Belg. J. Zool., 138 (1) : 13-19 January 2008

Shell utilization by the land hermit crab *Coenobita scaevola* (Anomura, Coenobitidae) from Wadi El-Gemal, Red Sea

Sallam WS[1], Mantelatto FL[2*] & Hanafy MH[1]

[1] **Department of Marine Science, Suez Canal University, Ismailia, Egypt. wafaasallam@yahoo.com**
[2] **Laboratory of Bioecology and Crustacean Systematics, Department of Biology, FFCLRP – University of São Paulo (USP), Av. Bandeirantes – 3900, CEP 14040-901, Ribeirão Preto, São Paulo, Brazil. Fax: + 55 16 36024396**

Corresponding author : * Mantelatto FL; e-mail: flmantel@usp.br

---

ABSTRACT. We conducted a study in order to determine the shell utilization pattern of the land hermit crab *Coenobita scaevola* (Forskäl, 1775), the only species representing the family Coenobitidae in the Red Sea. Hermit crabs were collected during July 2003 and January 2004 along the sandy shores of protected area of Wadi-Elgemal, south Red Sea. Animals were fixed in 10% formalin and transported to the laboratory where they were weighed and measured for cephalothoracic shield length (CSL) and width, left propodus length and height. Gastropod shells species were identified, weighed and measured for shell aperture width and length and shell internal volume. A total of 391 individuals were collected (219 females, 172 males) and were found occupying ten shell species, with clear significant occupation of *Nerita undata*. A positive relationship was obtained between the size of the shells occupied and the hermit crabs. Analysis of shell internal volume and crab dimensions demonstrated that this shell dimension constitutes mainly the determinant for *C. scaevola* shell utilization. With respect to the size of the animals and the occupied shell type, *Nerita undata* was occupied by a wide range of CSL (2.5–8.5mm). Small sized crabs (2.5–3.5mm CSL) occupied *Planaxis sulcatus* and *Nassarius arcularius plicatus* while larger specimens (8.5–9.5mm CSL) occupied *Turbo radiatus*, *Polinices milanostomus* and *Monodonta canilifera*. Variations in the shell occupation were also recognized among male and females. Comparisons among populational and shell use features led us to suggest the use of this land hermit crab as key-species in the preserving program of shores and protected areas, since this species is the first organism to disappear from any shore when a new tourist establishment is implemented.

KEY WORDS : Crustacea, Decapoda, population, hermit crab.

INTRODUCTION

Among Decapod Crustacea, terrestrial and semi-terrestrial members are unusual and only small numbers of species from various taxa, including here the hermit crabs, have been more or less successful in occupying the land (Wilde, 1973). On the contrary, hermit crabs represent an important portion of the many intertidal and moderately deep benthic marine communities worldwide, where they play an important role in the food chain (Fransozo & Mantelatto, 1998). Although one family, the Coenobitidae, composed of two phylogenetic closer genera, i.e. the monotypic coconut *Birgus* and *Coenobita* (Morrison et al., 2002), both well adapted for semi-terrestrial conditions, other families and genera are almost exclusively marine, and the majority have gastropod-shell-inhabiting species with soft and asymmetrical abdomens (Forest et al., 2000).

The genus *Coenobita* currently contains 16 species (Tudge & Lemaitre, 2006), and is a wide-ranging, largely tropical and subtropical genus of typical land hermit crabs inhabiting insular and coastal regions (Kurta, 1982; Hartnoll, 1988). This semi-terrestrial hermit crabs show ubiquitous pattern of movement and migrations tendencies that are influenced by many factors as food, water, tide rhythms, rainfall, including shell exchange and availability (see Kurta, 1982; Barnes, 2003 for review).

The subject of this study is *Coenobita scaevola* (Forskäl, 1775), the only coenobitid species in Red Sea waters from a total 31 hermit crab species previously recorded (Lewinsohn, 1969; Vine, 1986). This semi-terrestrial species is very abundant above the sea levels on the beaches of the Red Sea and the highly arid shores of Sinai Peninsula, but is totally dependent on the sea for water and consequently limited to the nearshore area (Achituv & Ziskind, 1985). It lives in burrows or rest in shaded areas among coastal vegetation during daytime and then emerge at night to scavenge close to high water (Vine, 1986).

Although shell utilization by hermit crabs has been examined in other areas of the world (see Mantelatto & Garcia, 2000 for review), little information is available to our knowledge about the pattern of shell utilization by hermit crabs of the Red Sea. El-Damhougy (1995) investigated the mouthparts structure and mechanisms of feeding of *Calcinus ornatus* and *Calcinus nitidus* from Hurgada while El Damhougy & Sadiq (2003) studied the factors affecting the age of glaucothöe stage of *Clibanarius signatus* at initial shell entry. On the other hand, six species has been reported further north the Red Sea from the Gulf of Suez and studied for their substrate preference (El-Damhougy & Haeba, 2003). Specifically on *Coenobita scaevola* the only work that we found was by Völker (1967) who reported this species to inhabit 29 shell species in Hurgada, based on a punctual sample.

In contrast, the gastropod fauna of the Red Sea has been well documented (Sharabati, 1984; Vine, 1986). Nevertheless, no information is available on that of the protected area of Wadi El-Gemal.

Gastropod shells are clearly important in all aspects of hermit life cycle as the main source utilized by these crustaceans to protect their soft and vulnerable abdomen. The crabs prefer to occupy shells of certain gastropod species to others, a preference not necessarily based on previous experience with these shell species but on certain shell properties that vary among gastropod species (CONOVER, 1978). Shells may function as a limiting resource to these crabs when in low abundance or adequacy (KELOGG, 1976). They may restrict crab growth (VANCE, 1972; BERTNESS, 1981), enhance their predation risk (VANCE, 1972), reduce fecundity (BERTNESS, 1981; ELWOOD et al., 1995), and modulate reproductive activity (BERTNESS, 1981; LITULO, 2004) and success (HAZLETT, 1989; HAZLETT & BARON, 1989). The patterns of shell utilization vary between hermit crab populations and are influenced by the type and size of shells available in the survey, the locality and the hermit crabs' shell preference (MANTELATTO & GARCIA, 2000; MEIRELES et al., 2003; MANTELATTO & MEIRELES, 2004).

On the other hand, research investigating aspects available worldwide on coenobitid hermits has focused on reproductive aspects (see TUDGE & LEMAITRE, 2006) and the mechanisms of migration (see BARNES, 2003 and NIEVES-RIVERA & WILLIAMS, 2003 for review). Nevertheless, the shell utilization approach for these land crustaceans has received little attention in recent years and is poorly known even though its significance. Since movement is particularly costly in the terrestrial environment, the crabs must carry their shells all the time and sometimes inadequate ones in function of their size and weight.

As an initial step to evaluate the ecological parameters affecting population of land hermit crabs in south Red Sea, we characterizes the shell utilization pattern of *C. scaevola* in a sandy beach in the protected area of Wadi El-Gemal at Marsa Alam, Red Sea.

MATERIALS AND METHODS

Hermit crabs were obtained from the protected area of Wadi El-Gemal in Marsa Alam, Red sea on July 2003 and January 2004. The animals were collected by hand at low tide from a sandy shore in the early morning by one person during a 20min walk over an area of 300m long. They were fixed in 10% formalin in seawater and transported to the laboratory. Processing started by careful removal of crabs from their shells in an anticlockwise fashion. Crab specimens were sexed by observing the position of the genital opening (gonopores). They were weighed (WW) and measured for cephalothoracic shield length (CSL=measured from the tip of the rostrum to the V-shaped groove at the posterior edge) and width (CSW), left chelar propodus length (LPL) and height (LPH). Shells were weighed (SWW) and measured for shell aperture width (SAW) and length (SAL) and shell internal volume (SIV=determined by the amount of water required to fill the empty shell by means of a measuring pipette). Measurements were carried out using a 0.1mm venier caliper. Gastropod shell species were identified according to SHARABATI (1984). The normality of hermit crab size (shield length) data was checked by Kolmogorov-Smirnoff test (ZAR, 1996). The chi-square test (χ^2) was used to compare the absolute frequency of occupation of shell species between sexes. To determine correlations between the dimensions of hermit crabs and occupied shells, regression analyses were performed (Spearman test) and by correlation coefficients using the power function equation ($Y=a.X^b$).

RESULTS

A total of 391 individuals of *C. scaevola* were collected (172 males and 219 females). No ovigerous females were observed in the samples. There was a unimodal size distribution for each sex and the size frequency distribution showed a prevalence of specimens measuring 3.5 to 8.0mm in shield length (Fig. 1). The size ranged from 2.5mm (males and females) to 9.0 and 9.5mm in shield length for females and males respectively. Overall sex ratio was 1: 1.2 in favour of females and was significantly different from the expected 1: 1 (χ^2=5.64, d.f.=1, P<0.05).

The hermit crabs were found occupying ten species of gastropod shells in different percentages (Table 1). *Nerita undata* was clearly the most occupied (86%), with no difference in shell use between sexes (χ^2=1.06, d.f.=1, P<ns), followed by *Turbo radiatus* (7.2%). On the other hand, there were significant differences in gastropod shell species occupation between sexes. *Littorina scabra, Monodonta canilifera* and *Nassarius arcularius plicatus* were occupied only by males (χ^2=16.9, d.f.=9, P<0.05). Regarding to the shell *versus* hermit correlations, shell utilization in *C. scaevola* was strongly associated with shell internal volume.

Shell species occupation as a function of hermit crab size is illustrated in Fig. 2. The diversity of shells utilized increased with the increasing of individual size. Among the occupied shells, *N. undata* dominated and was occupied by a wide range of size classes (2.5–8.5mm CSL). Small sized crabs (2.5–3.5mm CSL) occupied *Planaxis sulcatus* and *Nassarius arcularius plicatus* while larger specimens (8.5–9.5mm CSL) occupied *Turbo radiatus, Polinices milanostomus* and *Monodonta canilifera.*

Since almost all individuals (86%) were found occupying *N. undata*, we presented the regression equations showing the relations between *C. scaevola* dimensions and *N. undata* (Table 2). The equations ranked the relationships between the crab dimensions and internal volume of the occupied shell as recognized by the high correlations (r>0.80).

DISCUSSION AND CONCLUSION

The population of *C. scaevola* showed unimodality in the size-frequency distribution for the total individual analyzed. This life trait is the most common pattern among the hermit crabs (see MANTELATTO & SOUZA, 2000 for review) and reflects continuous recruitment and mortality of the species (DÍAZ & CONDE, 1989). Sexual size dimorphism was observed in *C. scaevola*, where males attained larger sizes than females. This dimorphism is a common one reported for marine hermit crabs (i.e, MANTELATTO & GARCIA, 2000; BIAGI et al., 2006), associated

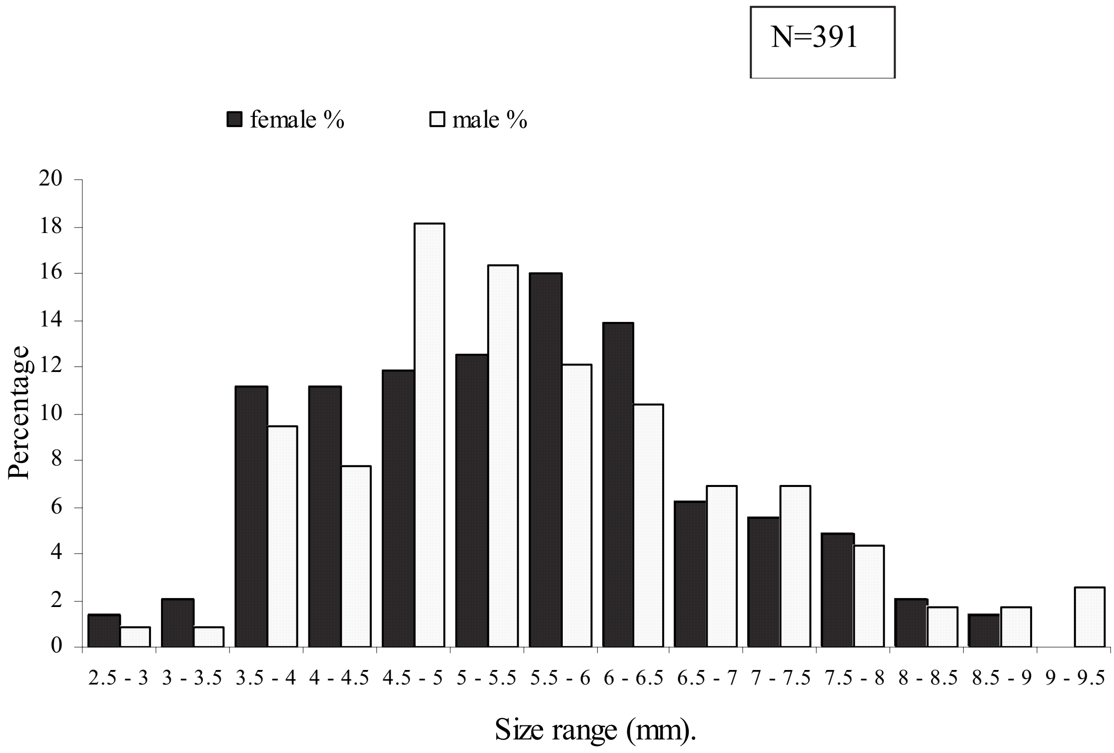

Fig. 1. – *C. scaevola.* Size frequency distribution (CSL) for the total number of individuals obtained from the protected area of Wadi El-Gemal in Marsa Alam, Red sea on July 2003 and January 2004.

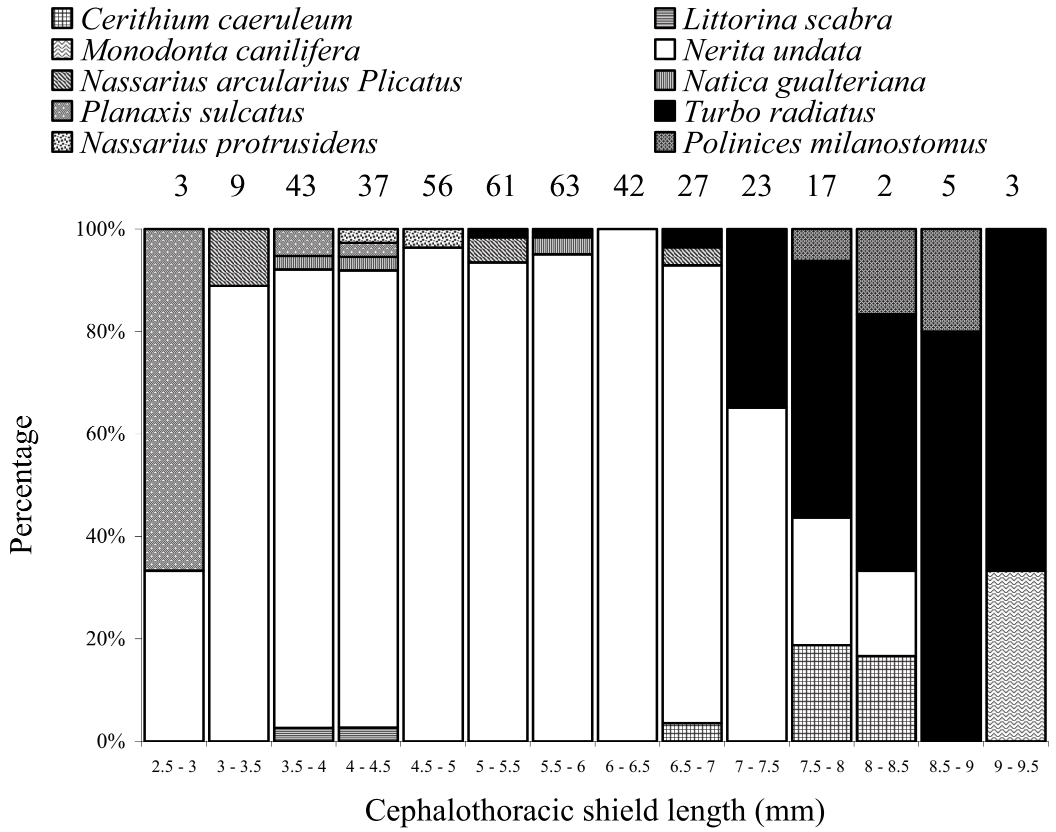

Fig. 2. – *C. scaevola*. Gastropod shell species occupation as a function of hermit crab size. The numbers above the bars indicate the total sample size for each size class.

TABLE 1

Total number and percentage of gastropod shells occupied by *Coenobita scaevola* in Wadi El-Gemal, Red Sea. (N=number of specimens).

Gastropod Shell Species	Males N (%)	Females N (%)	Total N (%)
Cerithium caeruleum (Sowerby, 1855)	3 (1.74)	2 (0.91)	5 (1.3)
Littorina scabra (Linnaeus, 1758)	2 (1.2)	–	2 (0.5)
Monodonta canilifera (Lamarck, 1816)	1 (0.6)	–	1 (0.3)
Nerita undata (Linnaeus, 1758)	138 (80.2)	197 (90.0)	335 (86.0)
Nassarius arcularius plicatus (Roding, 1798)	5 (3.0)	–	5 (1.3)
Natica gualteriana (Recluz, 1844)	2 (1.2)	2 (0.9)	4 (1.0)
Planaxis sulcatus (Born, 1778)	3 (1.7)	2 (0.9)	5 (1.3)
Turbo radiatus (Gmelin, 1791)	14 (8.1)	14 (6.4)	28 (7.2)
Polinices milanostomus (Gmelin, 1971)	2 (1.2)	1 (0.5)	3 (0.8)
Nassarius protrusidens (Melvill, 1888)	2 (1.2)	1 (0.5)	3 (0.8)
Total	**172 (43.99)**	**219 (56.01)**	**391**

TABLE 2

Regression equations for the relations between hermit crab *Coenobita scaevola* dimensions and the most occupied shell *Nerita undata* (**R^2**=determination coefficient; CSL=cephalothoracic shield length; CSW=cephalothoracic shield width; LPL=left propodus length; LPH=left propodus height; WW=hermit crab wet weight; SAW=shell aperture width; SAL=shell aperture length; SWW=shell wet weight; SIV=shell internal volume; N=391).

Relations	$Y= a.X^b$	R^2
SAW x CSL	$SAW=0.6401CSL^{0.9586}$	0.49
SAW x CSW	$SAW=0.4293CSW^{0.9681}$	0.49
SAW x LPL	$SAW=0.7574LPL^{0.9469}$	0.53
SAW x LPH	$SAW=0.4910LPH^{1.0645}$	0.50
SAW x WW	$SAW=0.0018WW^{2.5603}$	0.48
SAL x CSL	$SAL=1.3051CSL^{0.7578}$	0.67
SAL x CSW	$SAL=0.8851CSW^{0.7631}$	0.67
SAL x LPL	$SAL=1.7377LPL^{0.6804}$	0.62
SAL x LPH	$SAL=1.1556LPH^{0.8064}$	0.66
SAL x WW	$SAL=0.0124WW^{2.016}$	0.66
SWW x CSL	$SWW=4.3139CSL^{0.3454}$	0.53
SWW x CSW	$SWW=2.9382CSW^{0.3542}$	0.56
SWW x LPL	$SWW=5.0633LPL^{0.3175}$	0.52
SWW x LPH	$SWW=4.1154LPH^{0.3723}$	0.55
SWW x WW	$SWW=0.2992WW^{0.9441}$	0.53
SIV x CSL	$SIV=5.8882CSL^{0.4691}$	0.79
SIV x CSW	$SIV=4.0399CSW^{0.4765}$	0.79
SIV x LPL	$SIV=6.747LPL^{0.4384}$	0.77
SIV x LPH	$SIV=5.7532LPH^{0.5065}$	0.79
SIV x WW	$SIV=0.6855WW^{1.2696}$	0.79

principally to differences in energetic repartition between sexes (Abrams, 1988) and is important in selective pressure as intra- and interspecific fights for food, copulation, territory and shell (Mantelatto et al., 2005). This dimorphism can be attributed to such factors as differential mortality and growth rates between sexes (Abrams, 1978) with males reaching larger sizes within a shorter time than females, but being influenced by shell limitation, a fact that may imply reduced survival (Fransozo & Mantelatto, 1998; Mantelatto & Garcia, 2000).

Coenobita scaevola has the greatest number of zoeal stages (7 stages) and the longest zoeal life span (54-80 days) among the members of genus *Coenobita* (see Al-Aidoroos & Williamson, 1989 and Wang et al., 2007). Comparatively, the larval development of *Coenobita clypeatus* and *C. rugosus* require about 22-30 days to attain the glaucothöe respectively, and at least an additional month to the first crab, the presumed settling stage (Provenzano, 1962; Shokita & Yamashiro, 1986). Since in the studied period we have not found ovigerous females we may expect that juveniles are not being recruited to the population all over the year. This condition was corroborated by a low number of small sized crabs (2.5–3.5mm CSL) found in the Wadi El-Gemal. Thus we infer that settlement could take place in a different habitat other than the usual one for the adults, due to the fragility of these organisms and necessity of small shells supply. The presented pattern has been reported for other marine hermit crabs (Mantelatto & Sousa, 2000; Garcia & Mantelatto, 2001a; Macpherson & Raventos, 2004). According to Ball (1972), it appears that small sized individuals of *C. compressus* are much more sensitive to desiccation than larger animals and great aggregations can be found under ledges, in small rocky caves where is slightly more moisture.

Differences in gastropod shells utilization can occur as a function of the area of occurrence of the hermit crabs (Garcia & Mantelatto, 2000). *Coenobita* species are frequently found in areas, such as sandy beaches, where shells are extremely scarce (Ball, 1972). Specimens of *C. scaevola* of Wadi El-Gemal were found occupying ten species of shells with relative differences between sexes. *Littorina scabra, Monodonta canilifera* and *Nassarius arcularius plicatus* were occupied only by males. This fact probably indicates the resource competition/partition occurring mainly to guarantee a good adequacy of individual size to shells available in the survey. Differences in shell utilization between sexes were also observed by Imazu & Asakura (1994) and Bertini & Fransozo (1999). These differences may be due to differences in body size, competitive ability or reproductive behaviour, respectively (Bertness, 1981; Blackstone, 1985; Imazu & Asakura, 1994). Also, in semi-terrestrial hermit crabs a well-fitting shell is essential for maintaining low evaporation rates and carrying ample water. An appropriately sized shell in good condition allows invasion of inland environments offering more shade, food, and fresh water for *C. clypeatus* studied on Curaçao (Wilde, 1973). According to this author, the hermit crabs with broken, ill-fitting shells are restricted to the coast, must rely on drinking seawater, and appear to be in relatively poor conditions.

A population of *C. scaevola* studied almost 40 years late by Völker (1967) in the close region of Hurgada were found occupying a greater diversity of gastropod shells species (n=29) than the population studied here on the sandy shore of Wadi El-Gemal (n=10). Several hypotheses are possible to explain this apparent discrepancy in gastropod shell occupancy rates found between the two populations: 1) Gastropod life cycle – availability of different shell types (species) in nature is determined by the relative abundance of different live gastropods and their mortality rates (Meireles et al., 2003); 2) Environmental conditions – differences in abiotic characteristics of these two areas in terms of water dynamics (wave activity, intensity of currents, food supply) are determinant of installation of some invertebrate species (Fransozo & Mantelatto, 1998); 3) Predation pressure – several combined actions from natural (crabs) and artificial (human tourism) predators can act in different ways to reduce the diversity of gastropod shells in the region.

Similarly as other marine hermit crabs, *C. scaevola* shows highlight occupation of one species of gastropod shells, *N. undata*, over other ones. This shell was occupied by a wide range of individuals of both sexes with CSL varying from 2.5 to 8.5mm, while large sized crabs (8.5–9.5mm CSL) occupied a variety of shells. Although that shell availability was not evaluated, this intense occupancy would indicate active selection behaviour in *C. scaevola* in the field. Interestingly, in the past study Völker (1967) found that shells generally used by *C. scaevola* were found in the same frequency in the gastropod fauna, revealing a close relationship between shell use and availability of the resources. According to the energy savings hypothesis, proposed by Osorno et al. (1998), *C. scaevola* of Wadi El-Gemal preferred *N. undata* because it's the lightest of the shells available thus reducing the cost of bearing and carrying a shell. Large sized crabs might have modified their shell preference and occupied other species when large shells of *N. undata* became no longer available. The energy saved by carrying a light shell may be used to increase growth rate and egg production of intertidal hermit crabs, which ultimately improve fitness (Guillén & Osorno, 1993; Bertness, 1981). Also, crabs occupying shells large enough that they can withdraw completely and block the shell aperture with the chelipeds are much harder to extract from their shells than crabs which are too large to withdraw completely, and for this reason they would presumably be less vulnerable to predators (Ball, 1972). In conclusion, this pattern should be associated with the availability of resources and/or to the better suitability of these shells species to the condition of the individuals in the natural habitat.

Competition for shells may not be as intense among land hermit crabs as among their aquatic relatives. Abrams (1978) reported no fights for shells among *Coenobita compressus* in the field in Panama, whereas marine hermit crabs frequently fight. In opposite way when compared with marine hermit crabs, larger individuals of land hermit crabs tend to inhabit shells nearer their preferred size, i.e., shells that are modified by previous hermit crab use. The new shells have too little interior volume and are enlarged by hermit use (Wolcott, 1988). In this connection it is interesting to note that the majority of the shells occupied by *Coenobita* seem to be missing the columella (Ball, 1972). A similar observation has been made by Kinosita & Okajima (1968) on shells of *Nerita striata* occupied by *Coenobita rugosus* from Japan. Abrams (1978) suggested that rather than competition, terrestrial hermits show "shell facilitation"; that is, larger populations of crab generate, through wear, larger numbers of shells suitable for adult crabs. He accounted for limited adult populations by limited "recruitment" of entry-level shells, or possibly by predation on or food competition between adult hermits.

Interestingly and on the contrary to the proposed by Völker (1967), that affirm "land hermit crabs seem to have no relation to the shells of a given snail species", we found that shell dimension constitutes mainly the determinant for *C. scaevola* shell utilization, adopting in the Red Sea similar strategy developed by some other tropical and subtropical marine hermit crabs (Garcia & Mantelatto, 2001b).

The absence of ovigerous females during the two sampled periods was also an interesting and important point in the present study indicating the need for further frequent and systematized studies on this population since this is a rare pattern for these crustaceans. The presence of ovigerous females in some populations studied around the world have been previously documented (Ball, 1972; Wilde, 1973; Vannini, 1976; Shokita & Yamashiro, 1986). So, despite the fact that reproduction in coenobitids has covered a range of topics in recent years (Tudge & Lemaitre, 2006), the factors responsible for the absence of egg-bearing females are not clear and may involve methodology design (only two sampled periods), shell resource availability, interspecific competition for food and shelters, and others. The data obtained from two dates by daylight collection provided limited information about the reason for this absence. However, some hypotheses can be raised taking in account the limited range of the collection: 1) peaks of presence of ovigerous females probably occurs in different periods; 2) ovigerous females may be taking shelter at other points along this beach showing a cryptic habit during daylight and active at night as *C. compressus* (Ball, 1972), a common occurrence observed among ovigerous females of crustaceans; Particularly for *C. scaevola*, and other coenobitids, Vannini (1975) showed either daily or seasonal migrations depending upon rainfall. Also, spawning females of *C. clypeatus* presented unusual pattern since they did not enter the water, but move toward the sea at low tide to drop or fling their eggs onto the wet rocks (Wilde, 1973).

As a result of the intensive unregulated tourist development in the Red Sea area, a shore-monitoring program was established for the protected area of Wadi-El-Gemal. Continuous surveying of shores and beaches by rangers has led to the observation that *C. scaevola* is the first organism to disappear from any shore when a new tourist establishment is constructed (W. Sallam, pers. comm.). Accordingly, this study suggests the possibility to this species to be used as a key-species in the preserving program of this protected area. Its rarity or abundance on any shore could reflect the degree of healthiness of that shore and might assist in assessing the amount of deterioration of the shoreline which has a considerable impact on the different biota.

ACKNOWLEDGEMENTS

The first author wishes to express her sincere gratitude to Ms Marwa Essam for her help. Fernando Mantelatto extends special thanks to Wafaa Sallam for graciously allowing combining data and observation in order to jointly prepare this report and is grateful to CNPq for on-going Research fellowship. The authors are grateful to Drs. Renata Biagi and Andrea Meireles, and anonymous reviewers, for valuable suggestions on the manuscript. All experiments conducted in this study comply with current applicable state and federal laws.

REFERENCES

Abrams P (1978). Shell selection and utilization in a terrestrial hermit crab, *Coenobita compressus* (H. Milne Edwards). Oecologia, 34: 239-253.

Abrams PA (1988). Sexual difference in resource use in hermit crabs: consequences and causes. In: Chelazzi G & Vannini M (eds), Behavioral adaptations to intertidal life. New York, Plenum Press: 283-296.

Achituv Y & Ziskind M (1985). Adaptation of *Coenobita scaevola* (Crustacea: Anomura) to terrestrial life in desert-bordered shoreline. Marine Ecology Progress Series, 25: 189-198.

Al-Aidaroos A & Williamson DI (1989). Larval development of the land crab *Coenobita scaevola* (Forskäl, 1775) (Crustacea: Anomura: Coenobitidae) reared in the laboratary. Journal of Natural History, 23: 111-128.

Ball EE (1972). Observations on the biology of the hermit crab, *Coenobita compressus* H. Milne Edwards (Decapoda; Anomura) on the west coast of the Americas. Revista de Biologia Tropical, 20(2): 265-273.

Barnes DKA (2003). Ecology of subtropical hermit crabs in SW Madagascar: short-range migrations. Marine Biology, 142: 549-557.

Bertini G & Fransozo A (1999). Population dynamics of *Petrochirus diogenes* (Crustacea, Anomura, Diogenidae) in the Ubatuba region, São Paulo, Brazil. In*:* Von Vaupel Klein JC & Schram FR (eds), The Biodiversity Crisis and Crustacea, Balkema, Rotterdam, Brookfield, The Netherlands, Crustacean Issues, 12: 331-342.

Bertness MD (1981). The influence of shell-type on hermit crab growth rate and clutch size. Crustaceana, 40: 197-205.

Biagi R, Meireles AL & Mantelatto FL (2006). Bio-ecological aspects of the hermit crab *Paguristes calliopsis* (Crustacea, Diogenidae) from Anchieta Island, Brazil. Anais da Academia Brasileira de Ciências, 78: 451-462.

Blackstone NW (1985). The effects of shell size and shape on growth and form in the hermit crab *Pagurus longicarpus*. Biological Bulletin, 168: 75-90.

Conover M (1978). The importance of various shell characteristics to the shell-selection behavior of the hermit crabs. Journal of Experimental Marine Biology and Ecology, 32: 131-142.

Diaz H & Conde JE (1989). Population dynamics and life history of the mangrove crab *Aratus pisonii* (Brachyura, Grapsidae) in a marine environment. Bulletin of Marine Science, 45: 148-163.

El-Damhougy KA (1995). The structure of the mouthparts and mechanism of feeding in *Calcinus ornatus* Roux and *Calcinus nitidus* Heller (Anomura, Diogenidae). Journal of the Faculty of Education, Ain Shams University, 20: 831-840.

El-Damhougy KA & Haeba H (2003). Diversity and substrate preference of hermit crabs (Anomura: Decapoda) at the northern part of Gulf of Suez. Journal of the Egyptian Academic Society for Environmental development, 4(2): 49-64.

El-Damhougy KA & Sadiq AG (2003). Factors affecting the age of the glaucothöe stage of the hermit crab *Clibanarius lineatus* (Milne–Edwards) at initial shell entry and at metamorphosis to the juvenile star. Journal of the Egyptian German Society of Zoology, 40 D: 77-87.

Elwood RW, Marks N & Dick JTA (1995). Consequences of shell-species preferences for female reproductive success in the hermit crab *Pagurus bernhardus*. Marine Biology, 123: 431-434.

Forest J, Saint Laurent M, McLaughlin PA & Lemaitre R (2000). The marine fauna of New Zealand: Paguridea (Decapoda: Anomura), exclusive of the Lithodidae. National Institute of Water and Atmospheric Research, Biodiversity Memoir, 114: 1-250.

Fransozo A & Mantelatto FL (1998). Population structure and reproductive period of the tropical hermit crab *Calcinus tibicen* (Decapoda, Diogenidae) in the Ubatuba Region, São Paulo, Brazil. Journal of Crustacean Biology, 18(4): 738-745.

Garcia RB & Mantelatto FL (2000). Variability of shell occupation by intertidal and infralitoral *Calcinus tibicen* (Anomura: Diogenidae) populations. Nauplius, 8(1): 99-105.

Garcia RB & Mantelatto FL (2001a). Population dynamics of the hermit crab *Paguristes erythrops* (Diogenidae) from Anchieta Island, southern Brazil. Journal of the Marine Biological Association of the United Kingdom, 81: 955-960.

Garcia RB & Mantelatto FL (2001b). Shell selection by the tropical hermit crab *Calcinus tibicen* (Anomura, Diogenidae) from southern Brazil. Journal of Experimental Marine Biology and Ecology, 265: 1-14.

Guillén F & Osorno JL (1993). Elección de concha en *Coenobita compressus* (Decapopda: Coenobitidae). Revista de Biologia Tropical, 41(1): 65-72.

Hartnoll RG (1988). Evolution, systematics, and geographical distribution. In: Burggren WW & McMahon BR (eds), Biology of the land crabs. Cambridge University Press. Cap. 2: 6-54.

Hazlett BA (1989). Mating success of male hermit crabs in shell generalist and shell specialist species. Behavioral Ecology and Sociobiology, 25: 11-128.

Hazlett BA & Baron LC (1989). Influence of shells on mating behavior in the hermit crab *Calcinus tibicen*. Behavioral Ecology and Sociobiology 24: 369-376.

Imazu M & Asakura A (1994). Distribution, reproduction and shell utilization patterns in three species of intertidal hermit crabs on a rocky shore on the Pacific coast of Japan. Journal of Experimental Marine Biology and Ecology, 184: 41-65.

Kellogg CW (1976). Gastropod shells: a potentially limiting resource for hermit crabs. Journal of Experimental Marine Biology and Ecology, 22: 101-111.

Kinosita H & Okajima A (1968). Analysis of shell-searching behavior of the land hermit-crab, *Coenobita rugosus* H.

Milne Edwards. Journal of Faculty of Science of University of Tokyo, 11: 293-358.

Kurta A (1982). Social facilitation of foraging behavior by the hermit crab *Coenobita compressus*, in Costa Rica. Biotropica, 14(2): 132-136.

Lewinsohn C (1969). Die Anomuren des rotten Meers (Crustacea Decapoda: Paguridae, Galatheidae, Hippidea). The second Israel South Red Sea expedition, 1965, report no. 6. Zoologische Verhandelingen, 104: 1-213.

Litulo C (2004). Fecundity and breeding biology of the hermit crab *Diogenes brevirostris* (Stimpson, 1858) (Anomura: Diogenidae) from southern Mozambique. Invertebrate Reproduction and Development, 46: 41-46.

Macpherson E & Raventos N (2004). Population structure and reproduction of three sympatric species of hermit crabs in north-western Mediterranean. Journal of the Marine Biological Association of the United Kingdom, 84: 371-376.

Mantelatto FL & Garcia RB (2000). Shell utilization pattern of the hermit crab *Calcinus tibicen* (Anomura) (Diogenidae) from Southern Brazil. Journal of Crustacean Biology, 20(3): 460-467.

Mantelatto FL & Sousa LM (2000). Population biology of the hermit crab *Paguristes tortugae* Scmitt, 1933 (Anomura, Diogenidae) from Anchieta island, Ubatuba, Brazil. Nauplius, 8(2): 185-193.

Mantelatto FL & Meireles AL (2004). The importance of shell occupation and shell availability in the hermit crab *Pagurus brevidactylus* (Stimpson, 1859) (Paguridae) population from Southern Atlantic. Bulletin of Marine Science, 75(1): 27-35.

Mantelatto FL, Christofoletti RA & Valenti WC (2005). Population structure and growth of the hermit crab *Pagurus brevidactylus* (Anomura, Paguridae) from the northern coast of São Paulo, Brazil. Journal of the Marine Biological Association of the United Kingdom, 85: 127-128.

Meireles AL, Biagi R & Mantelatto FL (2003). Gastropod shell availability as a potential resource for the hermit crab infralittoral fauna of Anchieta Island (SP), Brazil. Nauplius, 11(2): 99-105.

Morrison CL, Harvey AW, Lavery S, Tieu K, Huang Y & Cunningham CW (2002). Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like form. Proceedings of the Royal Society of London B, 269: 345-350.

Nieves-Rivera AM & Williams Jr EH (2003). Annual migrations and spawning of *Coenobita clypeatus* (Herbst) on Mona Island (Puerto Rico) and notes on inland crustaceans. Crustaceana, 76(5): 547-558.

Osorno JJ, 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.

Provenzano Jr AJ (1962). The larval development of the tropical land hermit crab *Coenobita clypeatus* (Herbst) in the laboratory. Crustaceana, 4(3): 207-228.

Sharabati DP (1984). Red Sea shells. KPI. London: 127pp.

Shokita S & Yamashiro A (1986). Larval development of the land hermit crabs, *Coenobita rugosus*, H. Milne Edwards and *C. caripes* Stimpson reared in the laboratory. Galaxea, 5: 267-282.

Tudge CC & Lemaitre R (2006). Studies of male sexual tubes in hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea). II. Morphology of the sexual tube in the land hermit crabs, *Coenobita perlatus* and *C. clypeatus* (Coenobitidae). Crustacean Research, Special Number 6: 121-131.

Vance RR (1972). The role of shell adequacy in behavioral interactions involving hermit crabs. Ecology, 53: 1062-1074.

Vannini M (1975). Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 5. Descriptions and rhythmicity of digging behaviour in *Coenobita rugosus* H. Milne Edwards. Monitore Zoologico Italiano, Supp. 6, 6: 233-242.

Vannini M (1976). Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 10. Sandy beach decapods. Monitore Zoologico Italiano, Supp. 8, 10: 255-286.

Vine P (1986). Red Sea Invertebrates. IMMEL Publishing, London: 107pp.

Völker L (1967). Zur gehäusewahl des land-einsiedlerkrebses *Coenobita scaevola* Forskäl vom Roten Meer. Journal of Experimental Marine Biology and Ecology, 1: 168-190.

Wang FL, Hsieh HL & Chen CP (2007). Larval growth of the coconut grab *Birgus latro* with a discussion on the development mode of terrestrial hermit crab. Journal of Crustacean Biology, 27(4): 616-625.

Wilde PAWJ (1973). On the ecology of *Coenobita clypeatus* in Curaçao with reference to reproduction, water economy and osmoregulation in terrestrial hermit crabs. Studies on Fauna Curaçao and other Caribbean Islands, 44: 1-138.

Wolcott TG (1988). Ecology. In: Burggren WW & McMahon BR (eds), Biology of the land crabs. Cambridge University Press. Cap. 2: 55-96.

Zar JH (1996). Biostatistical analysis. Prentice-Hall. New Jersey, USA: 1-907.

Received: November 18, 2005
Accepted: June 26, 2007