0.9839	0.7996	***P* < 0.0005**		
	*Volema**	110	Y = 1.6856X + 2.9886	0.6226	***P* < 0.0005**		

Further testing using the multiple comparison Turkey test, showed that *M. brevispina* had significantly greater shell length (over *V. pyrum*; $P < 0.025$) and width (over *T. carinfera*; $P < 0.001$), and consequently over all other species. *T. carinfera* had significantly greater weight (over *V. pyrum*; $P < 0.025$, and all other species) and *P. mamilla* had significantly greater aperture width ($P < 0.05$) in relation to *T. palustris*, but not in relation to *V. pyrum* ($P > 0.2$).

Shell Preference Experiments

C. longitarsus clearly preferred *V. pyrum* shells over all other shell species tested (Table 4). Shell preference order was *Volema* > *Thais* > *Terebralia* > *Polinices* > *Murex*, although *Thais* was not significantly preferred over *Terebralia*. *Polinices* and *Murex* were the least preferred shell species.

Table 4. Results of selection experiments. Numbers of *C. longitarsus* changing to the various types of shells (replicates pooled in each treatment; treatments are as in Table 1).

Number of crabs (out of 10) that changed to shells of:							
Treatment	**1**		**2**	**Treatment**	**2**		**4**
	Polinices		*Thais*		*Thais*		*Terebralia*
Alone	7		6	Alone	6		6
Treatment		**6**		**Treatment**		**11**	
Together	0		3	Together	4		3
P		< 0.01		*P*		> 0.25	
Treatment	**1**		**3**	**Treatment**	**2**		**5**
	Polinices		*Murex*		*Thais*		*Volema*
Alone	7		5	Alone	6		7
Treatment		**7**		**Treatment**		**12**	
Together	4		1	Together	3		6
P		> 0.5		*P*		< 0.05	
Treatment	**1**		**4**	**Treatment**	**3**		**4**
	Polinices		*Terebralia*		*Murex*		*Terebralia*
Alone	7		6	Alone	5		6
Treatment		**8**		**Treatment**		**13**	
Together	1		2	Together	3		5
P		< 0.01		*P*		> 0.10	
Treatment	**1**		**5**	**Treatment**	**3**		**5**
	Polinices		*Volema*		*Murex*		*Volema*
Alone	7		7	Alone	5		7
Treatment		**9**		**Treatment**		**14**	
Together	0		4	Together	1		7
P		< 0.001		*P*		< 0.01	
Treatment	**2**		**3**	**Treatment**	**4**		**5**
	Thais		*Murex*		*Terebralia*		*Volema*
Alone	6		5	Alone	6		7
Treatment		**10**		**Treatment**		**15**	
Together	1		1	Together	1		5
P		> 0.9		*P*		< 0.025	
Order of preference (= denotes not significantly different): *Volema pyrum* > *Thais carinfera* = *Terebralia palustris* > *Polinices mamilla* = *Murex brevispina*							

DISCUSSION

Shell Availability, Utilisation and Human Exploitation

The results of the transect sampling agreed with reports from other geographic areas suggesting that gastropod shells are a limiting resource for hermit crab populations (Vance, 1972a; Abrams, 1978; Emmerson & Alexander, 1986; Borjesson & Szelistowski, 1989; Liszka & Underwood, 1990), with very few (7.9% of total) empty shell being found and the great majority of those were unavailable shells (broken or filled with sand). Although shell exchange and aggressive removal by other hermit crabs could occur frequently (Borjesson & Szelistowski, 1989) within the natural community, the low availability of empty shells suggests that choice may be limited and that crabs probably do not occupy optimal shells. This idea was also supported by the fact that even low preferred species e.g. *Murex brevispina* (Table 4) were commonly used in the field (Table 2). The mechanisms by which gastropod shells become available are not known for local shores. Human collection may be one of them, but this is very unlikely, for although gastropod mollusks collected by locals constitute less than 5 % of total, depending on the season, the gastropod collection may reach considerable amounts (Oliveira, 1972; pers. obs.). The low number of gastropod species, hence low availability of empty shells at Praia da Costa do Sol, might be explained by other factors beside human exploitation. The low complexity of the substrate (Praia da Costa do Sol is basically an intertidal sandflat) and the natural low diversity of this typical estuarine habitat, subjected to high variations of salinity, temperature, turbidity and turbulence (Oliveira, 1972) could explain the low number of gastropod species in this area.

Bivalves are the most important resource collected at Costa do Sol. This seems to be a general pattern of mollusc exploitation in Maputo Bay. As reported by Pereira (1998), at Inhaca Island there is a clear dominance of bivalves in terms of total number of individuals collected (Longamane, 1995; de Boer & Longamane, 1996; Pereira, 1998). Bivalves (mainly the asiatic hard clam *Meretrix meretrix*) are heavily exploited in Praia da Costa do Sol especially for its high commercial value (Oliveira, 1972). It's common practice to see this clam exposed for selling at the local markets. Gastropods are occasionally sold at the local markets (Oliveira, 1972; pers. obs.), but its commercial value is not as high, so this resource is mainly collected for domestic consumption, a fact also observed by Oliveira (1972). From the interview data, the most collected species, in terms of number of individuals, were *V. pyrum, P. mamilla* and *T. carinfera* which corresponded with the data on availability of gastropods in the field and the occurrence of shells in the mangrove (Table 2). This suggests that human collection has a minimal effect on the availability of gastropod shells, notwithstanding the fact that it is carried out on a daily basis.

The 23 species of gastropod shells used in the field by *C. longitarsus* compares well with the 23 species used by *C. longitarsus* in the Quirimbas Archipelago (Barnes, 1997b), and with those of other hermit crab species which have been shown to utilise from 4 to 34 species of gastropod shells (Hazlett, 1981). Orians & King (1964) and Emmerson & Alexander (1986) for example, reported that *Diogenes* species occupied respectively 16 and 33 shells species. As the sampled area is very small and the availability of shells species in the field is quite low, it is very likely that *C. longitarsus* might use more shell species in other surrounding areas. Reese (1962), Scully (1979) reported that shell use was related to the availability of shell species. This was the case in the present study, where *Volema pyrum* was the most common in the field and simultaneously the most used and preferred shell species (Tables 2 and 4).

Shell Morphology and Preference

It has been shown that shell selection by hermit crabs is based on a number of shell morphological characteristics including weight, volume, overall shell size, aperture width, or a combination of these factors (Vance, 1972a; Shaw & Hoggarth, 1981; Borjesson & Szelistowski, 1989 and references therein; Barnes, 1997b). in our study, *C. longitarsus* significantly selected *V. pyrum* shells. This could be explained by the low overall size of the shell, particularly the streamlined architecture. This could be an important shell characteristic, as *C. longitarsus* inhabits dense mangrove roots and pneumathophores at Costa do Sol and very long or large shells, such as *Murex brevispina*, may be constrained in their mobility.

Shell aperture width is an important shell characteristic for hermit crabs because it influences the "wetness" of the shell internal volume thus, avoiding dissecation, predation and crab mobility. For the two first reasons it desirable that the aperture width is as small as possible, but for the last is should not be very small. A combination of these would provide the best shell fit for the hermit crab. *P. mamilla* had the greatest aperture width of all shells studied (Table 3) and was the least preferred shell (Table 4). This gives a good indication of the importance of shell aperture width for hermit crabs and that dissecation might be more important than mobility.

Weight is another important shell characteristic especially for its role on the energy expenditure and growth of hermit crabs (Osorno *et al*., 1998). *T. carinfera* was significantly the heaviest shell studied, followed by *V. pyrum* (Table 3). These were also, the two most preferred shell species (Table 4). According to Barnes (1997b), *C. longitarsus* is able to use heavier shells because it is only active when it is submerged (all *C. longitarsus* observed during this study were clustered under mangrove roots and pneumathophores) and the shell mass is partly supported by water.

Other shell characteristics that could influence hermit crab selection, but not studied, were shell physical strength and presence of appendices and other external morphological characteristics that could help reduce predation. It has been reported for tropical regions that puffer fishes and xanthid and portunid crabs are the major predators of hermit crabs (Borjesson & Szelistowski, 1989). As observed in the Quirimbas Archipelago (Barnes, 1997b), puffer fishes are relatively rare locally. However crabs, especially portunid species (*Portunus* spp., *Scylla serrata*), are abundant and could be important predators of hermit crabs. Physical strength, as measured by Barnes (1997b), is very high in *Volema* and *Thais* species. Both species also have (especially *Thais*) a very rough surface covered with spines. These two, could be another important characteristics that influenced their selection by *C. longitarsus*.

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