

# Population biology and growth of the hermit crab *Dardanus insignis* at Armação do Itapocoroy, southern Brazil

Joaquim Olinto Branco\*, Alexander Turra<sup>††</sup> and Flávio Xavier Souto\*

\*Centro de Ciências Tecnológicas da Terra e do Mar/CTTMar/UNIVALI, Caixa Postal 360, 88301-970, Itajaí, Santa Catarina, Brazil.

<sup>†</sup>Departamento de Zoologia, PG-Ecologia, IB, Unicamp, Campinas, SP, Brazil 13080-970.

<sup>‡</sup>Corresponding author, e-mail: turra@unicamp.br

This study was conducted between January and December 1995 at Armação do Itapocoroy, Penha, Santa Catarina, southern Brazil. Monthly samples were carried out in the morning, afternoon, and evening using two over-trawls with 6 m at the opening, 3.0-cm mesh at the outer part and 2.0-cm mesh in the bag. *Dardanus insignis* was collected year round but with higher densities in September and October. The hermit crabs were more abundant during the evening than the afternoon but no differences were recorded between morning and both evening and afternoon. Females were slightly more abundant than males but the sex ratio did not differ from 1:1. Females were more abundant in the smallest size-classes (<1.8 cm) while males outnumbered females in the largest ones (>2.2 cm). The individuals of this population of *D. insignis* have a mean cephalothoracic length of  $1.89 \pm 0.40$  cm (range 1.00 to 3.90 cm) and a mean weight of  $40.26 \pm 27.06$  g. The size distribution showed an unimodal pattern, with males being larger than ovigerous females, which, in turn, were larger than non-ovigerous females. *Dardanus insignis* showed a seasonal reproductive pattern with a peak from September to November and complete absence of ovigerous females from April to August. The von Bertalanffy growth function (VBGF) with temporal oscillation fitted for this population of *D. insignis* had the following parameters:  $L_{\infty}=4.40$  cm,  $K=0.60$ ,  $C=0.95$ ,  $WP=0.35$ . Recruitment was estimated to start in September and was extended to the following months. Estimates of longevity ranged from 20 to 62 months. A mortality rate of 2.21 was estimated based on the length converted catch curve. The cephalothoracic length of males and females showed, respectively, positive and negative allometry with both cephalothoracic width and crab weight.

## INTRODUCTION

The studies on populations generally present descriptions of density, size distribution, dispersion patterns, sex ratio and reproductive 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, at least partially, the environmental and/or biological constraints that are shaping the structure of these populations, i.e. the selective forces that are selecting particular populational traits. Moreover, the study of dominant populations may be very important to elucidate the structure and function of communities.

Hermit crabs are a very abundant group in macroinvertebrate assemblages in intertidal and subtidal areas (Wenner & Read, 1982; Branco et al., 1998; Martinez-Iglesias & García-Raso, 1999; Fernandes-Góes, 2000). They are an interesting group of crustaceans that depend almost exclusively on gastropod shells resources to shelter their soft abdomen. The hermit crabs have elaborated shell fighting and mating behaviours (Hazlett, 1966a,b) and may present short or long-range daily movements (Hazlett, 1981) and even seasonal migrations (Fotheringham, 1975; Rebach, 1978, 1981; Asakura & Kikuchi, 1984; Asakura, 1987). Seasonality is also recorded for the reproductive period of hermit crabs both in temperate and tropical areas (Turra & Leite, 2000). Although a large number of studies on population biology have been conducted recently

(see Turra & Leite, 2000 for a review), the evaluation of population growth was undertaken only for the temperate hermit crabs *Cestopagurus timidus* (Roux, 1830) (Manjón-Cabeza & García-Raso, 1994) and *Diogenes pugilator* (Roux, 1829) (Manjón-Cabeza & García-Raso, 1998) and for the tropical hermit crabs *Clibanarius antillensis* (Stimpson, 1859), *Clibanarius scolopetarius* (Herbst, 1796) and *Clibanarius vittatus* (Bosc, 1802) (Turra & Leite, 2000).

*Dardanus insignis* (Saussure, 1858) is an occidental Atlantic oceanic hermit crab occurring in eastern United States, Gulf of Mexico, Antilles, Brazil (from Rio de Janeiro to Rio Grande do Sul), Uruguay and Argentina in different substrate types from depths of 1.5 to 500 m (Rieger, 1997). According to Hazlett (1966b), this species also occupies worm tubes and had a behavioural repertoire very similar to *Petrochirus diogenes* (Linnaeus, 1758), another oceanic hermit crab species. The complete description of the larval development of this species enabled its clear distinction from *Dardanus arrosor* (Herbst, 1796) (Hebling & Mansur, 1995), a hermit crab species common to north and north-eastern Brazilian waters (Rieger, 1997). More recently, the biology of a tropical population of *D. insignis* was studied by Fernandes-Góes (1997, 2000) in the Ubatuba region, south-eastern Brazil.

The aim of this study was to describe the population structure of the subtidal hermit crab *D. insignis* at the Armação do Itapocoroy, a subtropical area in southern Brazil. In this way, we describe the seasonal and daily variation in abundance of the studied population as well

as its size structure, sex ratio, relative growth and reproductive period. The monthly data on the population size structure were used to estimate population growth using the von Bertalanffy growth function (VBGF).

## MATERIALS AND METHODS

This study was conducted between January and December 1995 at Armação do Itapocoroy, Penha (26°46'S 48°36'W and 26°47'S 48°37'W), southern Brazil. The bottom of this area is composed of sand in the shallowest parts and by biotrititic sediment in the deepest ones. Monthly samples were collected in three periods (morning, afternoon, and evening) using two over-trawls with 6 m at the opening, 3-cm mesh at the outer part and 2-cm mesh in the bag. The sediment was trawled from depths of 6 to 10 m during 30 min at a constant speed of 2 knots. The abundance of individuals was compared among periods of the day using a paired *t*-test and considering months as temporal replicates. Three samples of water temperature were recorded in each sampling month (one for each sampling period of the day).

The individuals of *Dardanus insignis* were removed from their shells and then measured (cephalothoracic length and width, cm) and weighed (g). The shells were also weighed (g). The sex of the crabs as well as the presence of eggs in female pleopods was recorded. The population sex ratio was compared to 1:1 with the log-likelihood *G*-test (Zar, 1996). The size and weight of males and females and of ovigerous and non-ovigerous females were compared through the Student *t*-test (Zar, 1996). The exponential regression model ( $y = a \cdot x^b$ ) was fitted for the relationships between the cephalothoracic length and width and between the cephalothoracic length and the weight of all individuals, of males and females and of ovigerous and non-ovigerous females. A Student *t*-test was used to test the null hypothesis of isometry ( $b=1$ ) in these models. All tests were conducted with the significant level fixed at 0.05. Mean  $\pm$  standard error is presented through the text.

The estimates of the parameters of the VBGF were based on the size–frequency distribution over time using the software FISAT (Gayanilo & Pauly, 1997). A growth function with temporal oscillation suggested by Gayanilo & Pauly (1997) was used:

$$L_t = L_\infty [1 - e^{-K(t-t_0) - CK/2\pi [\sin 2\pi(t-WP+0.5) - \sin 2\pi(t_0-WP+0.5)]}] \quad (1)$$

where  $L_t$  is the length at a given time  $t$ ,  $L_\infty$  the asymptotic length (mm),  $K$  the growth constant or curvature parameter (rate at which  $L_\infty$  is approached),  $t_0$  the starting sample through which the growth curve passes,  $C$  the amplitude of seasonal growth (0, minimum; 1, maximum) and  $WP$  (winter point) the proportion of the year when growth rate is slowest. The goodness-of-fit of the VBGF was accessed by the calculation of  $R_n$  (0, minimum; 1, maximum) of the ELEFAN I routine (Gayanilo & Pauly, 1997). Two estimates of longevity considered the time necessary to a given individual to reach a given size-class under which 95 and 99% of the individuals were represented. This calculation was based on the equation above. A third longevity estimate was made through the length

converted catch curve, as proposed by Gayanilo & Pauly (1997), based on the parameters of the VBGF. A fourth way to estimate longevity was based on the direct observation of the oldest cohort in the fitted VBGF. The total mortality rate ( $Z$ ) was estimated using linear regression analysis obtained in the length converted catch curve in the software FISAT (Gayanilo & Pauly, 1997). The index of Munro & Pauly (1983) modified by Sparre (1987) ( $\phi' = \text{Ln}K + 2\text{Ln}L_\infty$ ) was calculated to draw interspecific comparisons.

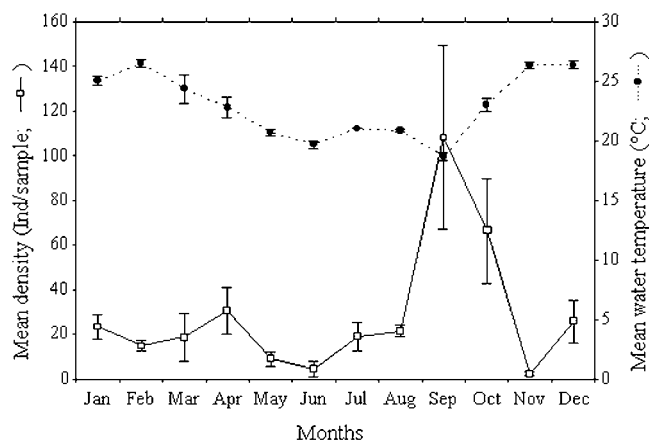
## RESULTS

### Temporal distribution

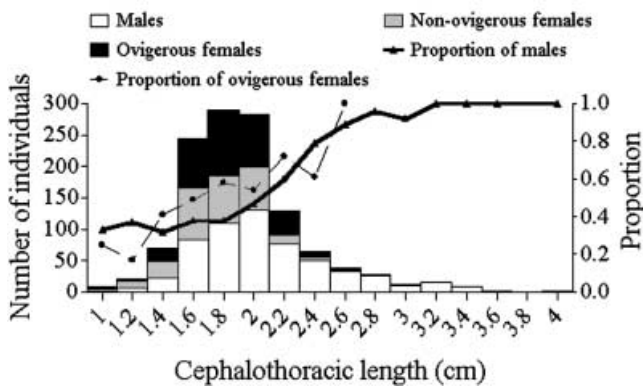
The crabs were collected year round but with higher densities in September and October (Figure 1). The temperature varied from 18.7°C to 26.5°C during the sampling period and the highest temperatures (25.0–26.5°C) were recorded in January, February, November and December (Figure 1). The temperature decreased throughout winter reaching the minimum value in September. The hermit crabs were more abundant during the evening (45.92  $\pm$  10.44 ind) than the afternoon (19.00  $\pm$  5.11 ind) (Paired *t*-test,  $t = -3.763$ ,  $df = 11$ ,  $P = 0.009$ ). No differences in abundance were recorded between the morning (34.92  $\pm$  13.97 ind) and both evening and afternoon (Paired *t*-test,  $t = -1.087$ ,  $df = 11$ ,  $P = 0.901$ ;  $t = 1.193$ ,  $df = 11$ ,  $P = 0.774$ , respectively).

### Sex ratio

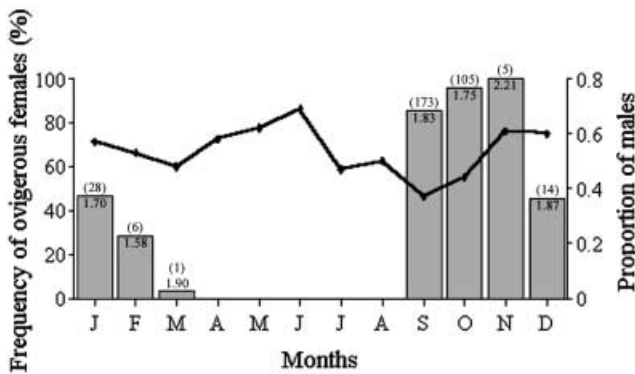
Females (617 ind) were slightly more abundant than males (579 ind) but the sex ratio was not different from 1:1 ( $G = 1.21$ ,  $df = 1$ ,  $P = \text{n.s.}$ ). The size of the hermit crabs had an influence on the sex ratio (Figure 2). Females were more abundant in the smallest size-classes (<1.8 cm) while males outnumbered females in the largest ones (>2.2 cm). Males and females were equally abundant at the 2.0 cm size-class. Sex ratio, indicated here by the proportion of males in the population, varied among the sampling months from 0.37 to 0.69 but did not show any clear seasonal pattern (Figure 3).



**Figure 1.** Annual variation in the mean density (individuals/sample  $\pm$  SE) of *Dardanus insignis* and in the mean water temperature (°C,  $\pm$  SE) at the Armação do Itapocoroy, southern Brazil.



**Figure 2.** Size–frequency distribution of the cephalothoracic length (mm) of males and ovigerous and non-ovigerous females of *Dardanus insignis* at the Armação do Itapocoroy, southern Brazil. The proportion of males in relation to all individuals and the proportion of ovigerous females in relation to all females are also shown through the size-classes.



**Figure 3.** Reproductive activity of *Dardanus insignis* indicated by the frequency of ovigerous females (bars) through the year at the Armação do Itapocoroy, southern Brazil. The proportion of males through the year (solid line) and the absolute number (in parentheses) and mean size of the ovigerous females are also shown.

*Size structure and reproductive period*

The individuals of this population of *Dardanus insignis* had a mean size of  $1.89 \pm 0.40$  cm (range 1.00–3.90 cm) and a mean weight of  $40.26 \pm 27.06$  g. The size distribution showed an unimodal pattern slightly skewed to the right (Figure 2), with males being larger (length and width) and heavier than females (Table 1). Ovigerous females were slightly larger than non-ovigerous females, but showed similar widths. The ovigerous females were also heavier than non-ovigerous females (Table 1). In fact, the proportion of ovigerous females increased with female size (Figure 2). The smallest ovigerous female was 1.00 cm long. *Dardanus insignis* showed a seasonal reproductive pattern with a peak from September to November and complete absence of ovigerous females from April to August (Figure 3).

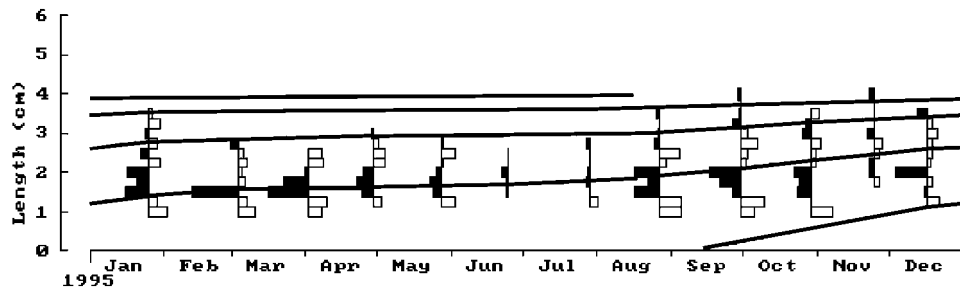
*Growth and mortality*

The VBGF fitted for this population of *D. insignis* (Figure 4) showed an adjust ( $R_n$ ) of 0.365. It was estimated an asymptotic length ( $L_\infty$ ) of 4.40 cm, a growth constant ( $K$ ) of 0.60 and a temporal oscillation with 0.95 of amplitude. The winter point was 0.35 indicating that the growth was slowest between April and May. Recruitment was estimated to start in September and was extended to the following months (Figure 4). Four estimates of longevity were done: 47 months by direct inspection of Figure 4; 62 months through the length converted catch curve; 32 months considering the time to a given individual to reach the size-class under which 99% of the individuals were represented; 20 months considering the time to a given individual to reach the size-class under which 95% of the individuals were represented. A mortality rate of 2.21 was estimated based on the length converted catch curve (Figure 5). The value of the index of Munro & Pauly was  $\phi' = 5.56$ .

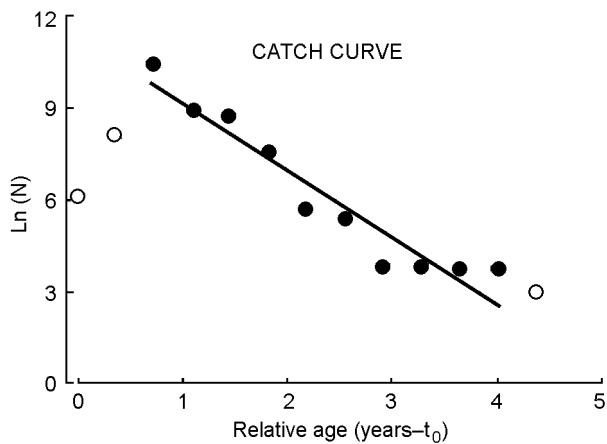
**Table 1.** Comparison of the cephalothoracic length (cm), cephalothoracic width (cm) and crab weight (g) of *Dardanus insignis* between males and females and between ovigerous and non-ovigerous females through Student t-test ( $t$ ). The number of observations in each reproductive class is shown in parentheses.

Parameter	Males (578)		Females (617)	
	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$t$	$P$
Cephalothoracic length (cm)	$2.03 \pm 0.02$	$1.76 \pm 0.01$	-12.706	<0.001
Cephalothoracic width (cm)	$1.30 \pm 0.02$	$1.04 \pm 0.01$	-14.533	<0.001
Crab weight (g)	$10.62 \pm 0.35$	$6.67 \pm 0.10$	-11.208	<0.001
Parameter	Non-ovigerous females (284)		Ovigerous females (333)	
	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$t$	$P$
Cephalothoracic length (cm)	$1.71 \pm 0.02$	$1.80 \pm 0.01$	-3.953	<0.001
Cephalothoracic width (cm)	$1.03 \pm 0.01$	$1.06 \pm 0.01$	-1.726	0.086
Crab weight (g)	$5.75 \pm 0.15$	$7.47 \pm 0.12$	-8.986	<0.001

$\bar{X}$ , mean; SE, standard error.



**Figure 4.** Size–frequency histograms for *Dardanus insignis* over the studied period and the fitted von Bertalanffy growth function (VBGF).

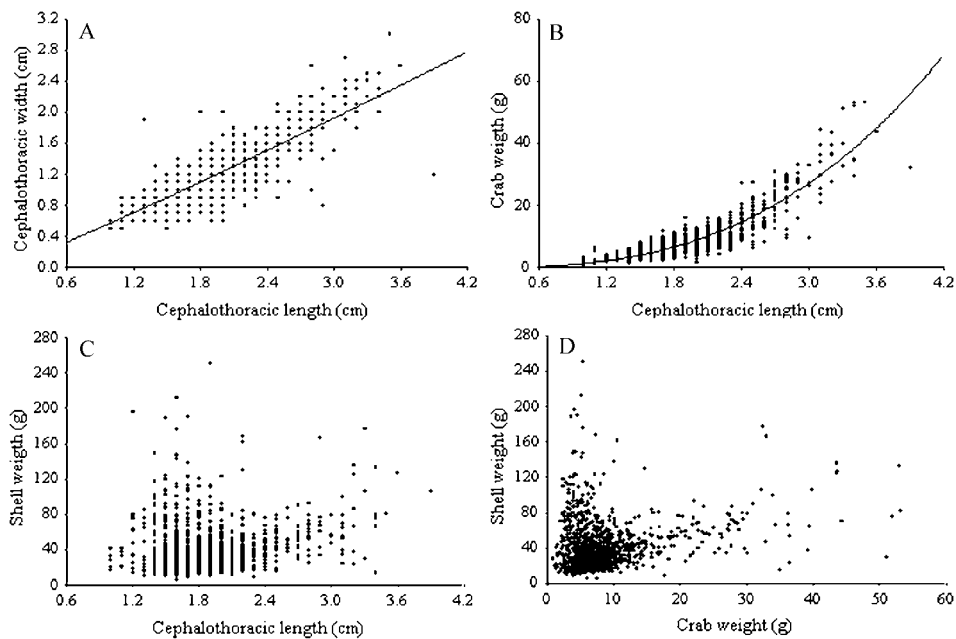


**Figure 5.** Length converted catch curve for *Dardanus insignis* based on the parameters of the von Bertalanffy growth function (VBGF). Estimated value of mortality ( $Z=2.21$ ) is equivalent to the module of the regression coefficient ( $b$ ) of the estimated curve.  $N$ , number of individuals;  $t_0$ , time (age) when size is minimum.

#### Relative growth and relationship with shell weight

The cephalothoracic length presented positive allometric relationships with both cephalothoracic width and crab weight (Student  $t$ -test for allometry:  $t=4.60$ ,  $df=1196$ ,  $P<0.001$ ;  $t=53.09$ ,  $df=1196$ ,  $P<0.001$ , respectively) (Figure 6). Positive allometry between cephalothoracic length and width was recorded only for the males while females showed a negative allometric relationship (Table 2). Both ovigerous and non-ovigerous females presented such negative allometry, but it was stronger for ovigerous females (Student  $t$ -test for regression coefficients:  $t=6.16$ ,  $df=612$ ,  $P<0.001$ ). Positive allometry was also recorded for the relationship between cephalothoracic length and crab weight for males and females and for ovigerous and non-ovigerous females (Table 2), but the allometry in ovigerous females was weaker than for non-ovigerous females (Student  $t$ -test for regression coefficients:  $t=8.83$ ,  $df=612$ ,  $P<0.001$ ).

It was not possible to fit any model for the relationship between crab size and shell weight and between crab weight and shell weight (Figure 6). The data are scattered



**Figure 6.** Relative growth of *Dardanus insignis* showing the relationships between cephalothoracic length and width (A;  $y=0.580 \times 1.092^x$ ,  $N=1197$ ,  $r^2=0.977$ ,  $P<0.001$ ) and between cephalothoracic length and crab weight (B;  $y=1.323 \times 2.752^x$ ,  $N=1197$ ,  $r^2=0.931$ ,  $P<0.001$ ). The scatter plots (lower graphs) also show the relationship between cephalothoracic length and shell weight (C) and between crab and shell weights (D).

**Table 2.** Non-linear regression model ( $y=ax^b$ ) fitted for the relationship between cephalothoracic length and width and between cephalothoracic length and crab weight for males and females and for ovigerous and non-ovigerous females of *Dardanus insignis*. The Student *t*-test compared the values of *b* with unit to test for positive or negative allometry.

Reproductive class	N	$r^2$	<i>P</i>	Equation	Student <i>t</i> -test (allometry)
Cephalothoracic length×width					
Males	579	0.724	<0.001	$y=0.597 \times 1.088$	3.26*
Females (all)	616	0.410	<0.001	$y=0.661 \times 0.814$	-4.65***
Ovigerous females	332	0.365	<0.001	$y=0.666 \times 0.791$	-3.54***
Non-ovigerous females	284	0.457	<0.001	$y=0.653 \times 0.848$	-2.66*
Cephalothoracic length×crab weight					
Males	579	0.842	<0.001	$y=1.269 \times 2.841$	37.79***
Females (all)	616	0.478	<0.001	$y=2.547 \times 1.689$	9.57***
Ovigerous females	332	0.354	<0.001	$y=3.610 \times 1.237$	2.49*
Non-ovigerous females	284	0.622	<0.001	$y=1.793 \times 2.116$	12.00***

\*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ .

**Table 3.** Parameters of the von Bertalanffy growth curves fitted for hermit crab populations using data on size–frequency distribution over time.

Species	$L_\infty$ (mm)	K	C	WP	Rn	Life span (months)*	$\Phi'$	Study
<i>Dardanus insignis</i> **	20.75	0.60	0.95	0.35	0.365	47	5.56	Present study
<i>Clibanarius antillensis</i>	7.39	0.60	1.0	0.9	0.228	48	3.49	Turra & Leite (2000)
<i>C. sclopetarius</i>	12.70	0.65	0.9	0.78	0.208	47	4.65	Turra & Leite (2000)
<i>C. vittatus</i>	10.67	0.96	1.0	0.7	0.232	42	4.69	Turra & Leite (2000)
<i>Cestopagurus timidus</i>	3.25	0.041	0	0	n.a.	21	-0.84	Manjón-Cabeza & García-Raso (1994)
<i>Diogenes pugilator</i> ***	4.70–5.08	0.14–0.27	0	0	n.a.	24–7	1.15–1.53	Manjón-Cabeza & García-Raso (1998)

$L_\infty$ , asymptotic length (mm); K, growth curvature parameter; C, amplitude of seasonal growth (0, minimum; 1, maximum); WP (winter point), the proportion of the year when growth rate is slowest; Rn, goodness-of-fit index (0, minimum; 1, maximum) of the ELEFAN I routine (Gayaniilo & Pauly, 1997);  $\Phi' = \ln K + 2 \ln L_\infty$ , index of Munro & Pauly (1983) after Sparre (1987).

\*, estimated from inspection of the fitted von Bertalanffy growth function; \*\*,  $L_\infty$  in mm as converted from 4.40 cm based on data in Fernandes-Góes (1997); \*\*\*, pooled data for males and females from two consecutive years; n.a., not available.

in two directions, i.e. the heaviest shells were occupied almost exclusively by small size or light crabs while the largest crabs used frequently shells with low or intermediate weight.

## DISCUSSION

Hermit crabs may undergo along-shore daily movements which can vary from half a metre (Hazlett, 1983) to a few hundred metres (Hazlett, 1981) in a single day. These daily movements may be responsible for the variation in abundance among different periods of the day reported for *Dardanus insignis* in the present study. Once lower abundances were recorded during the day the crabs may move apart from the sampling area (5–10 m depth) in this period either to deeper areas or to sites near the rocky shores. However, there are no records of daily movements for this species to strengthen this hypothesis. Moreover, it is not possible to address the role of digging behaviour, displayed by many subtidal species and probably by *D. insignis*, may play on preventing their capture by the sampling procedure. Despite the possibility of short-range movements, hermit crabs such as *Clibanarius vittatus* (Fotheringham, 1975), *Pagurus longicarpus* Say, 1817 (Rebach, 1978, 1981) and *Diogenes nitidimanus* Terao, 1913

(Asakura & Kikuchi, 1984; Asakura, 1987) may undergo seasonal migrations from shallow to deep waters. These migratory movements may be evidenced by marked variations in the abundance of individuals during specific periods in a given site as recorded for *Dardanus insignis* (Fernandes-Góes, 1997; present study). *Dardanus insignis* presented higher abundances associated to the lowest water temperatures in Armação do Itapocoroy (September and October) and in Ubatuba Bay (August–October, Fernandes-Góes, 1997). This may evidence that these populations leave the shallow embayed waters in the summer months and then return in the colder periods, when they initiate their reproductive period (see below). However, a more recent study in the Ubatuba region presented data on the abundance on *D. insignis* for five locations in two subsequent years (Fernandes-Góes, 2000) showing that the pattern of annual variation in abundance for these populations may vary among areas and between consecutive years and did not show clear relationships with water temperature.

Sexual dimorphism in the study population of *D. insignis* 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 suggested by previous reports for other species (Fernandes-Góes, 1997;



Bertini & Fransozo, 2000; Turra & Leite 1999, 2000; Turra et al., in press). Ovigerous females were also longer than non-ovigerous females although they showed similar widths. This was caused by the stronger negative allometry between cephalothorax length and width for ovigerous in relation to non-ovigerous females.

Data on the relationships between crab dimensions revealed a positive allometry between cephalothoracic length, and both width and crab weight. This means that individuals of this population of *D. insignis* become proportionally wider and heavier as growth proceeds. However, females showed a negative allometric relationship between cephalothoracic length and width. The positive allometric relationship between size and weight is well known among animals and is a direct consequence of the modification of the surface/volume ratios during growth. On the other hand, the positive or negative allometric relationship between cephalothoracic length and width is not a general assumption among hermit crabs once populations of *Petrochirus diogenes* (Bertini & Fransozo, 1999; Turra et al., in press) and another populations of *D. insignis* (Fernandes-Góes, 1997) present isometric relationships between these dimensions. This variation between populations, species, and sexes suggests the plasticity in this character, which is probably modulated by the shells used. In fact, Blackstone (1985) evidenced the effects of shells in modelling the shape of hermit crabs.

Once the cephalothorax instead of the shield was measured in the present study, a conversion is needed to compare the size distribution of this population of *D. insignis* with others previously studied. The conversion index of 2.12 from shield to cephalothoracic length was estimated based on information presented in Fernandes-Góes (1997). The shield length of the study population ranged from 4.72 to 18.40 mm, the smallest ovigerous female was 4.72 mm and the mean size of the individuals was 8.92 mm. These data differed slightly from the results presented by Fernandes-Góes (1997) for the population of *D. insignis* at Ubatuba Bay. She recorded a lower mean shield length of 8.31 mm and a wider size range 3.40–22.8 mm.

The lack of large individuals in the study population of *D. insignis* is also evidenced by its skewed size–frequency distribution. This also can be noted by the high mortality rate estimated for this population from the length converted catch curve. The low frequency of large sized individuals may be a consequence of the over-fishing on the soft bottoms of the studied area by traditional and commercial fishing industry. If this species of hermit crab uses shells of interest as habitats (see Fernandes-Góes, 1997), they, and the gastropod shells used become important by-catch products. This probably controls population size and the size of the individuals in this population. In fact, large shells are generally in lower supply in nature (Reese, 1969; Vance, 1972; Spight, 1977), so that the largest hermit crabs are thought to be under heavier shell limitation (Spight, 1977, 1985).

Hebling & Mansur (1995) described the larval development of *D. insignis* and showed that the cephalothoracic length of the megalopa is about 0.33 cm. The smallest individual sampled in the present study was 1.0 cm. In the same way, the smallest individual recorded by Fernandes-Góes (1997) in the Ubatuba region was 0.72 cm (converted from a shield length of 3.4 mm to cephalothoracic length). The absence of such small-sized individuals or juveniles

may be caused by the mesh size of the sampling devices employed in these studies. In contrast, this may also suggest habitat partitioning between small-sized/juveniles and large-sized/mature individuals as previously suggested by Turra & Leite (2000) for three intertidal populations of the genus *Clibanarius*, a hypothesis that requires further attention.

Hermit crabs have different patterns for the relationship between sex ratio and crab size (Wenner, 1972; Bertini & Fransozo, 2000). *Dardanus insignis* at Armação do Itapocoroy presented the standard pattern, with females dominating the smallest and males the largest size-classes. The standard pattern of sex ratio is uncommon among hermit crabs (Bertini & Fransozo, 2000) and was recorded only for the large-sized hermit crabs *D. insignis* (Fernandes-Góes, 1997; present study) and *P. diogenes* (Bertini & Fransozo, 2000; Turra et al., in press) and for the polychaete tube dwelling *Discorsopagurus schimitti* (Stevens, 1925) (Gherardi & Cassidy, 1995). According to Wenner (1972), this pattern may be caused by a faster growth of males in relation to females. Despite this possibility, there is no information on the growth rates of males and females for these species to reinforce this assumption. On the other hand, the inclusion of small-sized sexually mature individuals in the samples of all these species may lead to the anomalous pattern (Wenner, 1972), which is the most common among hermit crabs (Bertini & Fransozo, 2000; Turra & Leite, 2000).

The growth parameters (growth curvature parameter, longevity and temporal oscillation) estimated for *Dardanus insignis* are very similar to those recorded for tropical intertidal populations of *Clibanarius antillensis*, *C. scolopetarius* and *C. vittatus* (Turra & Leite, 2000) but quite distinct from the temperate hermit crabs *Cestopagurus timidus* (Manjón-Cabeza & García-Raso, 1994) and *Diogenes pugilator* (Manjón-Cabeza & García-Raso, 1998) (see Table 3). The asymptotic length of *Dardanus insignis* was markedly larger than all the other species. The index of Munro & Pauly (1983) calculated for *D. insignis* was also larger than those recorded for the *Clibanarius* populations cited above and for the temperate *Cestopagurus timidus* and *Diogenes pugilator* (Table 3). These data indicate that the population of the subtidal *Dardanus insignis* has a higher asymptotic length in relation to the growth curvature parameter (K) when compared to these other hermit crab species. Estimates of longevity may vary considerably from 20 to 62 months, depending on the method used, but all of them indicate cohort overlap. The longevity of 47 months calculated from the VBGF suggests an overlap of at least three cohorts. However, these values of longevity in the population were probably underestimated due to the low frequency of large size crabs. Recruitment of *D. insignis* was estimated to begin in September, the month equivalent to the reproductive peak of this population.

According to Bertini & Fransozo (2000) and Turra & Leite (2000), hermit crabs may have continuous or seasonal reproductive patterns. Turra & Leite (2000) revealed that continuous reproduction is markedly more common in tropical waters and that seasonal reproduction is an important strategy both in tropical and temperate regions. This is reinforced by *D. insignis*, which shows a seasonal reproductive period in both tropical (Fernandes-Góes, 1997) and subtropical (present study) waters.

Moreover, it is important to note that these two populations have coincident peaks of ovigerous females between September and October and absence or low number in the rest of the year.

No model could be fitted between the shell weight and both cephalothoracic length and crab weight considering all shell types. The inspection of Figure 6 reveals that the points are scattered in two directions as also recorded for another population of *D. insignis* in south-eastern Brazil (Fernandes-Góes, 1997). This was probably caused by the use of different shell species by the crabs. In fact, Fernandes-Góes (1997) analysed separately the relationship between crab size and shell weight for each shell type used by the crabs. She revealed that the relationship with shells of *Olivancillaria urceus* (Röding, 1798) have a greater slope than those with *Buccinanops gradatus* (Deshayes, 1844) and *Tonna galea* (Linnaeus, 1758) and that such differences were a direct consequence of the high weight of *O. urceus* in relation to the two other shell types.

## REFERENCES

- Asakura, A., 1987. Preliminary observations on the offshore mass migration of the sand-dwelling hermit crab, *Diogenes nitidimanus* Terao (Crustacea: Decapoda: Anomura). *Journal of Ethology*, **5**, 207–209.
- Asakura, A. & Kikuchi, T., 1984. Population ecology of the sand dwelling hermit crab, *Diogenes nitidimanus* Terao. 2. Migration and life history. *Publication of the Amakusa Marine Biology Laboratory*, **2**, 109–123.
- Bertini, G. & Fransozo, A., 1999. Relative growth of *Petrochirus diogenes* (Linnaeus, 1758) (Crustacea, Anomura, Diogenidae) in the Ubatuba region, São Paulo, Brazil. *Revista Brasileira de Biologia*, **59**, 617–625.
- Bertini, G. & Fransozo, A., 2000. Population dynamics of *Petrochirus diogenes* (Decapoda, Anomura, Diogenidae) in the Ubatuba region, São Paulo, Brazil. In *The biodiversity crisis and Crustacea* (ed. J.C. von V. Klein and F. Schram), pp. 331–342. Rotterdam: A.A. Balkema.
- Blackstone, N.W., 1985. The effects of shell size and shape on growth and form in hermit crabs *Pagurus longicarpus*. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **168**, 75–90.
- Branco, J.O., Lunardon-Branco, M.J., Peret, A.C., Souto, F.X., Schweitzer, R. & Vale, W.G., 1998. Associações entre macroinvertebrados e peixes demersais na Armação do Itapocoroy, Penha, SC, Brazil. *Brazilian Archives of Biology and Technology*, **41**, 268–277.
- Fernandes-Góes, L.C., 1997. *Distribuição e biologia populacional de Dardanus insignis (Saussure, 1858) (Crustácea: Decapoda: Anomura) na região de Ubatuba, SP*. MSc thesis, Universidade Estadual Paulista, Botucatu, Brazil.
- Fernandes-Góes, L.C., 2000. *Diversidade e bioecologia das comunidades de anomuros (Crustácea, Decapoda) do substrato não consolidado da região de Ubatuba, SP*. PhD thesis, Universidade Estadual Paulista, Botucatu, Brazil.
- Fotheringham, N., 1975. Structure of seasonal migrations of the littoral hermit crab *Clibanarius vittatus* (Bosc). *Journal of Experimental Marine Biology and Ecology*, **18**, 47–53.
- Gayanilo, F.C. Jr & Pauly, D., 1997. *FAO-ICLARM stock assessment tools (FiSAT) reference manual*. Rome: FAO Computerized Information Series (Fisheries) 8.
- Gherardi, F. & Cassidy, P.M., 1995. Life history patterns of *Discorsopagurus schmitti*, a hermit crab inhabiting polychaete tubes. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **188**, 68–77.
- Hazlett, B.A., 1966a. Social behavior of the Paguridae and Diogenidae of Curaçao. *Studies on the Fauna of Curaçao and other Caribbean Islands*, **23**, 1–143.
- Hazlett, B.A., 1966b. The behavior of some deep-water hermit crabs (Decapoda: Paguridae) from the Straits of Florida. *Bulletin of Marine Science*, **16**, 76–92.
- Hazlett, B.A., 1981. Daily movements of the hermit crab *Clibanarius vittatus*. *Bulletin of Marine Science*, **31**, 177–183.
- Hazlett, B.A., 1983. Daily movement in the hermit crabs *Clibanarius tricolor* and *Calcinus tibicen*. *Journal of Crustacean Biology*, **3**, 223–234.
- Hebling, N.J. & Mansur, C.B., 1995. Desenvolvimento larval de *Dardanus insignis* (Saussure) (Crustacea, Decapoda, Diogenidae) em laboratório. *Revista Brasileira de Zoologia*, **12**, 471–491.
- Manjón-Cabeza, M.E. & García-Raso, J.E., 1994. Estructura de uma población del cangrejo ermitaño *Cestopagurus timidus* (Crustacea, Decapoda, Anomura) de fondos de *Posidonia oceanica* del SE de España. *Cahiers de Biologie Marine*, **35**, 225–236.
- Manjón-Cabeza, M.E. & García-Raso, J.E., 1998. Population structure and growth of the hermit crab *Diogenes pugilator* (Decapoda: Anomura: Diogenidae) from the northeastern Atlantic. *Journal of Crustacean Biology*, **18**, 753–762.
- Martinez-Iglesias, J.C. & García-Raso, J.E., 1999. The crustacean decapod communities of the coral reefs from southwestern Caribbean sea of Cuba: species composition, abundance and structure of the communities. *Bulletin of Marine Science*, **65**, 539–557.
- Munro, J.L. & Pauly, D., 1983. A simple method for comparing the growth of fishes and invertebrates. *Fishbyte*, **1**, 5–6.
- Rebach, S., 1978. The role of celestial cues in short range migration of the hermit crab, *Pagurus longicarpus*. *Animal Behavior*, **26**, 835–842.
- Rebach, S., 1981. Use of multiple cues in short-range migrations of crustacea. *American Midland Naturalist*, **105**, 168–180.
- Reese, E.S., 1969. Behavioral adaptations of intertidal hermit crabs. *American Zoologist*, **9**, 343–355.
- Rieger, P.J., 1997. Os “ermitões” (Crustacea, Decapoda, Parapaguridae, Diogenidae e Paguridae) do litoral brasileiro. *Nauplius*, **5**, 99–124.
- Sparre, P., 1987. Computer programs for fish stock assessment. Length-based fish stock assessment for Apple II Computers. *Food and Agriculture Organization, Fisheries Technical Papers*, **2**, 1–218.
- Spight, T.M., 1977. Availability and use of shells by intertidal hermit crabs. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **152**, 120–133.
- Spight, T.M., 1985. Why small hermit crabs have large shells? *Research on Population Ecology*, **27**, 39–54.
- Turra, A., Branco, J.O. & Souto, F.X., in press. Biology of the hermit crab *Petrochirus diogenes* (Linnaeus, 1758) in southern Brazil. *Revista Brasileira de Zoologia*.
- Turra, A. & Leite, F.P.P., 1999. Population structure and fecundity of the hermit crab *Clibanarius antillensis* Stimpson 1862 (Anomura, Diogenidae) southeastern Brazil. *Bulletin of Marine Science*, **64**, 281–289.
- Turra, A. & Leite, F.P.P., 2000. Population biology and growth of three sympatric intertidal hermit crabs in south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, **80**, 1061–1069.
- Vance, R.R., 1972. Competition and mechanisms of coexistence in three sympatric species of intertidal hermit crabs. *Ecology*, **53**, 1062–1074.
- Wenner, A.M., 1972. Sex ratio as a function of size in marine crustacea. *American Naturalist*, **106**, 321–350.
- Wenner, E.L. & Read, T., 1982. Seasonal composition and abundance of Decapod Crustacean assemblages from the South Atlantic Bridge, USA. *Bulletin of Marine Science*, **32**, 181–206.
- Zar, J.H., 1996. *Biostatistical analysis*. New Jersey: Prentice-Hall.

Submitted 3 February 2002. Accepted 31 May 2002.