Reproductive biology of *Calcinus laevimanus* (Randall, 1840) (Decapoda: Anomura: Diogenidae) from Inhaca Island, southern Mozambique

Carlos Litulo, Daniela Abreu and Christopher C. Tudge

Abstract.—Hermit crabs are one of the most abundant taxa in the intertidal habitats of tropical estuarine areas. Despite this situation, many aspects concerning their population ecology and reproduction are still poorly known. In this study, the reproductive biology of the diogenid hermit crab, *Calcinus laevimanus* was studied with emphasis on size structure, sex ratio, recruitment, breeding season and fecundity. Monthly samplings were conducted between January and December 2003 at Inhaca Island, southern Mozambique. A total of 1966 crabs were collected, represented by 760 males and 1206 females. The size frequency distribution of the present population showed an unimodal pattern skewed to the right, suggesting increased mortality in the largest size classes. Sexual dimorphism was evidenced by the larger sizes attained by males in relation to females. Moreover, sex ratios were female-biased during most of the study period. Juvenile recruitment was constant with major peaks in March and May, ovigerous females were present year-round peaking February and April and egg number increased with female size. The present results show that reproduction and recruitment of *Calcinus laevimanus* displays high reproductive activity in the study area, as evidenced by the constant presence of ovigerous females and the high number of eggs carried by females.

INTRODUCTION

Decapod crustaceans represent a large number of living species that inhabit a wide variety of biotopes. Consequently, the study on decapod crustaceans is promising because the establishment of these animals in such diverse habitats derives from the evolution of adaptive population strategies (Mantelatto & Sousa,

2000). Hermit crabs are anomuran decapod crustaceans that developed some strategies to utilize gastropod shells and other type of cavities to shelter their uncalcified abdomen. According to Litulo (2005), there are currently more than 900 species of hermit crabs worldwide, ranging from the deeper parts of the oceans to intertidal habitats. Despite this situation, the population biology aspects of these organisms are still poorly known, principally in tropical environments.

The large number of studies on hermit crabs mostly focused on behavioural features such as the use of gastropod shells and habitat selection in both the field and laboratory (e.g., Tunberg *et al.*, 1994; Barnes, 1999; Turra & Leite, 2001a). However, studies on population structure and reproduction of hermit crabs have been conducted for European and Mediterranean (Lancaster, 1988; Manjón-Cabeza & Garcia Raso, 1994, 1995, 1998), temperate (Asakura & Kikuchi, 1984; Imazu & Asakura, 1994), tropical (Kamalaveni, 1949; Ameyaw-Akumfi, 1975; Bertness, 1981) including South American (Fransozo & Mantelatto, 1998; Mantelatto & Garcia, 1999; Bertini & Fransozo, 2002; Martinelli *et al.*, 2002) and African species (Gherardi & Vannini, 1989; Gherardi *et al.*, 1994; Litulo, 2004; Litulo & Tudge, 2005).

Breeding periods of hermit crabs have been frequently described and reveal continuous to seasonal patterns (Bertness, 1981; Bertini & Fransozo, 1999; Turra & Leite, 2000). Reproductive activity can also be influenced by the adequacy of shells used by the crabs (Bertness, 1981; Mantelatto *et al.*, 2002). Moreover, breeding activity can vary in re-

sponse to competition for shells in natural habitats (Ameyaw-Akumfi, 1975).

In East African region, studies on hermit crab biology are scarce (e.g., Ameyaw-Akumfi, 1975; Emmerson & Alexander, 1986; Reddy & Biseswar, 1993) and, in particular reference to Mozambique, they have been restricted to behaviour and ecology (Barnes, 1997, 1999).

Calcinus laevimanus (Randall, 1840) is one of the most common hermit crabs in the Indo-Pacific region (Gherardi & Vannini, 1989; Reddy & Biseswar, 1993; Tudge, 1995a). At both ebb and flood tides, *C. laevimanus* disperse to feed on the substrate, picking at the detritus-covered rocks and pebbles with its chelipeds (Gherardi & Vannini, 1989). With the incoming high tide, it retreats into the rocks or pebbles. Often research on this species has been concerned with behaviour (Gherardi & Vannini, 1989) and patterns of shell utilization (Reddy & Biseswar, 1993). With the exception of research on spermatozoal and spermatophore ultrastructure (Tudge, 1995b, c), there is no information available on the general reproductive biology of *C. laevimanus* assessed by systematized study performed over a long period. This study addresses the paucity of information and describes the reproductive biology of *C. laevimanus* from Inhaca Island, an estuarine region in southern Mozambique, with emphasis on population size structure, sex ratio, juvenile recruitment, breeding season and fecundity.

MATERIALS AND METHODS

This study was conducted monthly from January to December 2003 on the full moon, during low tide in the exposed pebble area in front of the Marine Biological Station of Inhaca, Island, southern Mozambique (26°00' S, 33°00' E). The climate at this location is a mixture of tropical and subtropical, partly influenced by the South-Eastern trade wind, and a northerly monsoon, but also occasionally by strong and cold South-West winds or cyclones from the North-East. The winter (April–September) is usually cold and dry, while summer (October–March) is warm and rainy.

Detailed information on weather conditions as well as detailed descriptions regarding the ecology, fauna and flora of the Island can be found in Guerreiro *et al.* (1996).

Sampling was performed by two people during a period of 1 hour, covering an area of 300 m². Almost all hermit crabs were found in small aggregations of 5 or more in small pools that were regularly searched during the study period as reported for *Calcinus tibicen* in the southern Atlantic (Fransozo & Mantelatto, 1998). After collection, all individuals were bagged and transported immediately to the laboratory where they were removed by carefully cracking each shell. Sex was determined based on the position of gonopores (coxae of pereopod 3 for females and pereopod 5 for males). The cephalothoracic shield length (SL = from the tip of the rostrum to the V-shaped groove at the posterior edge of the carapace) was measured with the aid of Vernier callipers (± 0.05 mm accuracy) or under a dissecting microscope equipped with an ocular micrometer. Specimens were grouped in 0.5 mm size-class intervals, from 2.0 to 10.5 mm.

Ten eggs were removed from each ovigerous female for egg staging. Three stages of embryonic development were microscopically identified based on the amount of yolk and the development of eye pigment (modified from Wada *et al.*, 1995 and Mantelatto & Garcia, 1999).

Stage I (Initial): light-red, newly deposited eggs completely filled with yolk and no signs of segmentation. Stage II (Intermediate): eggs with less than 80% of yolk, and the development of zoea observed. Stage III (Final): dark-grey eggs with less than 5% of yolk and zoea fully developed just a few days from hatching.

Twenty-five ovigerous females with eggs at stage I were selected for egg counting. Pleopods were removed from females, placed in petri dishes filled with seawater, and eggs detached by the gradual addition of a solution of sodium hypochlorite (7%). Bare pleopods were then discarded by gently stirring in a beaker filled with 200 ml seawater. Three 1.5 ml subsamples were taken using a pipette, with eggs

counted under a dissecting microscope. The average value obtained was then extrapolated for the whole suspension to estimate the number of eggs (Ramirez Llodra, 2002).

The reproductive activity of the population was assessed as the percentage of females carrying eggs relative to the total number of females collected (Fransozo & Mantelatto, 1998; Turra & Leite, 2000; Martinelli *et al.*, 2002). The monthly occurrence of ovigerous females was assessed through one-way ANOVA followed by a Scheffé's test for multiple comparisons. The Chi-square test (χ^2) was used to evaluate sex ratio (M:F) and to compare male and female percentages per month. Data was assessed for normality and homogeneity of variance through the Kolmogorov-Smirnov and Levene tests and the mean size of individuals is compared by the Student's *t*-test (Underwood, 1997). The occurrence of juveniles (here defined as individuals of both sexes smaller than the smallest ovigerous female) characterized the recruitment in the population (Turra & Leite, 2000).

For fecundity analysis, data were analysed using the linear function ($Y = a + bX$) of egg number (EN) versus shield length (SL). Mean $\pm$ standard deviation (SD) is presented throughout the text.

RESULTS

A total of 1966 crabs were sampled from which 760 were males (38.7%), 866 non-ovigerous females (44.0%) and 340 ovigerous females (17.3%). Data was homogeneously distributed (Levene test, $p > 0.05$). Animal size (minimum, maximum, and mean $\pm$ SD) was 2.5, 9.8, and 4.91 ± 1.48 mm for males; 2.0, 5.5, and 4.27 ± 0.71 mm for non-ovigerous females; and 4.0, 8.2 mm, and 4.83 ± 0.78 mm for ovigerous females respectively. Males were on average larger than ovigerous females ($t = 56.28$, $p < 0.001$), which in turn were larger than non-ovigerous females ($t = 48.78$, $p < 0.05$).

Figure 1 depicts the yearly size frequency distribution for all hermit crabs sampled during

Fig. 1. *Calcinus laevimanus*. Overall size frequency distribution of individuals sampled at Inhaca Island, southern Mozambique.

the study period. There was a unimodal size distribution with normal distribution slightly skewed to the right for males (Kolmogorov-Smirnov test, $KS = 0.986$, $p > 0.05$), non-ovigerous females ($KS = 0.982$, $p > 0.05$) and ovigerous females ($KS = 0.977$, $p > 0.05$). The size frequency histogram shows a clear prevalence of individuals of both sexes measuring 3.5 to 5.5 mm SL. The modal size ranged from 3.5 to 4.5 mm SL for males and 4.5 to 5.5 mm SL for non-ovigerous females and ovigerous females (Fig. 1).

Monthly size frequency distributions for males, non-ovigerous females and ovigerous females are shown in Fig. 2, where major differences can be seen between each demographic category. Males often displayed uni and bimodal distribution, while non-ovigerous and ovigerous females tended to be largely unimodal. Larger males were scarce in the population mainly in March, April, May, July and September.

Overall sex ratio (M:F) was 1: 1.59 in favour of females and significantly differed from the expected 1:1 ($\chi^2 = 18.18$, $p < 0.05$). Monthly sex ratios were female-biased during the study period except for the month of January, and during the remainder of the year the percentage of females was significantly

Fig. 2. *Calcinus laevimanus*. Monthly size frequency distributions of individuals sampled during the study period at Inhaca Island, southern Mozambique. (White bars = males, grey bars = non-ovigerous females, black bars = ovigerous females).

higher than that of males except in June, July and December (Table 1).

Juveniles (all crabs of both sexes < 4.0 mm SL) appeared year-round with higher incidence in March and May (Fig. 3). The lowest num-

bers were observed in August and December.

Calcinus laevimanus breeds continuously with peaks in February, April and October. The months of July, August and November, showed the lowest frequency of egg-bearing females

(Fig. 4).

The number of eggs ranged from 600 (SL = 4.0 mm) to 3000 (SL = 8.2 mm), with an average of 1504 ± 872 eggs. There was a strong positive relationship between increasing egg number (EN) and increasing shield length (SL) ($N = 25$, $r^2 = 0.96394$, $p < 0.001$) (Fig. 5).

DISCUSSION

The overall size frequency distribution of both sexes was unimodal with males reaching larger sizes than both ovigerous and non-ovigerous females. This condition has been reported in other populations of *Calcinus laevimanus* in East Africa (Gherardi & Vannini, 1989) and in other sub-tropical and tropical hermit crabs: *Calcinus tibicen* (Herbst, 1791) (see Fransozo & Mantelatto, 1998), *Clibanarius antillensis* (Stimpson, 1859), *Clibanarius scolopetarius* (Herbst, 1796), *Clibanarius vittatus* (Bosc, 1802) (see Turra & Leite, 2000), and *Loxopagurus loxochelis* (Moreira, 1901) (see Martinelli *et al.*, 2002). According to Diaz & Conde (1989), unimodality of size frequency distributions generally characterizes a dynamic equilibrium for a certain population, and the occurrence of slight variations could reflect recruitment pulses, growth or different mortality rates. Moreover, this may indicate that settle-

Fig. 3. *Calcinus laevimanus*. Percentage of juveniles (all crabs < 4.0 mm SL) sampled at Inhaca Island, southern Mozambique.

ment of megalopae occurs in the same habitat as that occupied by the adults.

The lack of larger individuals in the present population of *Calcinus laevimanus* is also evidenced by its skewed size frequency distribution. Gherardi and colleagues (Gherardi & Vannini, 1989; Gherardi *et al.*, 1994) found a similar skewed size frequency in their populations of *C. laevimanus* and *Clibanarius laevimanus*, respectively. Branco *et al* (2002) reported the same phenomenon while studying a population of *Dardanus insignis* (Saussure,

Table 1. *Calcinus laevimanus*. Total number of individuals, percentage and sex ratio of crabs sampled at Inhaca Island, southern Mozambique from January to December 2003. (N = sample size; ns = not significant, * = significant deviation from the 1:1 ratio through the χ^2 test, $p < 0.05$).

Month	Males		Females		Total (N)	Sex ratio (M:F)
	(N)	%	(N)	%		
January	58	56.31	45	43.69	103	1:0.78 ns
February	31	18.79	134	81.21	165	1:4.32*
March	44	26.83	120	73.17	164	1:2.73*
April	60	32.61	124	67.39	184	1:2.07*
May	66	42.04	91	57.96	157	1:1.38*
June	74	45.96	87	54.04	161	1:1.18 ns
July	94	49.47	96	50.53	190	1:1.02 ns
August	53	36.05	94	63.95	147	1:1.78*
September	57	34.54	108	65.45	165	1:1.89*
October	52	36.36	91	63.64	143	1:1.75*
November	72	39.13	112	60.87	184	1:1.56*
December	99	48.77	104	51.23	203	1:1.05 ns
Total	760	38.66	1206	61.34	1966	1:1.59*

Fig. 4. *Calcinus laevimanus*. Reproductive activity indicated by the frequency of ovigerous females through the study period at Inhaca Island, southern Mozambique. (Labels indicate significant differences calculated by the Scheffé's test for multiple comparisons).

1858) in Brazil. Right-skewed distributions may be evidence of high mortality rates in certain populations (Underwood, 1997). Branco *et al.* (2002) suggest that a lack of larger individuals in a population might be physiological or be caused by a deficiency of shells in nature. In fact, large shells are often in limited supply in nature, so that hermit crabs are thought to be under heavy shell limitation (Reddy & Biseswar, 1993). This situation may be taking place at Inhaca Island because many people collect shells during low tide periods to sell in the markets and hotels for subsistence. This activity may be contributing to the skewness in the size frequency distribution of *C. laevimanus*.

Calcinus laevimanus at Inhaca Island, Mozambique, is sexually dimorphic with males being generally larger than both ovigerous and non-ovigerous females (Fig. 1). A situation also seen in the Somalian populations of *C. laevimanus* (Gherardi & Vannini, 1989). Abrams (1988) states that three factors can influence the sexual dimorphism of hermit crabs: 1) the difference in energy available for growth, with males growing more because they do not expend energy in egg production, but use

Fig. 5. *Calcinus laevimanus*. Regression analysis between egg number (EN) and shield length (SL) in females.

their energy for structural metabolism; 2) the larger reproductive effort exhibited by males may be due to their ability to fertilize more than one female; 3) males of larger dimensions have a greater chance on obtaining females for copulation as a function of intraspecific fights. Moreover, smaller growth rates of females would be a consequence of the utilization of relatively small shells and of the higher energy allocation to reproduction in relation to males (Asakura, 1992; Bertini & Fransozo, 2000). We believe that all these factors may influence the size of females in the present population of *C. laevimanus*.

The overall and monthly sex ratios differed from the expected 1:1 proportion (Table 1). Several causes may lead to this discrepancy, such as differences between sexes in longevity and growth rate, differential migration, mortality and sex reversal. Sex reversal (hermaphroditism) has been occasionally reported in hermit crabs (Turra, 2004) but the causes ruling its occurrence are still poorly known (Mantelatto & Sousa, 2000). According to Werner (1972), sex ratios differing from the 1:1 are widespread among crustaceans. In hermit crabs, females tend to be more abundant than males (Ameyaw-Akumfi, 1975; Imazu & Asakura, 1994; Martinelli *et al.*, 2002). Turra & Leite (2000) state that this may be explained by higher mor-

tality acting on males or by habitat partitioning, differential feeding restriction or spatial dispersion between sexes. Also important to address is the search for and utilization of shells, which are a limiting resource that may influence the sex ratio, with males being more successful in obtaining adequate shells in relation to females (Asakura, 1992).

In our study juvenile recruitment was continuous. These observations and the maximum size attained by the specimens may support the hypothesis that recruitment may occur in the same habitats from those occupied by adults. Looking at Fig. 3, it can be seen that juveniles recruit mostly during winter (March–June) in the study area. At Inhaca Island, phyto- and zooplankton growth occurs from September to November and a major period of plankton abundance occurs by March due to nutrient accumulation along the winter season (Paula *et al.*, 1998). These observations may lead us to suggest that juvenile recruitment is synchronized with the abundance of food resources, which are crucial for larval and juvenile growth.

Hermit crabs may display continuous (with or without peaks) or seasonal reproductive patterns (Bertness, 1981; Tunberg *et al.*, 1994; Manjón-Cabeza & Garcia Raso, 1998) regardless of the taxonomic group. As noted by Sastry (1983), populations of a given species at different latitudes subjected to particular environmental conditions may display different reproductive patterns. Continuous or wide reproductive periods shown by hermit crabs may be a result of multiple spawnings or asynchrony in reproduction.

Ovigerous females of *C. laevimanus* were found year-round in the study area but with peaks in February, April and October, suggesting a continuous reproductive pattern (Fig. 4). A similar pattern was found in *Paguristes tortugae* studied by Mantelatto & Sousa (2000) and *Clibanarius antillensis* studied by Turra & Leite (2000). Continuous reproduction is important for the determination of several characteristics of a population such as continuous larval supply and juvenile recruitment, which

are important mechanisms to stabilize a population. Discontinuous or prolonged reproduction is also common among subtropical and tropical hermit crabs. According to Turra & Leite (2000), any hypothesis to explain the occurrence of populations with seasonal reproductive patterns in the tropics and with continuous patterns in temperate regions may be based on the evolutionary histories of population although local factors such as competition and shell use, should also be considered when assessing the reproductive traits of a species or population.

Fecundity (number of eggs per egg clutch) increased in proportion with female shield length (Fig. 5). This was to be expected as the egg number of most hermit crabs increases in parallel with female size (Mantelatto & Garcia, 1999; Turra & Leite, 2001b; Mantelatto *et al.*, 2002; Litulo, 2004; Macpherson & Raventos, 2004). Small variations in the number of eggs were observed within the same size classes. According to Sastry (1983) and Mantelatto *et al.* (2002), this can be related to accidental loss of eggs, incomplete fertilisation or multiple spawnings. Multiple spawnings (here defined as females spawning several times after each release of previous larvae) are generally characteristic in tropical hermit crabs due to small variations in environmental parameters, which are very important for egg and larval development (Sastry, 1983). The large jump (doubling) in egg number observed at about 6mm (SL) (Fig. 5) could represent the difference between first mating (primiparous) and already mated (multiparous) females, or more likely is a consequence of a gastropod host shell switch to a larger species providing more egg space (Mantelatto & Garcia, 1999).

The characterization of populations in natural habitats is important to understand their life cycle and ecological stability. This can be accomplished by describing patterns of distribution, density, dispersion, sex ratio and breeding periods that can be compared to other populations of the same species, genus or other taxonomic level. Such comparisons are an important strategy to verify differences among populations and to understand the environmen-

tal constraints that are shaping the structure of these populations (Branco *et al.*, 2002). This data on *Calcinus laevimanus* is a starting point to gaining this understanding for tropical hermit crabs, especially in the poorly studied region of East Africa.

Acknowledgements.—We thank the Marine Biological Station of Inhaca Island (EBMI) for logistical support, and WIOMSA (Western Indian Ocean Marine Science Association) for financial support. CCT wishes to acknowledge the support of Rafael Lemaitre and previous IZ Department chairs at NMNH, Smithsonian Institution, for access to resources. This manuscript was substantially improved by the comments of two anonymous referees.

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- Ciências Biológicas, Faculdade de Ciências, Universidade Eduardo Mondlane, Caixa Postal 257, Maputo, Mozambique; e-mail: (CL) Litos@uem.mz. CCT, Invertebrate Zoology, MRC 163, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, U.S.A., and Department of Biology, American University, Washington, D.C. 20016-8007, U.S.A.; e-mail: tudgec@si.edu

*Author for correspondence

Addresses: *CL, DA, Departamento de