Population features and breeding season of the land hermit crab *Coenobita scaevola* (Forskäl, 1775) (Anomura, Coenobitidae) from Wadi El-Gemal, South Red Sea, Egypt

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Abstract

Population dynamics of the land hermit crab *Coenobita scaevola* was evaluated focusing on size structure, sex ratio and breeding season. Specimens were randomly and monthly collected – from January to December 2007 – at Wadi El-Gemal, Marsa Alam, South Red Sea. From a total of 1088 obtained crabs, 496 were males (45.6%), 557 were non-ovigerous females (51.2%) and 35 (3.2%) were ovigerous females. The overall size frequency distribution was unimodal for males, non-ovigerous females and ovigerous females. The overall sex ratio (1:1.9) favored females. The population profiles of *C. scaevola* show some peculiarities when compared with congenerics and other diogenids. Both the low reproductive rate and the early maturation of females particularly inspire caution regarding the maintenance of this population. It can be hypothesized that these are strategies to minimize energy investment on growth and reproduction according to the environmental conditions to which this population is submitted during its life cycle.

Key words: Crustacea, Decapoda, reproduction, sex ratio.

Introduction

When compared with the high diversity of decapod crustaceans distributed worldwide, terrestrial and semi-terrestrial members represent a small portion of these taxa, including the true crabs and the less diverse hermit crabs. However, these latter represent an important portion of the many intertidal and moderately deep benthic marine communities (Fransozo and Mantelatto, 1998) and are promising examples of study since their establishment in marine, estuarine, and semi-terrestrial habitats derives from the evolution of adaptive population strategies (Mantelatto and Sousa, 2000).

Population features such as size structure, sex ratio, and reproductive patterns have been considered some of the most important data to assess differences among populations and to understand both the adaptive mechanisms of establishment in different areas (Mantelatto *et al.,* 2010) and the biological constraints that shape the structure of these populations (Branco *et al.,* 2002). Moreover, the study of dominant populations may be very important to elucidate the structure and function of communities.

Family Coenobitidae consists of two phylogenetically close genera: the monotypic coconut crab *Birgus* and the land hermit crab *Coenobita* (Morrison *et al.,* 2002) – both well adapted to life on land. Other families and genera are almost exclusively marine and encompass more than 90% of the hermit crabs studied in the literature. *Coenobita scaevola* (Forskäl, 1775) – the only coenobitid species in the Red Sea waters from a total of 31 marine hermit crab species previously recorded in this region (Lewinsohn, 1969; Vine, 1986) – is a member of this small group of semi-terrestrial hermit crabs currently represented by 16 recognized species (Tudge and Lemaitre, 2006). This species is very abundant above sea level on the beaches of the Red Sea and on the highly arid shores of the Sinai

Peninsula. It is totally dependent on the sea for water and consequently limited to the nearshore area (Achituv and Ziskind, 1985). It lives in burrows or rests in shaded areas among coastal vegetation during daytime and then emerges at night to scavenge close to the high water mark (Vine, 1986).

To date, the biological aspects of *C. scaevola* have only been studied in terms of life adaptation (Achituv and Ziskind, 1985), larval development (Al-Aidaroos and Williamson, 1989) and shell utilization (Völker, 1967; Sallam *et al.,* 2008), with a paucity of information on the population's features. Considering this promising scenario and as a part of a long-term effort to expand the knowledge on the life history of *C. scaevola,* this paper concentrates on the sex ratio, size frequency distribution and the reproduction pattern of *C. scaevola* at the protected area of Wadi El-Gemal, South Red Sea.

Material and Methods

Area of study

The study was conducted on a sandy beach of the protected area of Wadi El-Gemal at Marsa Alam, South Red Sea (35°04'0"E, 24°42'0"N) (Fig. 1). Wadi El-Gemal falls within the hyper arid region characterized by an arid climate and dominated by hot, rainless summers and mild winters. Precipitation falls mainly in the autumn and in the winter months, but it is not an annual event, being rather episodic and localized; it is often received in the form of short, heavy downpours that cause flash flooding. The monthly mean temperature varies between 24-38°C during summer and 12-26°C during winter. The relative humidity is around 28% during the summer and 57% in winter. Northwesterly winds predominate most of the year. Wind velocity is distinctly higher in the daytime, a phenomenon that can be explained by the high temperature differences between the heated landmass and the cool seawater throughout the day.

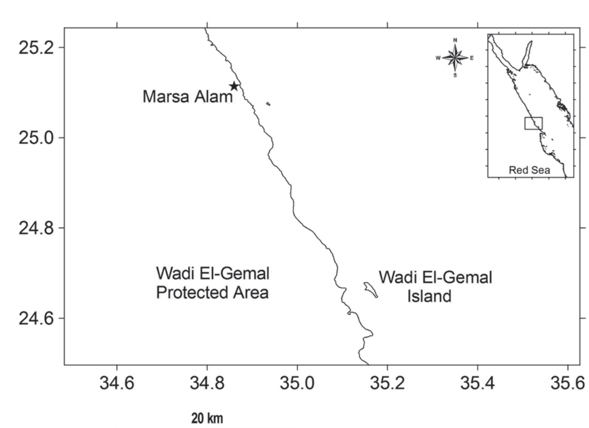

Figure 1. Map indicating the area of sampling at Wadi El-Gemal, Marsa Alam, Red Sea, Egypt.

Analysis of specimens

Hermit crabs were collected monthly for one year – from January to December, 2007. Collection was performed during daylight by one person covering an area of 300 m long for 30 min. Collected specimens were fixed in a 10% formalin-seawater solution and transported to the laboratory. Processing started with a careful removal of the crabs from their shells in an anticlockwise fashion. Sex was checked based on the presence of gonopores. The cephalothoracic shield length (SL = dorsally from the tip of the rostrum to the V-shaped groove at the posterior edge) was measured with the aid of a Vernier caliper (± 0.1 mm accuracy).

The population structure was analyzed according to the total distribution of individuals in the size classes (SL). Sex ratio was based on the number of males and females, considering the total of individuals collected in months and size classes (Mantelatto *et al.,* 2007a). The breeding period of the population was assessed as the percentage of females carrying eggs in relation to the total number of females collected (Fransozo and Mantelatto, 1998; Turra and Leite, 2000; Martinelli *et al.,* 2002). The settlement season, i.e., individuals in the first size class (*see* Pardo *et al.,* 2007 for concept and revision) was determined based on the occurrence of individuals in the first size class (SL < 4.0 mm) and on its monthly fluctuation. The chi-square test ($\chi 2$) was used to evaluate the sex ratio and to compare the male and the female percentages per month (Zar, 1996).

Results

Population structure

From the total of 1088 crabs that were sampled, 496 were males (45.6%), 557 were non-ovig-

Table I. *Coenobita scaevola* (Forskäl, 1775). Total number, percentage and sex ratio of individuals collected monthly at Wadi El-Gemal, Marsa Alam, South Red Sea.

Month	Males	%	Non-ovigerous females	%	Ovigerous females	%	Total	Sex ratio (M:F)	X^2
January	47	36.7	81	63.3	0	0	128	1:1.72	9.03*
February	36	40	54	60	0	0	90	1:1.50	3.60
March	49	49.5	50	60.5	0	0	99	1:1.02	0.01
April	48	42.5	65	57.5	0	0	113	1:1.35	2.56
May	31	31.3	52	52.5	16	16.2	99	1:2.19	13.82*
June	35	34.7	66	65.3	0	0	101	1:1.89	9.51*
July	44	57.1	18	23.4	15	19.5	77	1:0.75	1.57
August	16	31.4	35	68.6	0	0	51	1:2.19	7.07*
September	39	54.2	29	40.3	4	5.5	72	1:0.85	0.50
October	46	58.2	33	41.8	0	0	79	1:0.72	2.14
November	61	61	39	39	0	0	100	1:0.64	4.84*
December	44	55.7	35	44.3	0	0	79	1:0.80	1.03
Total	496		557		35		1088	1:1.19	8.47*

*Significantly different from the expected 1:1 sex ratio (X^2 test, $P < 0.05$)

erous females (51.2%) and 35 (3.2%) were ovigerous females (Table I). Animal size – minimum, maximum, and mean ± SD, respectively – was 3.0, 10.5, 5.47 ± 1.07 mm regarding males; 3.0, 9.3, 5.55 ± 0.98 mm regarding non-ovigerous females and 4.1, 7.3, and 5.84 ± 0.63 mm regarding ovigerous females. The number of collected individuals ranged from 51 (August) to 128 (January).

Figure 2 depicts the yearly size frequency distribution of all hermit crabs sampled during the study period. There was a unimodal size distribution regarding males, ovigerous females and non-ovigerous females. The size-frequency histogram shows a clear prevalence of individuals with 5.1-6.0 mm SL. Modal size ranged from 5.1 to 6.0 mm SL for each demographic category.

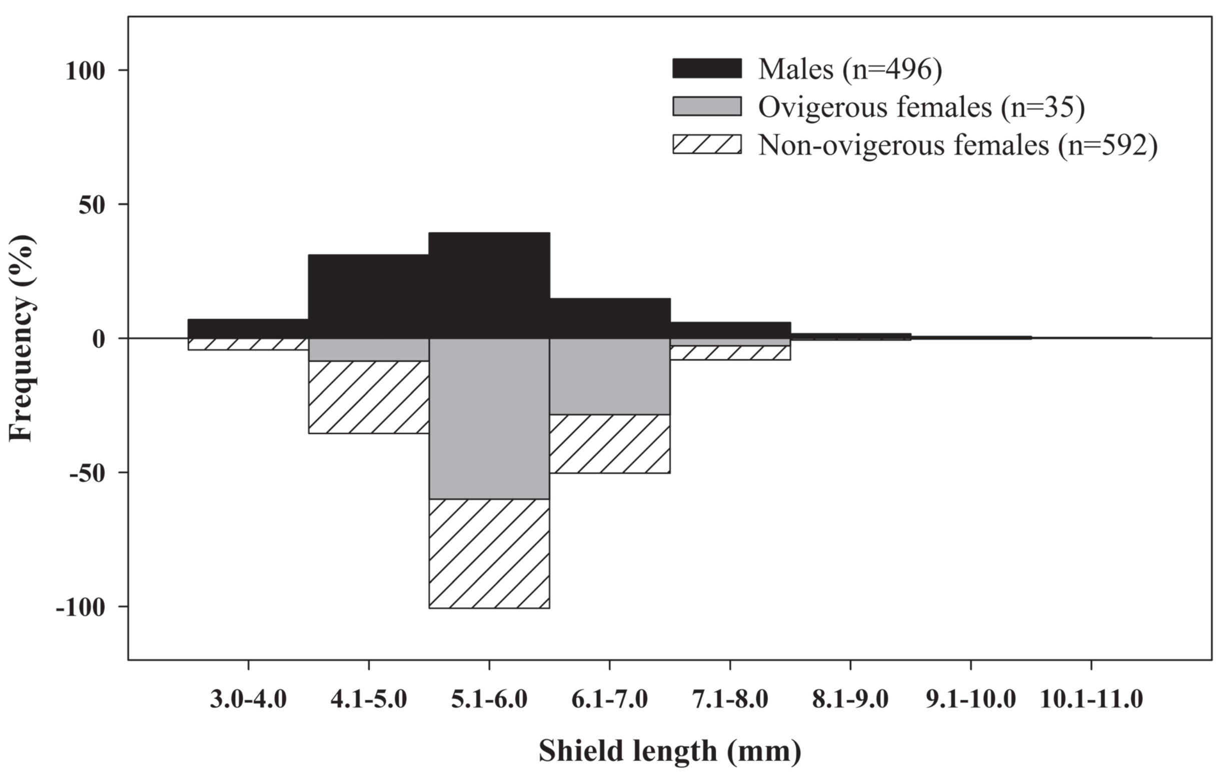

Figure 2. *Coenobita scaevola* (Forskäl, 1775). Overall size-frequency distribution of the total sample collected from January to December 2007 at Wadi El-Gemal, Marsa Alam, Red Sea.

The mean size of males was insignificantly larger than that of non-ovigerous females (t = 1.39, $P > 0.05$) and significantly larger than that of ovigerous females (t = 3.21, $P < 0.05$).

Monthly size frequency distributions with 1 mm class intervals of SL concerning males, non ovigerous females and ovigerous females were constructed (Fig. 3). Juveniles (SL < 4.0 mm) were represented by a total of 60 individuals in the first size class (5.0% of the total sampled) and occurred in almost all months.

Sex Ratio

Overall sex ratio (M:F) was 1:1.9 in favor of females and differed insignificantly from the expected 1:1 (X^2 = 19.68, $P > 0.05$). Monthly sex ratios (percentage of males) ranged from 31.3 to 61.0% while the percentage of non-ovigerous females ranged from 23.4 to 68.6%. In the smallest (3.0 to 4.0 mm SL) and in the last three larger size classes (8.1 to 11.0 mm SL) the proportion of males reached values higher than 50% and it reached a maximum of 100% in the last class (Fig. 4).

Reproductive season

Ovigerous females were only found in three non-successive months (May, July and September), with percentages ranging from 5.5% in September to 19.5% in July in relation to the total number of

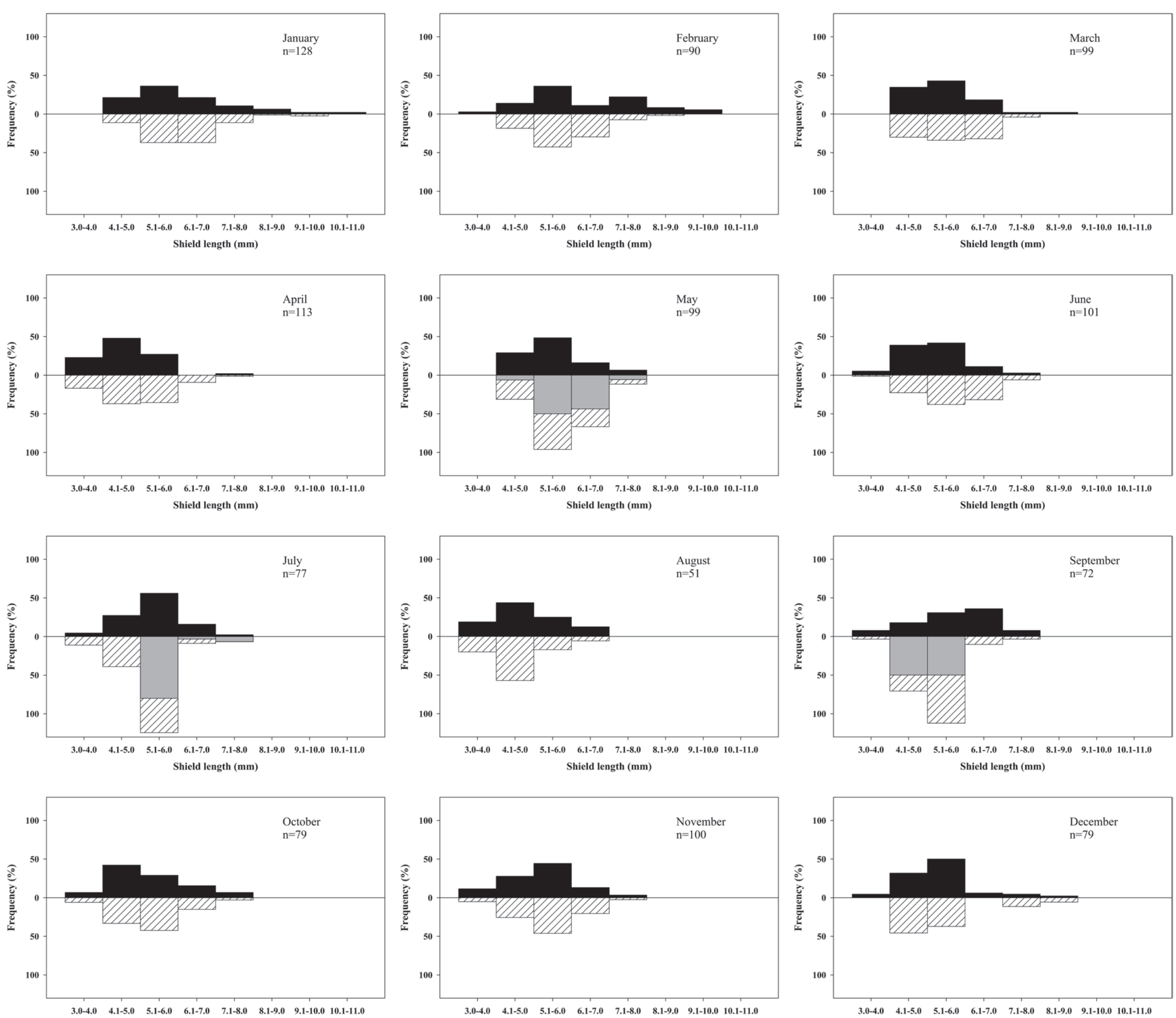

Figure 3. *Coenobita scaevola* (Forskäl, 1775). Monthly size-frequency distributions of sampled individuals – from January to December 2007 – at Wadi El-Gemal, Marsa Alam, Red Sea. Black bars – males; grey bars – ovigerous females; dashed bars – non-ovigerous females.

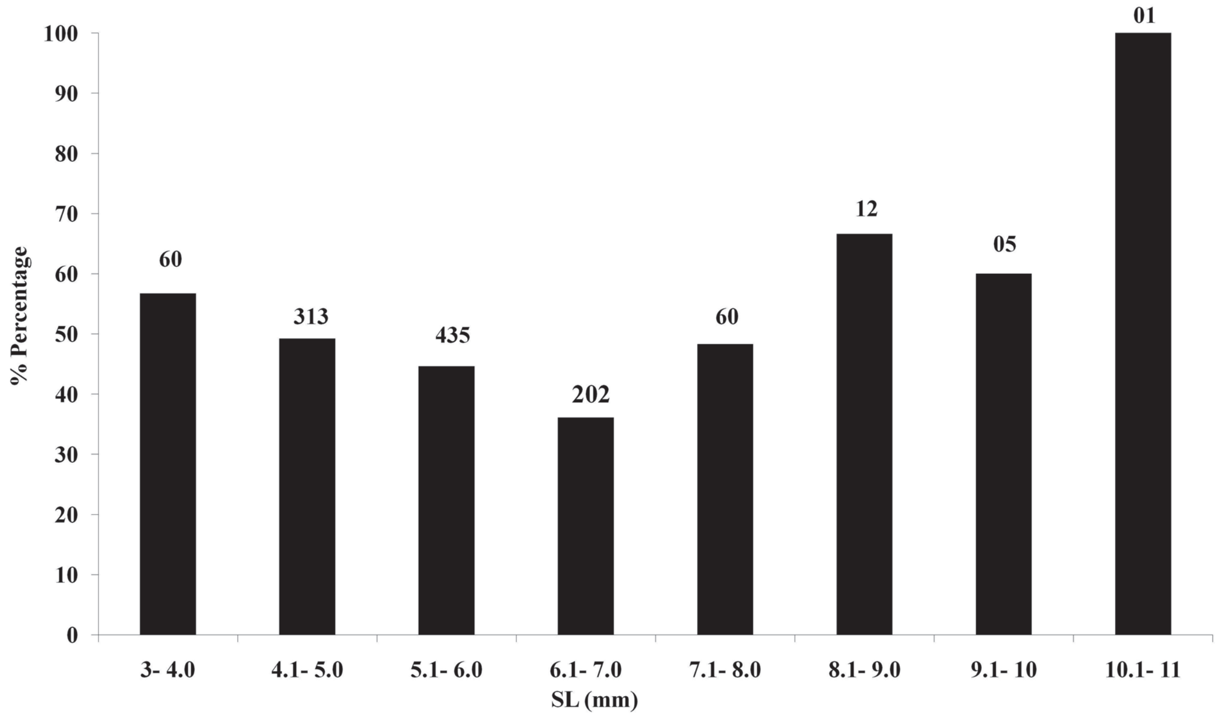

Figure 4. *Coenobita scaevola* (Forskäl, 1775). Sex ratio (percentage of males in relation to size). Values above columns correspond to the total number of individuals in each size class.

individuals collected (Fig. 5). The percentage values of females carrying eggs to the total number of females collected ranged from 12% in September to 46% in July (Table I), which represents a considerable increment in the reproductive effort.

Ovigerous females started to appear in the second size class (4.1-5.0 mm SL) and their percentage gradually increased in relation to larger females (Fig. 2). The median size of the 35 ovigerous females was 5.8 mm SL, ranging from 4.1 to 7.3 mm. The smallest ovigerous female (SL = 4.1 mm) was collected in September and was used as a morphological parameter to establish the size at sexual maturity (transition from juvenile phase to adult).

Discussion

The population profiles of *C. scaevola* inhabiting Wadi El-Gemal showed some peculiarities – low reproductive rate and early maturation of females – when compared with coenobitids.

Coenobita scaevola is sexually dimorphic in relation to size. The larger size reached by males is a consistent feature not only for this land hermit crab demography, but indeed for the majority of hermit-crab species that have been studied (*see* Biagi *et al.,* 2006; Mantelatto *et al.,* 2007b and Fantucci *et al.,* 2009 for references). It allows us to infer that they have a faster growth rate than the females, which may be interpreted as (a) strategy(ies) related to the differential energy consumption between the sexes and to several implications in the life cycle (*see* Mantelatto *et al.,* 2010). Concerning the *C. scaevola* that live in the studied region, we detected previously that size differences between sexes had caused a differential shell-occupation pattern (Sallam *et al.,* 2008).

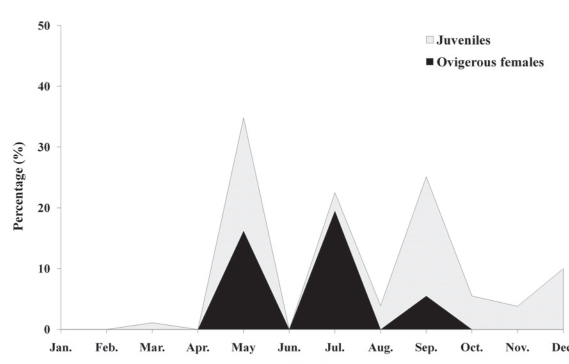

Figure 5. Relative month percentage of ovigerous females and of juveniles/total collected individuals, during the study period.

Among carcinologists, the population information has been assessed in several ways. Size frequency distribution is the most used parameter to characterize the population structure since it changes throughout the year as a result of reproduction, recruitment from larvae and death (Thurman, 1985). In the present study, the population presented a unimodal pattern of distribution which usually characterizes the occurrence of slight monthly variations. It may be a result from the balance between the continuous recruitment without class disruption and mortality rates. This pattern has been observed in some tropical hermit crab species, such as *Paguristes erythrops* Holthuis, 1959, *Pagurus brevidactylus* (Stimpson, 1879) and *Pagurus criniticornis* (Dana, 1852) [Garcia and Mantelatto (2001a), Mantelatto *et al.* (2005), and Mantelatto *et al.* (2007b), respectively].

Since we have found a low percentage of ovigerous females in the studied period, we may expect that juveniles are not being recruited to the population throughout the year. The low number of small sized crabs (2.5-3.5 mm SL) found in the Wadi El-Gemal corroborate this condition. As previously hypothesized by us (Sallam *et al.,* 2008), we can infer either that the adults' settlement could have taken place in some unexamined habitat other than the usual one, as analogously described for other *Coenobita* species (Wilde, 1973) or that they are genuinely very scarce due to their fragility and their dependence on the supply of small shells. These possible explanations had been reported for other marine hermit crabs (Mantelatto and Sousa, 2000; Garcia and Mantelatto, 2001b; Macpherson and Raventos, 2004). In addition, some *Coenobita* species, including *C. scaevola,* were observed to regulate their shell water salinity by replenishing or diluting it with fresh water (obtained from different areas) to attain the best osmotic performance, especially during egg bearing periods (*see* Wilde, 1973; Hartnoll, 1988 for revision). That can explain why some individuals prefer particular localities. Moreover, we cannot discharge a hypothetical influence of our daylight period sampling methods, since most of the coenobitids are nocturnal, although they might be active during the day under humid conditions or under rain (Wilde, 1973).

Ovigerous females were found only in three non-successive months – May, July and September – suggesting that reproduction is interrupted during some periods of the year. Considering the occurrence of small sized ovigerous females (SL = 4.1 mm), the low number of juveniles and the non-continuous reproductive pattern observed in the population studied, we can infer that sexual maturity may occur early in the life cycle of *C. scaevola* in the protected area of the South Red Sea in Egypt. This hypothesis is also supported by the pattern of larval development with respect to the genus. *Coenobita scaevola* has the greatest number of zoeal stages (7 stages) and the longest zoeal life span (54-80 days) among the members of the genus *Coenobita* (Al-Aidaroos and Williamson, 1989; Wang *et al.,* 2007). The larval development of *Coenobita clypeatus* (Fabricius, 1787), *C. rugosus* (H. Milne Edwards, 1837) and *C. compressus* H. Milne Edwards, 1837 requires respectively 22-32 days to attain the glaucothöe and it requires at least an additional month to the first crab, when the presumed settling stage occurs (Provenzano, 1962; Shokita and Yamashiro, 1986; Brodie and Harvey, 2001). In addition, *Coenobita variabilis* McCulloch, 1909 is the only member of the Coenobitidae reported to undergo abbreviated development, reaching the megalopal stage in only six days at after two nonfeeding zoeal stages (Harvey, 1992).

The reproductive patterns of this species could be explained as an adaptation to terrestrial habits. Thurman (1985) reported that both the size and the number of the produced eggs appeared to correspond to the environmental conditions, and that the apparent expense in producing an egg brood in semi terrestrial species was no greater than that of the other species that carried a large number of smaller eggs. Crane (1975) stated that semi and fully terrestrial crab species were smaller in body and clutch size.

It has been demonstrated that most tropical and subtropical hermit crab species have an extended reproductive period (*see* Turra and Leite, 2000 and Garcia and Mantelatto, 2001a for review) and show similarities in some other aspects of reproduction, such as a high reproductive investment and a high brood number per life time (Mantelatto *et al.,* 2002; Torati and Mantelatto, 2008). On the other hand, diogenid species from temperate environments often have their reproductive activity restricted or reduced to some season/period (*see* Table I in Miranda *et al.,* 2006 for review), which is the case of *C. scaevola.* In the same way, the reproduction events of *Coenobita clypeatus* in the Caribbean waters took place in summer and autumn and were dispersed over several months (*see* review in Wilde, 1973). Thus, it can be speculated that the lower intensity of reproduction shown by the females of *C. scaevola* in some periods (May and September) may be related to their higher energy requirements to cope with the environmentally related stress conditions in the hyper arid region (*see* details in M&M). This results in a different strategy of reproduction to equate the optimum physiological performance of the species. In another way, it was observed that almost 50% of the females showed an ovigerous condition in July, which can be understood as the peak of the reproductive effort.

Temperature is considered an important environmental factor in shaping life-history traits in decapods (Wear, 1974; Sastry, 1983).The reproductive season of *C. scaevola* occurs during the hottest months of the year (temperatures between 24-38°C), but the climate in the study area is also favorable for reproduction in the other seasons, particular during the warm winter (12-26°C). This means that the conditions are suitable for continuous reproduction all year round and that the hermit could have avoided the harsh summer temperature. The same pattern was reported for *Dotilla sulcata* from South Sinai (Sallam, 2005). Ovigerous females appeared between April and August and had a reduced fecundity. The author stated that breeding during spring and early summer had been advantageous for *D. sulcata* in order to ensure the development of their offspring before the colder months, what was considered a marked ability to adapt to the surrounding environment.

The sex-ratio analysis by size classes revealed an anomalous pattern proposed by Wenner (1972), which is characterized by a decrease in the males/females ratio in the intermediary classes and subsequent increase in the largest size classes. Probably, the deviation of the males/females proportion found in the present study (females more abundant in the middle-sized classes) may be attributed to a faster growth of males, to sexual selection and to a shorter longevity of females (Bertness, 1981; Abrams, 1988; Benvenuto and Gherardi, 2001). This pattern has been the most commonly reported in the literature (*see* Mantelatto *et al.,* 2007b for review) for hermit crab populations that inhabit both the intertidal and infralittoral areas. Despite the punctual sampling data, a similar pattern was detected for *C. clypeatus* in the Caribbean region (Wilde, 1973), with specific differences and peculiarities according to the site of occurrence (land side or sea side) and the season.

Unfortunately, other geographic distributions of *C. scaevola* lack information about population demographics, which limits any solid conclusion concerning intraspecific variability in the life history traits of this intriguing genus. This scenario makes our study the second attempt to enhance our knowledge on this poorly studied species. The low reproductive ratio and rate and the early maturity of females regarding the maintenance of this population inspire caution. This pattern can be hypothesized as a reproductive strategy to minimize costs during the life cycle stress. All population aspects treated here need further attention and confirm that several reproductive features of *C. scaevola* (and probably many other *Coenobita* species) are still unclear. Further studies that compare other species in detail are needed and will undoubtedly contribute to the greater understanding of semiterrestrial hermit crab life cycles.

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