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Population dynamics and reproduction of the hermit crab *Calcinus gaimardii* (Anomura: Diogenidae) at Inhaca Island, southern Mozambique

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Abstract

The population dynamics and reproduction of *Calcinus gaimardii* were studied at Inhaca Island, southern Mozambique. Crabs were sampled monthly from January to December 2003 in order to assess abundance, size distribution, sex ratio, reproduction and juvenile recruitment. *Calcinus gaimardii* is sexually dimorphic in relation to size, with males reaching larger size than females. Sex ratios were female-biased during most months of the study period. Females were more abundant in the intermediate size classes while males outnumbered females in the largest ones. Reproduction took place year-round with peaks of breeding activity between August and October. Likewise, juvenile recruitment was continuous for both sexes with high intensity in winter (May and June). Egg number increased with female size.

Keywords: *Breeding activity, Calcinus gaimardii, hermit crabs, Mozambique, population dynamics*

Introduction

Among the marine Crustacea, anomuran crabs represent one of the most diverse and abundant groups, inhabiting tropical and temperate waters all around the world. Hermit crabs are anomuran decapod crustaceans that have developed strategies to inhabit gastropod shells and other types of cavity to shelter their uncalcified abdomen (Litulo 2004, 2005a). There are currently more than 900 species of hermit crabs already described worldwide, ranging from the deeper parts of the ocean to intertidal habitats (Litulo 2004, 2005a), where they play an important role in the marine food chain (Fransozo and Mantelatto 1998). Consequently, they represent promising material for study because the establishment of these organisms in such environments derives from the evolution of adaptive population strategies (Garcia and Mantelatto 2001).

The characterization of populations in natural habitats is important in order to understand their life cycles and ecological stability. This can be accomplished by describing

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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 (Branco et al. 2002). Such comparisons are an important strategy to verify differences among populations and to understand the environmental constraints that are shaping the structure of these populations (Branco et al. 2002).

Traditionally, breeding seasons of hermit crabs have been analysed based on the occurrence of egg-bearing females during different months of the year (e.g. Manjón-Cabeza and Garcia-Raso 1994, 1998; Turra and Leite 2000; Garcia and Mantelatto 2001; Litulo 2004, 2005a; Macpherson and Raventos 2004) or by means of gonad analysis (Kamalaveni 1949; Lancaster 1990; Bertini and Fransozo 2002; Bertini et al. 2004). At present, most work carried out on the population dynamics and reproduction of hermit crabs has been conducted mainly in temperate and subtropical environments (e.g. Nyblade 1987; Turra and Leite 1999; Mantelatto and Sousa 2000; Squires et al. 2001; Martinelli et al. 2002; Macpherson and Raventos 2004), while very little is known about tropical species (but see Kamalaveni 1949; Amayaw-Akumfi 1975; Turra and Leite 2000; Litulo 2004, 2005a).

Breeding periods of hermit crabs have been frequently described and reveal continuous to seasonal patterns (Bertness 1981; Bertini and Fransozo 1999; Turra and 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 response to competition for shells in natural habitats (Ameyaw-Akumfi 1975).

Calcinus gaimardii (H. Milne Edwards, 1848) is one of the most abundant hermit crabs on East African shores. It inhabits eulittoral rocky platforms, coral reefs, coral rubble, pebble areas, debris and adjacent sandy areas. Its distribution ranges from the Western Indian Ocean through to Hawaii, north to Japan, south to Queensland and the central Pacific Ocean (Tudge 1995; McLaughlin 1997). The only works available on the reproductive biology of this species are those by Tudge (1997) and Jamieson and Tudge (2000) who described its spermatozoa and spermatophore morphology. No information is available on population dynamics, breeding season and fecundity of *C. gaimardii* in Indian Ocean waters.

This work analyses the population dynamics and breeding biology of *C. gaimardii* at Inhaca Island, southern Mozambique.

Materials and methods

The present study was conducted in an exposed pebble area in front of the Marine Biological Station of Inhaca Island (EBMI), 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 cold south-west winds or cyclones from the north-east (Litulo 2005b). The winter season (April to September) is usually cold and dry, while summer (October to March) is warm and rainy. Tides are semi-diurnal with maximum amplitude of about 3.5 m.

Hermit crabs were sampled between January and December 2003 during spring low tide periods and at full moon. At each sampling survey, 10 1.0-m² (1.0 m × 1.0 m) quadrats were sampled by two people over a period of 1 h and covering the same area of about 300 m². Collected crabs were bagged and stored in 70% ethanol until further processing. Upon return to the laboratory, all individuals were removed from the shells by carefully cracking each shell. Sex was determined based on the location 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 Vernier callipers (± 0.05 mm). The presence of ovigerous females was recorded.

Between 10 and 15 eggs were removed from each female for egg staging. The embryo mass of each female was examined under the stereomicroscope on the basis of amount of yolk and the development of eye pigment, following Litulo (2004, 2005a). Stage I (Initial): light red, newly deposited eggs, completely filled with yolk, no signs of segmentation; Stage II (Intermediate): eggs with less than 80% yolk and the development of the zoea begun; Stage III (Final): dark grey eggs with less than 5% yolk and are a few days from hatching. The fecundity of *Calcinus gaimardii* was determined by counting all embryos carried by 50 females bearing eggs at stage I. For this purpose, 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 discarded by gently stirring in a beaker filled with ~ 200 ml seawater. Three 1.5-ml sub-samples were taken using a pipette, and eggs were counted under a dissecting microscope. The average value obtained was then extrapolated for the whole suspension to estimate the total number of eggs (Litulo 2004, 2005a).

Whisker plots were performed for males and females in each month to analyse the population structure through the study period. A Student's t test was employed to detect differences between sexes. The population sex ratio was compared to 1:1 with the log-likelihood G test. The breeding season was determined using the proportion of ovigerous females captured over the study period and their monthly fluctuation was assessed using ANOVA, followed by Scheffé's test for multiple comparisons. Animals smaller than the smallest ovigerous female were considered as juveniles. The power function ($Y = ax^b$) was fitted to estimate the relationships between egg number (EN) and female size (SL). The Student's t test was also used to test the null hypothesis of isometry ($b=3$) for this relationship (Underwood 1997).

Results

A total of 793 crabs was obtained throughout the study period comprising 295 males (37.2%), 285 non-ovigerous females (35.9%) and 213 ovigerous females (26.9%). Males (mean = 8.96 mm, SD = 1.66, range = 1.5–17.1 mm) were, on average, larger than females (mean = 7.12 mm, SD = 2.43, range = 1.5–15.2) ($t = 11.38$, $P < 0.05$).

Immature males were dominant between May and June whereas adults peaked from January to April (Figure 1A). High frequency of immature females was observed in June and adults were dominant from August to October (Figure 1B).

Females ($n = 498$) were more abundant than males ($n = 295$) and the sex ratio differed from 1:1 ($G = 111.36$, $df = 1$, $P < 0.05$). The percentage of females was relatively higher throughout the study period and monthly sex ratios were female-biased (Figure 2).

The size of hermit crabs had an influence on the sex ratio (Figure 3). Females were more abundant in the intermediate size-classes (4.0–10.5 mm) while males outnumbered females in the largest ones (12.0–16.0 mm).

Calcinus gaimardii showed a continuous reproductive pattern with peaks of occurrence of ovigerous females from August to October (Figure 4). Low frequency of ovigerous females was recorded in June and November to December.

The number of eggs ranged from 609 (SL = 5.0 mm) to 6835 (SL = 15.0 mm), with an average of 2085 ± 693 eggs and increased with size ($b > 3.0$, $t = 7.18$, $P < 0.05$) (Figure 5).

Figure 1. Whisker plots (mean $\pm$ SD) representing size variation of *Calcinus gaimardii* (H. Milne Edwards, 1848) of males (A) and females (B).

Discussion

Sexual dimorphism in the present population of *C. gaimardii* was evidenced by the larger average sizes attained by males in relation to females. This kind of sexual dimorphism seems to be a constant in hermit crabs as reported in previous studies for other species: *Petrochirus diogenes* (Linnaeus, 1758) (Bertini and Fransozo 1999), *Paguristes tortugae* (Schmitt, 1933) (Mantelatto and Sousa 2000), *Clibanarius antillensis* (Stimpson, 1859), *C. scolopetarius* (Herbst, 1796) and *C. vittatus* (Bosc, 1802) (Turra and Leite 2000), and *Clibanarius longitarsus* (De Haan, 1849) (Litulo 2005a). The most prominent factors regulating sex in hermit crabs are: difference in energy available for growth, with males

Figure 2. *Calcinus gaimardii* (H. Milne Edwards, 1848). Frequency of crabs sampled at Inhaca Island during the study period.

Figure 3. *Calcinus gaimardii* (H. Milne Edwards, 1848). Relationship between sex ratio and crab size.

Figure 4. Reproductive activity of *Calcinus gaimardii* (H. Milne Edwards, 1848) at Inhaca Island, southern Mozambique. Bars sharing the same letter do not differ statistically (Scheffé's test, $P>0.05$).

Figure 5. *Calcinus gaimardii* (H. Milne Edwards, 1848). Relationship between egg number (EN) and female size (SL).

growing faster as they do not allocate their energy for egg production, but direct it for structural growth; the larger reproductive effort belongs to the males due to their ability to fertilize more than one female; males of larger dimensions have a greater chance of obtaining females for mating as a function of intra-specific fights (Abrams 1988). All these factors can interfere with the size of *C. gaimardii* males.

Size frequency distributions for the present species showed small variations, suggesting that recruitment, growth and mortality follow seasonal trends. Temporal variation in abundance and size of a given species in a given site may be associated with harsh environmental conditions in some periods of the year (Turra et al. 2002). In the case of *Calcinus gaimardii*, results indicate that recruitment of young crabs takes place mostly during winter. Moreover, no adult crabs were found for either sex in winter, suggesting that mortality may be higher at the end of summer.

According to Hazlett (1981), hermit crabs may undergo along-shore daily movements, which can vary from half a metre to a few hundred metres in a single day. These daily movements may be responsible for the variation in the abundance and size of hermit crabs at different periods of the day. Such movements may be caused by natural lack of adequate shells in the study area or the present hermit crabs are under heavier shell limitation.

The overall and monthly sex ratios differed significantly from 1:1 with females appearing in larger numbers in relation to males. Several causes are responsible for this discrepancy, and the most frequent are differences between sexes in longevity and time for growth, differential mortality, sex reversal (Turra 2004) and differential production of gametes. Alternatively, female-biased sex ratios as recorded in the present study may be intrinsic, resulting from a greater production of female offspring in the study area (Litulo 2005a). In the analysis of sex ratio by size-classes males tended to dominate over females in the larger classes whereas females tended to be abundant in the intermediate size classes. Garcia and Mantelatto (2001) obtained the same pattern while studying a population of the hermit crab *Paguristes erythrops* (Holthuis, 1959). According to Asakura (1995), this trend is widespread among hermit crabs and may be explained by the higher mortality acting on males, habitat partitioning and differential spatial dispersion between sexes. On the other hand, males are larger than females, a fact that makes sex ratio at high size-classes skewed for males (Turra and Leite 2000).

Each organism inhabits a definite habitat, in which abiotic and biotic factors are suitable for reproduction and growth. Studies of reproductive patterns can supply basic knowledge on the biology and ecology of a species in a determined place (Bertini et al. 2004). In tropical habitats, reproduction occurs year-round or is more intense during the warmer months, when food sources are abundant in the planktonic communities.

Calcinus gaimardii breeds continuously as evidenced by the presence of egg-bearing females. This ensures a continuous larval supply, which is essential for settlement and juvenile recruitment of the species in the study area. Higher frequencies of breeding females were recorded in summer, suggesting that the present species shows rapid embryonic development. To date, most hermit crabs studied display continuous (with or without peaks) or seasonal reproductive patterns (Imazu and Asakura 1994; Bertini and Fransozo 1999; Turra and Leite 2000). It is also known that tropical and subtropical species breed for longer periods, probably due to narrow variations observed in abiotic factors (Litulo 2004, 2005a), but there are species breeding in winter such as *Cestopagurus timidus* (Roux, 1930) (Manjón-Cabeza and Garcia-Raso 1994) and *Loxopagurus loxochelis* (Moreira, 1901) (Martinelli et al. 2002; Bertini et al. 2004). The occurrence of winter breeding species in subtropical and tropical habitats may be associated with the populations' evolutionary life

histories, although abiotic and biotic factors should also be considered when assessing the reproductive patterns of a species or population.

Knowledge of the fecundity of a species is important in order to compare its reproductive potential and, according to Sastry (1983), the number of eggs and the rate at which they are produced are characteristic of a species and have significance for its life history strategy and ecology. In hermit crabs, fecundity can vary inter- and intra-specifically and can be affected in different ways by particular conditions within each environment (Turra and Leite 2001). In the present study, the number of eggs increased with female size as previously reported in other hermit crabs (see Mantelatto et al. 2002; Macpherson and Raventos 2004). However, small variations were observed within the same size-classes. These variations can be caused by accidental egg losses, incomplete fertilization or multiple spawnings (Litulo 2004, 2005a).

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