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Breeding season of the hermit crab *Dardanus deformis* H. Milne Edwards, 1836 (Anomura, Diogenidae) in Maputo Bay, southern Mozambique

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Abstract
The breeding season of the hermit crab *Dardanus deformis* is studied based on the occurrence of ovigerous females, in relation to temperature and rainfall. Monthly samples were obtained between January and December 2003 at Costa do Sol, Maputo Bay, southern Mozambique. A total of 331 female individuals was analysed of which 164 were non-ovigerous females and 167 were ovigerous females. *Dardanus deformis* breeds continuously in the study area with peaks of spawning from August to October and a slight decrease from May to July. Both temperature and rainfall were positively correlated with percentages of ovigerous females. Multiple linear regressions suggest that rainfall is the main factor controlling the breeding activity of *D. deformis* in Maputo Bay. This species may have a rapid and high reproductive activity in the study area as observed by the higher number of ovigerous females relative to non-ovigerous females which may contribute to a constant larval supply and recruitment of this species in the study area.

Keywords: *Breeding biology,* Dardanus deformis*, hermit crabs, Maputo Bay, southern Mozambique*

Introduction

Evaluation of breeding seasons is important for a better understanding of biological processes that take place in organisms or populations. In marine invertebrates, breeding may take place year-round (continuous pattern) or can be restricted to a few months (discontinuous pattern) due to fluctuations in environmental conditions (Sastry 1983).

The decapod Crustacea comprises a large number of species which inhabit a wide variety of biotopes (Mantelatto and Sousa 2000). Consequently, this group represents a promising field of study because the establishment of these animals in such diverse habitats derives from the evolution of adaptive population strategies (Mantelatto and Sousa 2000). Hermit crabs are anomuran decapod crustaceans that have developed strategies to utilize gastropod shells and other types of shelters for their uncalcified abdomen. There are currently more than 900 species of hermit crabs worldwide, ranging from the deeper parts of the oceans to

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intertidal and supratidal habitats (updated from Hazlett 1981; Martinelli et al. 2002). Despite this diversity, the reproductive biology of these crustaceans is still poorly known, although there are many studies on different biological aspects, mostly related to behavioural characteristics such as use of gastropod shells and habitat selection (e.g. Tunberg et al. 1994; Barnes 1999; Mantelatto and Garcia 1999; Turra and Leite 2001). However, studies on the reproductive biology of hermit crabs have only been conducted for European (Carlon and Ebersole 1995; Manjón-Cabeza and Garcia-Raso 1998; Pessani et al. 2000; Macpherson and Raventos 2004) and South American species (Fransozo and Mantelatto 1998; Bertini and Fransozo 2000; Turra and Leite 2000; Garcia and Mantelatto 2001; Branco et al. 2002; Martinelli et al. 2002).

Breeding seasons of hermit crabs have in some cases been frequently described and reveal continuous to seasonal patterns (Manjón-Cabeza and Garcia-Raso 1998; Turra and Leite 2000; Martinelli et al. 2002; Turra et al. 2002; Macpherson and Raventos 2004; Litulo 2005). Reproductive activity has been shown to be influenced by morphology of the shell used by the crabs (Carlon and Ebersole 1995; Turra and Leite 1999; Mantelatto et al. 2002). Furthermore, breeding seasons may vary between populations in response to variations of environmental parameters in a given area.

In southern Africa, studies on hermit crab biology are limited (e.g. Emmerson and Alexander 1986; Walters and Griffiths 1987; Reddy and Biseswar 1993) and with particular reference to Mozambique, they are restricted to behavioural and ecological studies (Barnes 1997, 2000; Barnes and De Grave 2000; De Grave and Barnes 2001).

Dardanus deformis (H. Milne Edwards, 1836) is one of the largest and most abundant hermit crabs inhabiting East African shores. It is generally found in the eulittoral zone in sandy, rocky substrate, and also in the shallow sublittoral. It occurs from the western Indian Ocean to the western Pacific Ocean (Kalk 1995). Nothing is known about the reproductive biology of this crab.

In the present study, the breeding biology of a population of *Dardanus deformis* inhabiting a sandy area of Costa do Sol, Maputo Bay, southern Mozambique is assessed, focusing on breeding season and possible influence of temperature and rainfall, on the occurrence of ovigerous females.

Materials and methods

This study was conducted in the intertidal area of Costa do Sol, Maputo Bay, southern Mozambique (25°55′–26°10′S, 33°40′′–32°55′E). Three rivers discharge into the area: Incomáti on the north, Maputo on the southern bank, and Umbeluzi flowing through the Espirito Santo estuary (Litulo 2004). The runoff of these rivers brings large amounts of nutrients into the area. The climate in Maputo Bay is tropical with an average yearly temperature of 25°C. Average rainfall is ~1000 mm per year. The tides are semidiurnal with maximal amplitude of 3 m. Small patches of seaweed and seagrass, namely *Ulva reticulata* (Forskåll), *Enteromorpha* spp. and *Zostera capensis* (Setchell), occur in the area.

Samples were taken monthly (full moon) during 1 year, from January to December 2003, in low-tide periods. Collection was performed by two people during a period of 1 h, covering an area of 300 m^2. Almost all hermit crabs were found in small aggregations of five or more in small pools that were regularly searched during the study period. After collection, all individuals were bagged and transported immediately to the Laboratory of Ecology of the University Eduardo Mondlane where they were removed 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 ($\pm$0.05 mm accuracy) or under a dissecting microscope equipped with an ocular micrometer.

The local meteorological station (INAM—Instituto Nacional de Meteorologia) provided the monthly average values of air temperature and rainfall. The reproductive period was determined using data on frequency of ovigerous female and embryonic development over the year.

The mean size of individuals of ovigerous and non-ovigerous females was compared by the Student's *t* test (Underwood 1997). The degree of association among egg-bearing females with environmental factors was assessed using simple linear regressions (Underwood 1997). Analyses of multiple regression by selection of variables were performed for the evaluation of association between the frequency of breeding females and the set of environmental variables (Underwood 1997). The significance of the multiple linear regression models obtained was tested using ANOVA, and the regression coefficients β_0 (constant), β_1 (temperature weight), and β_2 (rainfall weight) estimated.

Results

A total of 331 crabs were collected during the study period and both non-ovigerous and ovigerous females were found in all months (Figure 1). Animal size (minimum, maximum, and mean $\pm$ SD) was 1.8, 13.5 and 4.78 $\pm$ 1.79 mm for non-ovigerous females and 2.8, 14.8 and 5.17 $\pm$ 2.40 mm for ovigerous females. Ovigerous females were on average larger than non-ovigerous females (t=3.65, P<0.001). *Dardanus deformis* breeds continuously with peaks of breeding between August and October and a decrease from May to July (Figure 1).

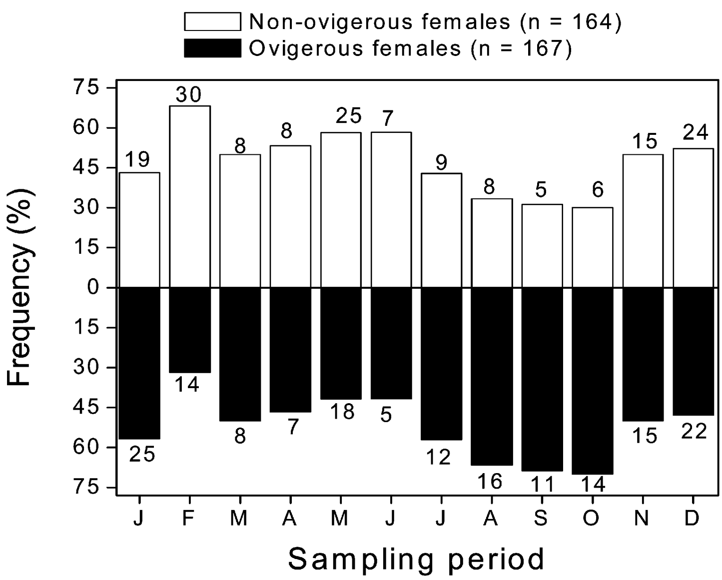

Figure 1. *Dardanus deformis* (H. Milne Edwards, 1836). Frequency of crabs collected during the study period at Costa do Sol, Maputo Bay, southern Mozambique. Values above and below columns correspond to the total number of non-ovigerous and ovigerous females sampled during the study period.

Temperature ranged from 19°C in July and reached maxima in January and September (Figure 2A). Higher peaks of rainfall were observed in January and December and decreased from May to September (Figure 2B).

The percentage of ovigerous females was positively correlated with temperature (r^2=0.949, P<0.0001) and rainfall (r^2=0.961, P<0.001) (Figure 3A, B). The analyses of variance demonstrated the validity of this observation (Table I), and the estimates of the regression coefficients are shown (Table II). From the data and analysis, it can be concluded that rainfall is the main factor controlling breeding of *Dardanus deformis* in the study area.

Discussion

Dardanus deformis breeds continuously as evidenced by the presence of ovigerous females. This ensures a constant larval supply and this may also be fundamental to understanding the recruitment of megalopae and juvenile crabs in the area.

Both temperature and rainfall were positively correlated with the relative frequency of ovigerous females. Sastry (1983) states that temperature may act as a metabolic, biochemical and hormonal modulator, triggering the processes of ecdysis, mating and

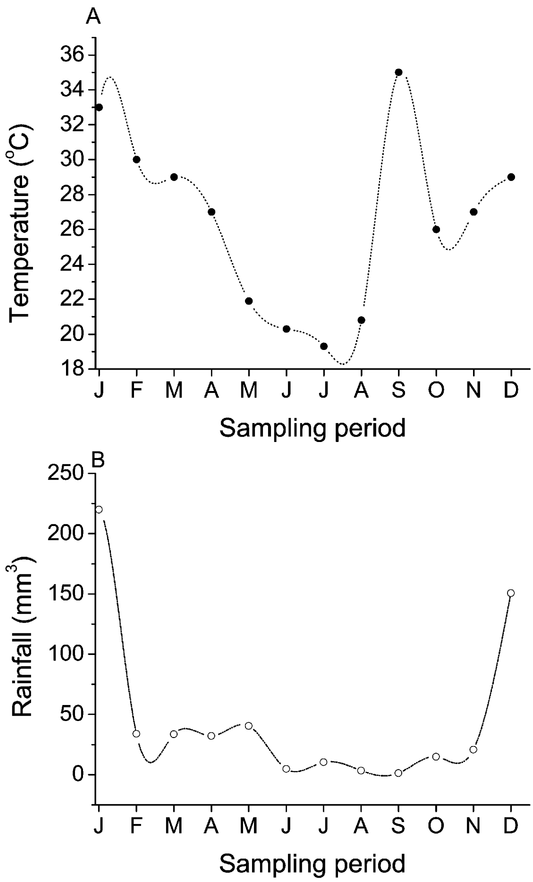

Figure 2. Monthly values of temperature (A) and rainfall (B) at Costa do Sol during the sampling period.

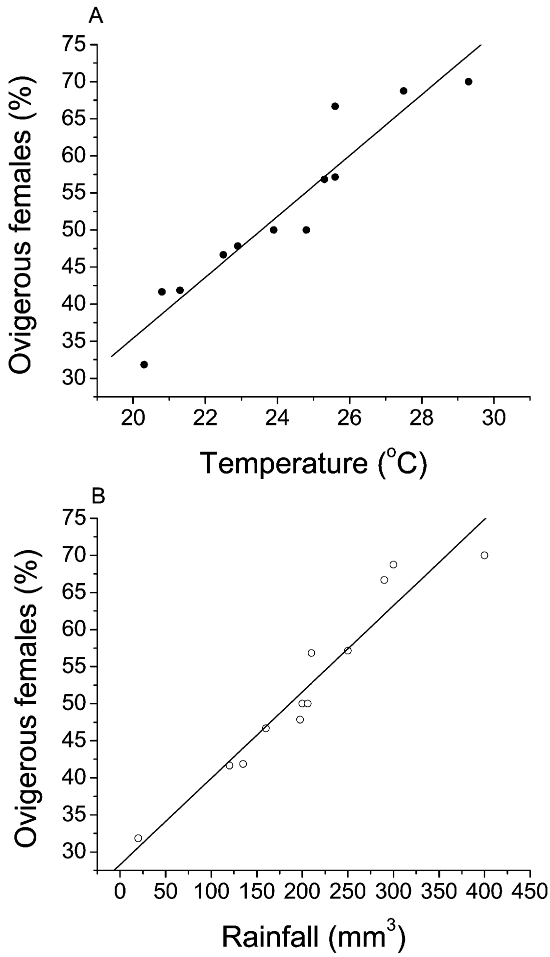

Figure 3. *Dardanus deformis* (H. Milne Edwards, 1836). Regression lines for the relationships between percentage of ovigerous females and (A) temperature ($Y=-46.71194+4.10545X$, $r^2=0.94922$, $P<0.0001$) and (B) rainfall ($Y=28.28968+0.11643X$, $r^2=0.96076$, $P<0.001$).

gonad development. At the same time, it is known that under low temperatures the speed of maturation of oocytes is low, leading to a longer period of incubation. On the other hand, rainfall may provide a selective advantage to intertidal anomuran populations since periods of higher rainfall rate can cause changes in the salinity of water and promote an increase in

Table I. *Dardanus deformis* (H. Milne Edwards, 1836): analysis of variance for the multiple linear regression $Y_j=\beta_0+\beta_1X_{1j}+\beta_2X_{2j}+\varepsilon_j$, where Y_j is percentage of ovigerous females, and the independent variables X_1 and X_2 are temperature and rainfall.

Source of variation	df	SS	MS	*F*
Model	2	1437.87223	718.93611	64.73148*
Error	9	99.95794	11.10644	
Total	11	1537.83917		

*$P<0.05$.

Table II. *Dardanus deformis* (H. Milne Edwards, 1836): regression coefficient (b_i) estimates, standard error and t values for the multiple linear regression $Y_j = \beta_0 + \beta_1 X_{1j} + \beta_2 X_{2j} + \varepsilon_j$, where Y_j is percentage of ovigerous females, and the independent variables X_1 and X_2 are temperature and rainfall, respectively.

Parameter	Estimate	SE	*t* value	*P* value
Constant	−0.98771	22.89444	−0.043314	0.96653
Rainfall	0.07438	0.03429	2.16891	0.04822
Temperature	1.57341	1.22392	1.28555	0.23069

nutrient concentration, favouring the development of planktonic larvae, and increase primary productivity of the seawater (Litulo 2004). Multiple linear models suggest that rainfall is probably the most important environmental parameter controlling breeding in this species in the study area.

Hermit crabs may display continuous (with or without peaks) or seasonal reproductive patterns (Tunberg et al. 1994; Fransozo and Mantelatto 1998; Manjón-Cabeza and Garcia-Raso 1998; Branco et al. 2002; Macpherson and Raventos 2004) regardless of the family (see review by Turra and Leite 2000).

According to Bertini and Fransozo (2002), most hermit crabs display a seasonal reproduction rather than a continuous one. However, both continuous and seasonal reproduction is also found in subtropical and tropical areas. Furthermore, tropical species breed for longer periods. This may be explained by the narrow variations observed in temperature, rainfall and nutrient input which are very important for reproduction and larval growth.

Continuous reproduction with breeding peaks is a well-known pattern present in many tropical hermit crabs. Sastry (1983) mentioned that a prolonged breeding period indicates that individuals produce several successive broods during the year or breed asynchronously. Such a reproductive pattern seems to apply to *D. deformis*, since several breeding peaks can be observed during the study period.

Turra and Leite (2000) hypothesized that 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 the populations, although local factors such as competition and shell use should also be considered when assessing the reproductive traits of a species or population.

This study constitutes the first account on the population biology and reproduction of hermit crabs in southern Africa. Further studies on gonad development, growth, larval ecology and morphology are needed to better understand the life cycle of *D. derformis* in the study area.

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