

# Population biology and fecundity of the Indo-Pacific hermit crab *Clibanarius longitarsus* (Anomura: Diogenidae)

Carlos Litulo

Departamento de Ciências Biológicas, Faculdade de Ciências, Universidade Eduardo Mondlane, Caixa Postal 257, Maputo, Mozambique. E-mail: Litos@imensis.net

The population biology and reproduction of the hermit crab *Clibanarius longitarsus* were studied with emphasis on size structure, sex ratio, breeding season and fecundity. Specimens were sampled monthly over a period of one year (January–December 2003) at Costa do Sol mangrove, Maputo Bay, southern Mozambique. A total of 597 individuals was obtained of which 202 were males, 192 non-ovigerous females and 203 ovigerous females. Annual size–frequency distributions were polymodal for males and bimodal for non-ovigerous and ovigerous females, respectively. Sexual dimorphism was recorded by the larger average size attained by males in relation to females. Sex ratio was female-biased during most months of the study. *Clibanarius longitarsus* showed a higher reproductive activity with two major peaks (March and October). Juvenile recruitment was continuous throughout the study period. Clutch size was positively associated with female size. The high number of ovigerous females as obtained in the present population may evidence a higher reproductive activity displayed by *C. longitarsus* at Costa do Sol mangrove.

## INTRODUCTION

Hermit crabs are Anomuran decapod crustaceans that have developed strategies to utilize gastropod shells and other types of cavities to shelter the uncalcified abdomen. According to Martinelli et al. (2002), there are currently more than 800 species of hermit crabs worldwide, ranging from the deeper parts of the oceans to intertidal habitats. Despite their importance, the population biology and reproductive aspects of these organisms are still poorly known, principally in tropical habitats.

There are many studies on different biological aspects of hermit crabs, mostly related to behavioural characteristics such as the use of gastropod shells and habitat selection in both field and laboratory (see reviews by Garcia & Mantelatto, 2001). Some studies on population structure of hermit crabs have been conducted in European, temperate, and South American species (Turra & Leite 2000; Garcia & Mantelatto, 2001; Branco et al., 2002; Martinelli et al., 2002; Macpherson & Raventos, 2004).

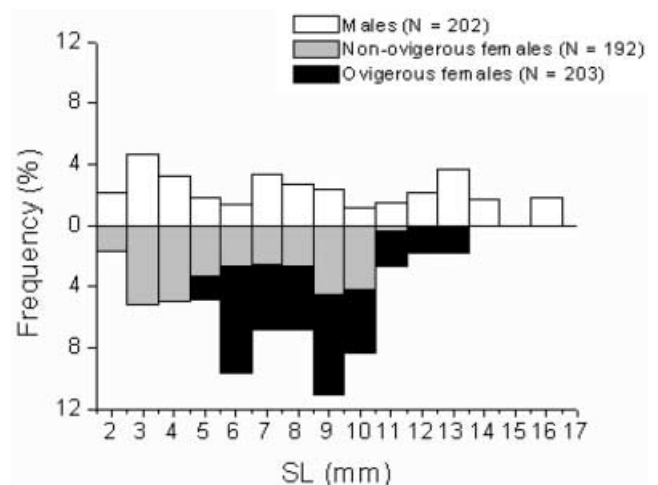
Breeding patterns of hermit crabs have been frequently described and reveal continuous to seasonal patterns (Turra & Leite, 2000). Reproductive activity has shown to be influenced by shell morphology used by the crabs (Mantelatto et al., 2002). Moreover, reproductive peaks may vary between populations in response to variation of environmental parameters of a given area.

*Clibanarius longitarsus* (De Haan, 1849) is the most abundant hermit crab in the Indo-Pacific region. It is mostly found in mud, sandy substrates or attached to mangrove roots. At present, the only research work available in East Africa on this species dealt with behaviour in natural habitats (Gherardi et al., 1990). Nothing is known about its population structure and reproduction. This information is important to understand several aspects concerning the life cycle of this crab in the region.

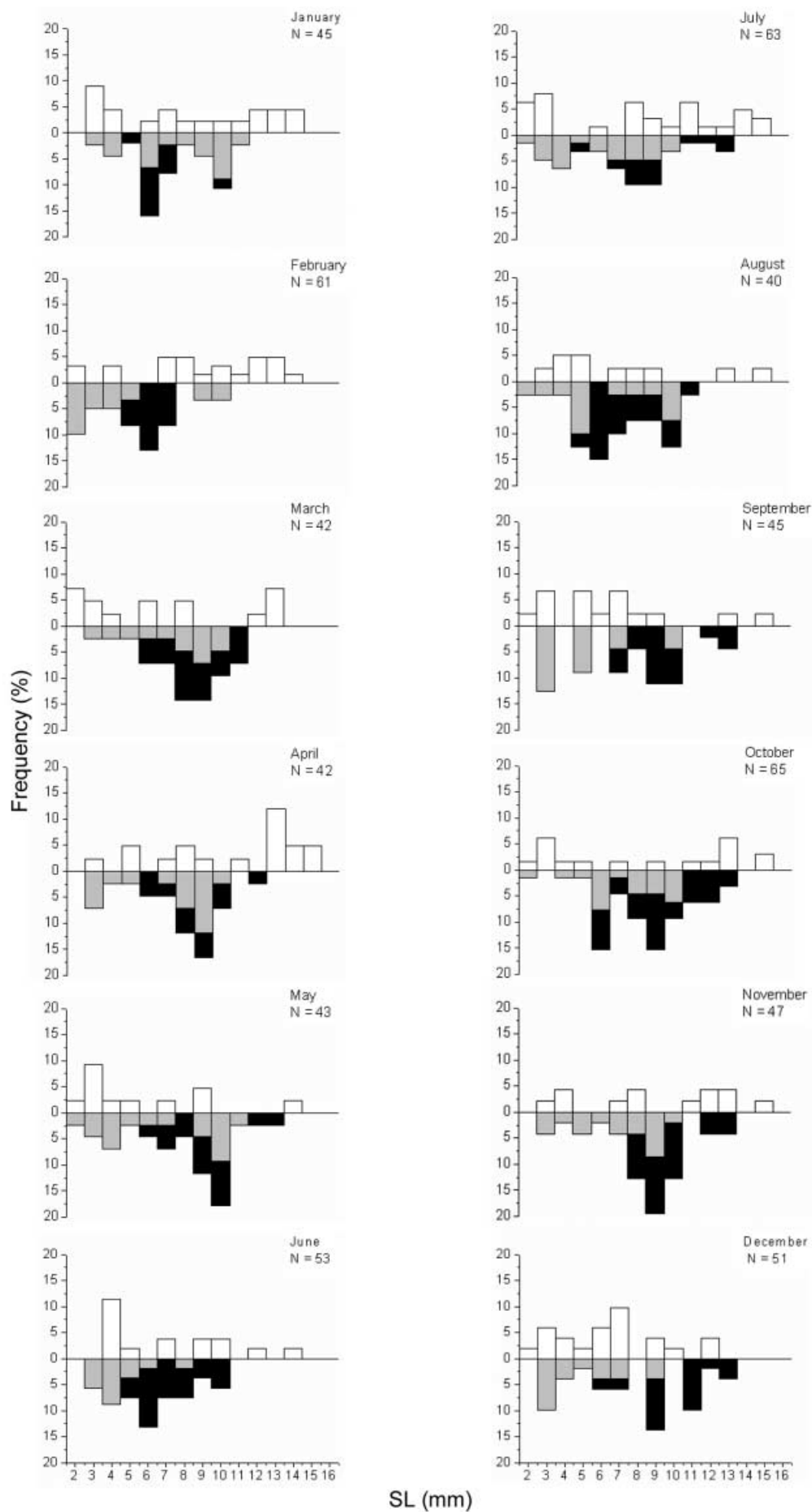
This study describes the population biology and reproduction of *C. longitarsus* at Costa do Sol mangrove, Maputo Bay, southern Mozambique, with emphasis on seasonal abundance, seasonal size–frequency distribution, sex ratio, reproductive season (based on the monthly variation of ovigerous females), juvenile recruitment and fecundity.

## MATERIALS AND METHODS

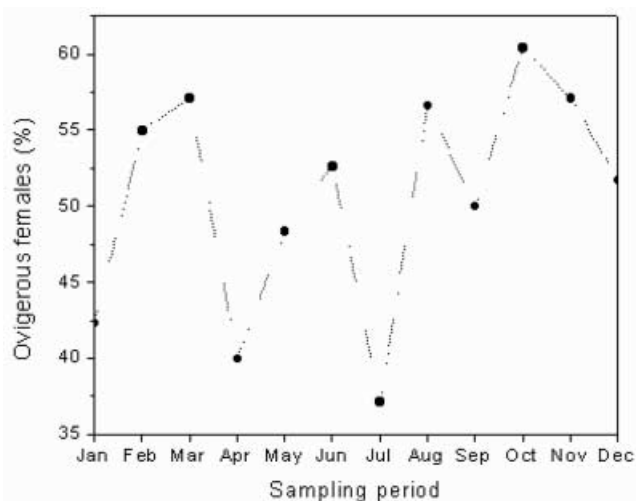
The fieldwork took place at Costa do Sol mangrove, Maputo Bay, southern Mozambique (25°51'S 26°18'S). Three rivers discharge into the area: the Incomati in the north, Maputo on the southern bank and Umbeluzi flowing through the Espirito Santo estuary. The mangrove



**Figure 1.** Overall size–frequency distributions of individuals of *Clibanarius longitarsus* sampled at Costa do Sol mangrove, Maputo Bay, southern Mozambique.



**Figure 2.** *Clibanarius longitarsus*. Monthly size–frequency distributions of crabs sampled at Costa do Sol mangrove, Maputo Bay, southern Mozambique. (White bars, males; grey bars, non-ovigerous females; black bars, ovigerous females.)



**Figure 3.** Breeding activity of *Clibanarius longitarsus* at Costa do Sol mangrove, Maputo Bay, southern Mozambique.

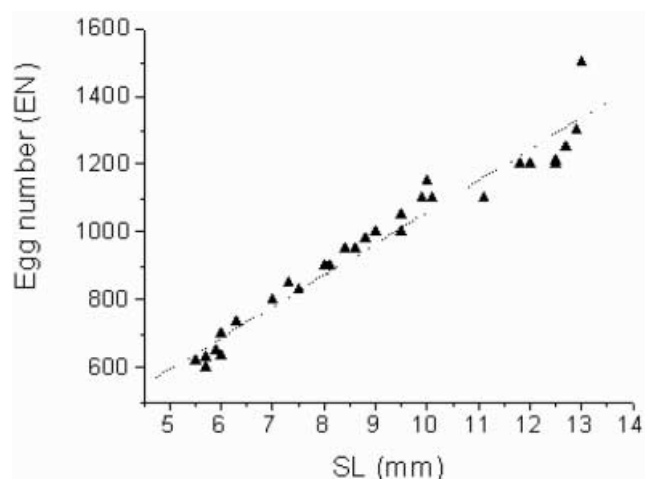
vegetation of this area is dominated by *Avicennia marina* (Forsk.) and small patches of *Rhizophora mucronata* (Lamk.) and *Ceriops tagal* (Perr.) (Litulo, 2004). The run-off of these rivers brings large amounts of nutrients into the area. The climate in Maputo Bay is tropical with an average yearly temperature of 25°C. Tides are semidiurnal with maximal tidal amplitude of 3.5 m. Average rainfall is of about 1000 mm  $y^{-1}$  (Litulo, 2004).

Collections were performed at spring low tides by one person during a period of 1 h, covering an area of 300 m<sup>2</sup>. 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 where they were removed by carefully cracking each shell. Sex was determined based on the presence of gonopores. The cephalothoracic shield length (SL=from the tip of the rostrum to the V-shaped groove at the posterior

**Table 1.** *Clibanarius longitarsus* (De Hann, 1849). Total number of individuals and sex ratios of crabs collected at Costa do Sol mangrove.

Month	Mal (N)	Nof (N)	Fov (N)	Total (N)	Sex ratio
January	19	15	11	45	1:1.4*
February	21	18	22	61	1:1.9*
March	14	12	16	42	1:2*
April	17	15	10	42	1:1.6*
May	12	16	15	43	1:2.6*
June	15	18	20	53	1:2.5*
July	28	22	13	63	1:1.3 <sup>n.s.</sup>
August	10	13	17	40	1:3*
September	15	15	15	45	1:2*
October	17	19	29	65	1:2.8*
November	12	15	20	47	1:2.9*
December	22	14	15	51	1:1.3 <sup>n.s.</sup>
Total	202	192	203	597	1:1.9*

Mal, males; Nof, non-ovigerous females; Fov, ovigerous females; N, sample size; \*, represents months with significant deviations from the expected 1:1 ratio through the  $\chi^2$ ,  $P < 0.05$ ; n.s., not significant.



**Figure 4.** *Clibanarius longitarsus*. Linear regression between egg number (EN) and female size (SL) ( $EN = 132.13995 + 92.73914SL$ ,  $r^2 = 0.97526$ ,  $P < 0.001$ ,  $N = 30$ ).

edge) was measured with the aid of Vernier callipers ( $\pm 0.05$  mm accuracy) or under a dissecting microscope equipped with an ocular micrometer.

Ten to fifteen 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; Turra & Leite, 2001).

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

To estimate fecundity, 30 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. Bare pleopods were then discarded by gently stirring in a beaker filled with 200 ml seawater. Three 1.5 ml sub-samples 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).

Specimens were grouped in 1.0 mm size-class intervals, from 1.5 to 16.5 mm.

The reproductive activity of the population was assessed as the percentage of females carrying eggs relative to the total number of females collected (Turra & Leite, 2000; Martinelli et al., 2002). The Chi-square test ( $\chi^2$ ) was used to evaluate sex ratio (M:F). Data were assessed for normality and homoscedacity through the D'Agostino and Levene tests and the mean size of individuals was compared using the non-parametric Kruskal–Wallis test followed by the non-parametric Tukey-type post-hoc test (Zar, 1999). The occurrence of juveniles (individuals of both sexes smaller than the smallest ovigerous female) characterized the recruitment in the population (Garcia & Mantelatto, 2001; Martinelli et al., 2002).

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 597 individuals was obtained of which 202 were males (34.0%), 192 non-ovigerous females (32.0%) and 203 ovigerous females (34.0%). Animal size (minimum, maximum, and mean SL  $\pm$  SD) was 1.5, 15.0 mm and 8.13  $\pm$  2.15 mm for males; 1.8, 11.0 mm and 5.77  $\pm$  2.65 mm for non-ovigerous females; 5.0, 13.0 mm and 7.62  $\pm$  4.10 mm for ovigerous females. The categories of this population of *Clibanarius longitarsus* differed in size ( $H=53.8436$ ,  $df=2$ ,  $P<0.0001$ ). Males were on average larger than ovigerous females (Tukey test,  $P<0.0001$ ), which were in turn larger than non-ovigerous females (Tukey test,  $P<0.0001$ ).

Figure 1 shows the size–frequency distributions for all hermit crabs sampled during the study period. There was a polymodal size distribution with non-normal distribution for males (DAgostino test,  $K^2=0.28703$ ,  $P<0.01$ ), non-ovigerous females ( $K^2=0.2866$ ,  $P<0.01$ ) and ovigerous females ( $K^2=0.28416$ ,  $P<0.01$ ) and departed significantly from homoscedacity for males, non-ovigerous females and ovigerous females (Levene test,  $P<0.005$ ) The size–frequency histograms show a prevalence of individuals measuring 2.5 to 11.5 mm. Modal size ranged from 2.5 to 3.5, 6.5 to 7.5 and 12.5 to 13.5 mm for males. The modal size range of non-ovigerous females was 2.5 to 3.5 mm and 8.5 to 9.5 mm whereas ovigerous females ranged from 5.5 to 6.5 mm and 8.5 to 9.5 mm, respectively.

Monthly size–frequency distributions of males, non-ovigerous females and ovigerous females collected during the study period are shown in Figure 2. Males often displayed bi- and polymodal distributions. Fairly unimodal distributions were observed in June, November and December. Non-ovigerous and ovigerous females tended to display unimodal distributions often skewed to the right.

*Clibanarius longitarsus* breeds continuously with high incidence of ovigerous females in March (57.5%) and October (60.6%) and a clear decrease of ovigerous females in April (40.0%) and July (37.1%) (Figure 3).

The number of eggs ranged from 618 (SL=5.5 mm) to 1500 (SL=13.0 mm), with an average of 957  $\pm$  241 eggs. There was a strong relationship between egg number (EN) and shield length (SL) ( $N=30$ ,  $r^2=0.97526$ ,  $P<0.0001$ ) (Figure 4).

## DISCUSSION

The overall size–frequency distribution of both sexes was bi- and polymodal with males reaching larger sizes than both ovigerous and non-ovigerous females. This condition has been reported in other tropical hermit crabs: *Clibanarius antillensis*, *C. scolopetarius*, *C. vittatus* (Turra & Leite, 2000), *Dardanus insignis* (Branco et al., 2002) and *Loxopagurus loxochelis* (Martinelli et al., 2002). Bi- and polymodality of size–frequency distributions generally characterizes recruitment pulses, different mortality rates between sexes or behavioural differences.

The lack of larger individuals in the present population of *Clibanarius longitarsus* is also evidenced by its skewed

monthly size–frequency distributions. Branco et al. (2002) and Turra et al. (2002) reported the same phenomenon while studying a population of *Dardanus insignis* and *Petrochirus diogenes*. Right-skewed distributions may evidence high mortality rates of a certain population (Zar, 1999). Branco et al. (2002) suggest that lack of larger individuals in a population may be caused by lack of shells in nature or may be under heavier shell limitation. It is possible that this situation may be taking place in the present population.

Sexual dimorphism in the present population of *C. longitarsus* was recorded by the larger average size attained by males in relation to females as previously observed in other hermit crabs (Garcia & Mantelatto, 2001; Macpherson & Raventos, 2004). Three factors interfere with sexual dimorphism of hermit crabs: (1) the difference in energy available for growth, with males growing more because they do not expend in egg production, but use their energy for structural metabolism; (2) the larger reproductive effort exhibited by males may be due to their ability to copulate more than one female; and (3) males of larger dimensions have greater chances in obtaining females for fertilization and to win intraspecific fights (Abrams, 1988). Additionally, smaller growth rates of females would be a consequence of utilization of relatively small shells in nature.

The overall and monthly sex ratios differed from 1:1 with females appearing in larger numbers in relation to males. This is a frequent phenomenon in hermit crabs. Several causes are responsible for this discrepancy and, the most addressed are differences between sexes in longevity and time for growth, differential migration, mortality, sex reversal (Wenner, 1972) and differential production of gametes. Alternatively, female-biased sex ratios as observed in the present study, may be intrinsic, resulting from a greater production of female offspring in the study area.

In hermit crabs, females often tend to be more abundant than males (Wada et al., 1995). Turra & Leite (2000) state that this may be explained by higher mortality rates 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. It is possible that individuals of *Clibanarius longitarsus* may move long distances searching for larger shells. These migratory movements may be reinforced by the marked differences observed in the size–frequency distributions as well as monthly abundance (see Table 1).

Few juveniles were obtained in the present study similar to Garcia & Mantelatto (2001) and Macpherson & Raventos (2004). The present results may lead us to suggest that recruitment occurs in the same habitat as that occupied by adults, contrasting with the results found by Garcia & Mantelatto (2001) who found juveniles of *Paguristes erythropus* on sea grass beds. According to Litulo (2004), the run-off of the three rivers that discharge in Maputo Bay brings large amounts of nutrients that are very important for larval development, thus contributing to the recruitment of decapod crustaceans in the study area.

Ovigerous females of *C. longitarsus* were found year-round in the study area. A similar pattern was

reported by Turra & Leite (2000), Bertini & Fransozo (2002) and Macpherson & Raventos (2004). This ensures constant larval supply, which may be important for the determination of some population characteristics (e.g. unimodal size distribution and juvenile recruitment), which are important tools to stabilize the population.

The high reproductive activity of *Clibanarius longitarsus* in the study area was evidenced by the large number of ovigerous females recorded in relation to the non-ovigerous females. Also, based on the smallest ovigerous females recorded in the present study (SL=5.0 mm) compared with that obtained by Gherardi et al. (1989) in Kenyan mangroves (SL=9.6 mm), it is possible to state that the sexual maturity occurs in small-sized individuals in the life cycle of this crab in Maputo Bay. Fecundity (number of eggs per egg clutch) increased in proportion with female shield length. This was to be expected: the egg number of most hermit crabs increases in parallel with female size (Turra & Leite, 2001; Mantelatto et al., 2002; Macpherson & Raventos, 2004). However, 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 fertilization or multiple spawnings.

Thanks go to the Laboratory of Ecology of the University Eduardo Mondlane for logistic support. Thanks are extended to Drs Rafael Lemaitre and Richard G. Hartnoll for useful comments on an earlier draft of the manuscript. The comments of two anonymous referees helped to improve an earlier version of this manuscript.

## REFERENCES

- Abrams, P.A., 1988. Sexual difference in resource use in hermit crabs: consequences and causes. In *Behavioural adaptation to intertidal life* (ed. G. Chelazzi and M. Vannini), pp. 283–296. New York: Plenum, Inc.
- Bertini, G. & Fransozo, A., 2002. Breeding season of the hermit crab *Petrochirus diogenes* (Anomura: Diogenidae) in the north coast of São Paulo State, Brazil. In *Modern approaches to the study of Crustacea* (ed. E. Escobar-Briones and F. Alvarez), pp. 145–150. The Netherlands: Kluwer Academic Publishers.
- Branco, J.O., Turra, A. & Souto, F.X., 2002. Population biology and growth of *Dardanus insignis* at Armação do Itapocoroy, southern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, **82**, 597–563.
- Garcia, R.B. & Mantelatto, F.L.M., 2001. Population dynamics of the hermit crab *Paguristes erythroptus* (Diogenidae) from Anchieta Island, southern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, **81**, 955–960.
- Gherardi, F., Micheli, F. & Vannini, M., 1990. Movement patterns and dispersal of the hermit crab *Clibanarius longitarsus* in a mangrove swamp. *Marine Behaviour and Physiology*, **16**, 209–223.
- Gherardi, F. & Vannini, M., 1989. Field observations on activity and clustering in two intertidal hermit crabs, *Clibanarius virens* and *Calcinus laevimanus* (Decapoda, Anomura). *Marine Behaviour and Physiology*, **14**, 145–159.
- Litulo, C., 2004. Breeding patterns of a tropical population of the fiddler crab *Uca inversa* (Hoffman, 1874) (Decapoda, Brachyura, Ocypodidae). *Crustaceana*, **77**, 1045–1054.
- Macpherson, E. & Raventos, N., 2004. Population structure and reproduction of three sympatric hermit crabs in the north-western Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*, **84**, 371–376.
- Mantelatto, F.L.M., Alarcon, V.F. & Garcia, R.B., 2002. Egg production strategies of the tropical hermit crab *Paguristes tortugae* from Brazil. *Journal of Crustacean Biology*, **22**, 390–397.
- Martinelli, J.M., Mantelatto, F.L.M. & Fransozo, A., 2002. Population structure and breeding season of the South Atlantic hermit crab *Loxopagurus loxochelis* (Anomura, Diogenidae) from the Ubatuba region, Brazil. *Crustaceana*, **75**, 791–802.
- Ramirez Llodra, E., 2002. Fecundity and life-history strategies in marine invertebrates. *Advances in Marine Biology*, **43**, 87–170.
- Sastry, A.N., 1983. Ecological aspects of reproduction. In *The biology of Crustacea*. Vol. 8. *Ecological aspects of reproduction* (ed. F.B. Vernberg and W.B. Vernberg), pp. 179–270. New York: Academic Press.
- Turra, A., Branco, J.O. & Souto, F.X., 2002. Population biology of the hermit crab *Petrochirus diogenes* (Linnaeus) (Crustacea, Decapoda) in southern Brazil. *Revista Brasileira de Zoologia*, **19**, 1043–1051.
- Turra, A. & Leite, F.P.P., 2000. Population biology and growth of three sympatric species of intertidal hermit crabs in southeastern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, **80**, 1061–1069.
- Turra, A. & Leite, F.P.P., 2001. Fecundity of three sympatric populations of hermit crabs (Decapoda, Anomura, Diogenidae). *Crustaceana*, **74**, 1019–1027.
- Wada, S., Goshima, S. & Nakao, S., 1995. Reproductive biology of the hermit crab *Pagurus niddendorffi* Brandt (Decapoda, Anomura, Paguridae). *Crustacean Research*, **24**, 12–32.
- Wenner, A.M., 1972. Sex ratio as a function of size in marine Crustacea. *American Naturalist*, **106**, 321–350.
- Zar, J.H., 1999. *Biostatistical analysis*. New Jersey: Prentice Hall.

Submitted 11 August 2004. Accepted 6 January 2005.