

Pattern of shell utilization by the hermit crab *Paguristes tortugae* (Diogenidae) from Anchieta Island, southern Brazil*

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SUMMARY: The objective of this study was to characterize the pattern of shell utilization by *Paguristes tortugae*, from infralittoral areas of Anchieta Island (Ubatuba, São Paulo State, Brazil) using the percentage of the different shell types occupied and the morphometric relationship between hermit crabs and occupied shells. Specimens were collected monthly (January to December 1998) by SCUBA diving. The animals and the shells were measured and weighed. A total of 2,429 hermit crabs were captured occupying 21 species of gastropod shells. The shells more occupied were *Pisania auritula* (35.49%), *Cerithium atratum* (27.83%), *Morula nodulosa* (12.70%) and *Leucozonia nassa* (6.83%), respectively. There was differential shell occupation between sexes: males and ovigerous females occupied in higher percentage *P. auritula* shells while the non-ovigerous females occupied *C. atratum*. Regression analysis showed best correlation between the size of the crabs (shield length) and shell dry weight. This study showed that shell occupation by *P. tortugae* involves inter- and intraspecific competition as well as shell type availability in the field.

Key words: Anomura, Crustacea, population, shell resource.

RESUMEN: PAUTAS DE UTILIZACIÓN DE CONCHAS POR EL CANGREJO ERMITAÑO *PAGURISTES TORTUGAE* (DIOGENIDAE) DE LA ISLA DE ANCHIETA, BRASIL MERIDIONAL. – El objetivo del presente estudio consistió en caracterizar las pautas de utilización de conchas por *Paguristes tortugae* en áreas infralitorales de la isla de Anchieta (Ubatuba, Estado de Sao Paulo, Brasil) utilizando el porcentaje de los distintos tipos de concha ocupados y la relación morfométrica entre los ermitaños y las conchas ocupadas. Los especímenes fueron muestreados mensualmente (enero a diciembre 1998) mediante inmersión con bombonas de aire comprimido. Los animales y las conchas fueron medidos y pesados. Un total de 2429 cangrejos ermitaños fueron capturados y se registraron un total de 21 especies de conchas de gasterópodos utilizadas por los mismos. Las conchas más ocupadas fueron *Pisania auritula* (35.49%), *Cerithium atratum* (27.83%), *Morula nodulosa* (12.70%) y *Leucozonia nassa* (6.83%). Se detectó una ocupación diferencial de conchas respecto al sexo del ermitaño: machos y hembras ovígeras ocuparon conchas de *P. auritula* en una mayor proporción, mientras que las hembras no ovígeras ocuparon preferencialmente *C. atratum*. Un análisis de regresión mostró la mayor correlación entre la talla de los cangrejos (longitud del escudo cefalotorácico) y el peso seco de la concha. Este estudio mostró que la ocupación de conchas por *P. tortugae* comporta competencia inter- e intraespecífica, y depende también de la disponibilidad de conchas en el campo.

Palabras clave: Anomura, Crustacea, poblaciones, recursos de conchas.

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INTRODUCTION

According to Conover (1978), the ability of hermit crabs to occupy and carry gastropod shells is one of the main reasons for their evolutionary success. Hermit crabs need increasingly larger shells during their life cycle, a fact that keeps them in constant activity searching for suitable shells (Bertness, 1981). Some species are adapted to occupying the shells more easily encountered in the field (Mesce, 1993), while others select shells according to their preference for type, size, shape and/or shell covering (Grant and Ulmer, 1974; García and Mantelatto, 2001). Therefore, hermits should modify their preference for shell size based on the availability of empty shells (Hazlett, 1992). At the same time, the gastropod shells can be a limiting resource to hermit crab populations (Vance, 1972).

Hermit crabs are entirely dependent on the processes that make suitable shells available for their use, including snail mortality and inter- and intraspecific shell exchanges (Hazlett, 1981). The hypothesis more commonly used to explain that shells are in short supply are that natural populations of crabs are often in smaller shells than preferred in laboratory experiments (Vance, 1972; Scully, 1979; Bertness, 1980), empty shells are often rare in the habitats that support hermit crab populations (Hazlett, 1970; Bertness, 1980) and, hermit crabs often have ritualized shell-exchange behavior that may be beneficial when shell resources are scarce (Carlson and Ebersole, 1995). Several authors have studied shell occupation by hermit crabs in the field (Walters and Griffiths, 1987; Gherardi and Vannini, 1989; Gherardi, 1991; Negreiros-Fransozo and Fransozo, 1992; Manjón-Cabeza and García Raso, 1999; Martinelli *et al.*, 1999; Bertini and Fransozo, 2000), and others have studied hermit crabs under laboratory conditions to verify the preference pattern by shells utilized (Lively, 1988; Hazlett, 1992; García and Mantelatto, 2001). Despite this background and considering the high number of hermit crab species described worldwide, few studies have evaluated comparatively shell occupation in the field and in laboratory conditions (see Mantelatto and García, 2000 for review).

Paguristes tortugae Schmitt, 1933 is a species relatively abundant, from Florida (U.S.A) to Brazil (Hebling and Rieger, 1986), and a reasonable number of studies have been conducted with this species: including larval development (Hebling and Negreiros-Fransozo, 1983), population aspects

(Negreiros-Fransozo and Fransozo, 1992; Mantelatto and Sousa, 2000), fecundity and reproductive potential (Negreiros-Fransozo *et al.*, 1992; Mantelatto *et al.*, 2002). The objective of the present study was to characterize the pattern of shell utilization in the field by *P. tortugae* inhabiting the infralittoral area of Anchieta Island, Brazil investigating the factors that influenced the occupation of gastropod-shell species by each sex and the morphometric relationships between hermit crabs and their shells assessed.

MATERIAL AND METHODS

Study Area

Anchieta Island (23°33'S, 45°05'W) (Fig. 1) has a total area of about 10 km² and was recently declared an ecological reserve of São Paulo State because the natural environment has been affected by anthropogenic factors such as tourism and fishery activities in coastal areas. This island is located landwards, separated from the coast by a 300 m long and 35 m deep canal. However, the decapod crustacean fauna from this area is poorly studied, and their scientific information scarce.

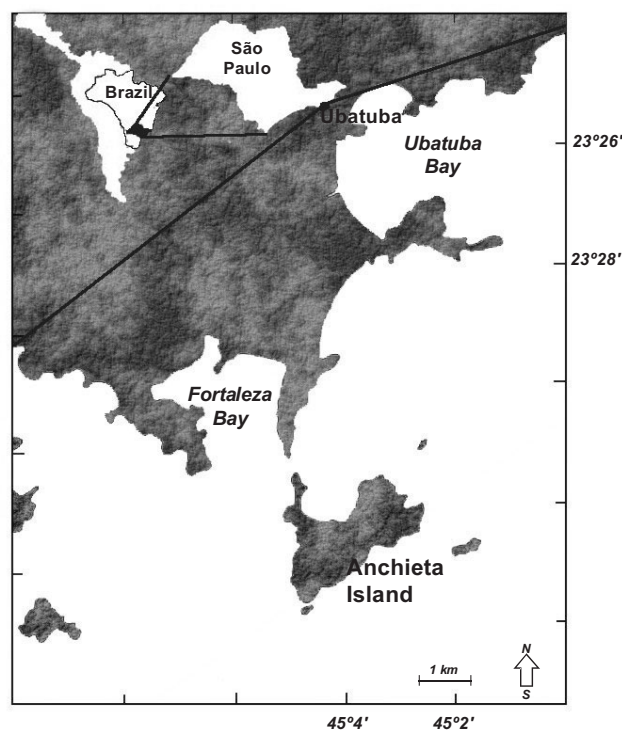


FIG. 1. – Map showing the localization of Anchieta Island, Ubatuba (São Paulo State), Brazil.

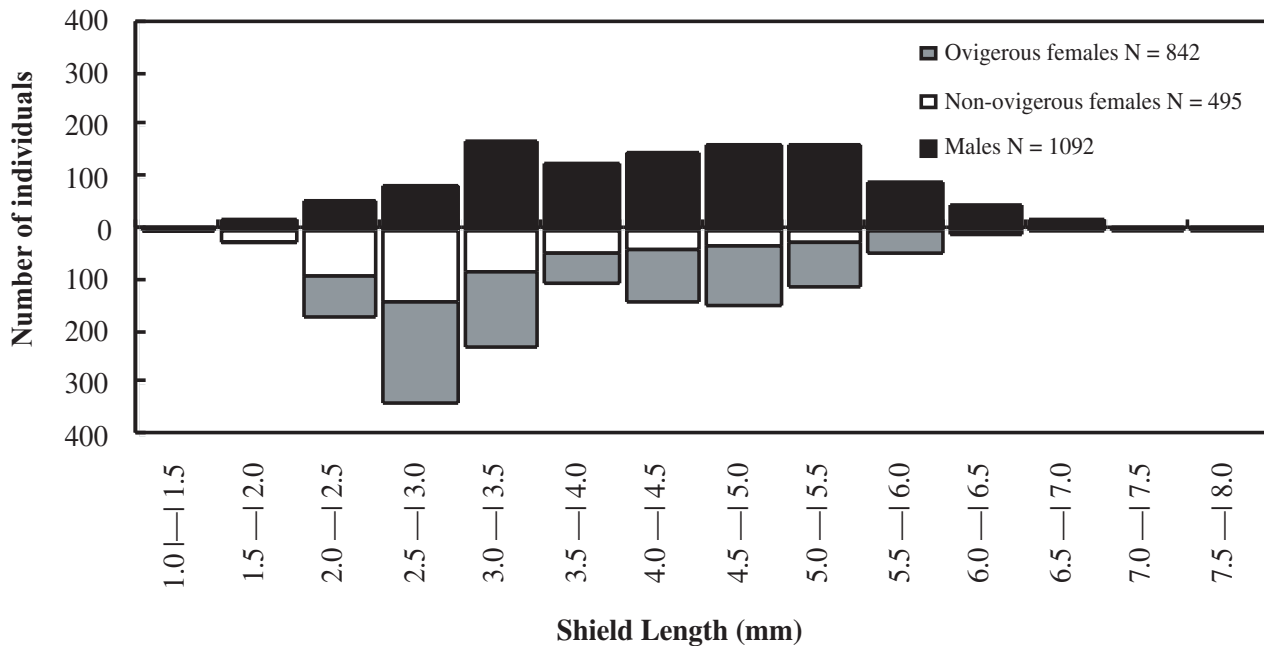


FIG. 2. – *P. tortugae*. Size frequency distribution for the individuals collected. (N = number of individuals).

Sampling and analysis

The hermit crabs were obtained monthly from January to December 1998 from four infralittoral rocky/sandy areas of Anchieta Island (East and South Beaches, Prainha and Saco do Vento), whose surface is irregular, with many huge boulders. Every month, at least one of these sites was sampled depending on ocean and weather conditions. Specimens were captured during the daytime by three SCUBA divers over a period of 30 min over an area of about 850 m². This methodology provided large amounts of material from this area of irregular surface and thus was considered efficient for the hermit crab population study (Mantelatto and Garcia, 2002). Animals were frozen and transported to the laboratory for analysis where they were carefully removed from their shells, weighed (WW = Wet Weight) and measured for shield length (SL), shield width (SW), propodus length (PL) and propodus height (PH). Shell species were identified by Rios (1994), confirmed by a specialist (Dr. Osmar Domaneschi, University of São Paulo), measured (SAW = shell aperture width; SAL = shell aperture length), and their dry weight (SDW) was determined. Measurements were made with a caliper (0.1 mm) or by drawing with the aid of a camera lucida. Shell internal volume (SIV) was measured on the basis of the volume of fine sand ($\emptyset = 0.25\text{--}0.105\text{ mm}^3$) required to fill the empty shell modified by Mantelatto and Garcia (2000).

The distribution frequency was tested by the Kolmogorov-Smirnov normality test (KS), and the Pearson Correlation was utilized to evaluate the relationship between the variables (hermit crab *versus* shell dimensions) (Zar, 1996). The best models obtained from Pearson analysis were checked by linear regression and by correlation coefficients. The shell type preference was estimated by the percentage of occupation of the chosen species and the chi-square test (χ^2) was used to compare occupancy rates of shell species.

RESULTS

A total of 2,429 individuals of *P. tortugae* was collected, 1,092 (44.96%) of them males, 495 (20.38%) non-ovigerous females, and 842 (34.66%) ovigerous females. The total size frequency distribution of the population sampled was non-normal (KS = 0.0969; $P < 0.05$), as were the males (KS = 0.0576; $P < 0.05$), ovigerous females (KS = 0.1334; $P < 0.05$), and non-ovigerous females (KS = 0.1271; $P < 0.05$). Males reached a larger size than females (7.0 to 8.0 mm SL) (Fig. 2).

Paguristes tortugae was found occupying a total of 21 gastropod shell species. *Pisania auritula* (35.49%), *Cerithium atratum* (27.83%), *Morula nodulosa* (12.70%), and *Leucozonia nassa* (6.83%) were the shells more frequently occupied. Males

TABLE 1. – Gastropod shell species and percentage of occupation by *P. tortugae* (N = total number of individuals; MA = males; NOF = non-ovigerous females; OF = Ovigerous females).

Shell Species	N	%	MA	%	NOF	%	OF	%
<i>Astraea latispina</i> (Philippi, 1846)	25	1.03	23	2.11	01	0.20	01	0.12
<i>Astraea tecta olfersii</i> (Philippi, 1846)	40	1.65	34	3.11	05	1.01	01	0.12
<i>Astraea phoebia</i> (Roding, 1798)	18	0.74	15	1.37	03	0.61	-	-
<i>Buccinanops gradatum</i> (Deshayes, 1844)	01	0.04	01	0.09	-	-	-	-
<i>Cerithium atratum</i> (Born, 1778)	676	27.83	223	20.42	195	39.40	258	30.64
<i>Cymatium parthenopeum</i> (von Salis, 1793)	22	0.91	19	1.74	02	0.40	01	0.12
<i>Chicoreus tenuivariocosus</i> (Dautzenberg, 1927)	13	0.54	10	0.92	01	0.20	02	0.24
<i>Coralliophila aberrans</i> (C. B. Adams, 1850)	05	0.21	02	0.18	02	0.40	01	0.12
<i>Fusinus brasiliensis</i> (Grabau, 1904)	09	0.37	06	0.55	01	0.20	02	0.24
<i>Favartia cellulosa</i> (Conrad, 1846)	01	0.04	01	0.09	-	-	-	-
<i>Leucozonia nassa</i> (Gmelin, 1791)	166	6.83	69	6.32	34	6.87	63	7.48
<i>Morula nodulosa</i> (Adams, 1845)	308	12.70	56	5.13	90	18.18	162	19.24
<i>Modulus modulus</i> (Linnaeus, 1758)	01	0.04	-	-	01	0.20	-	-
<i>Muricopsis necocheanus</i> (Pilbry, 1900)	01	0.04	-	-	01	0.20	-	-
<i>Phalium granulatum</i> (Born, 1778)	01	0.04	01	0.09	-	-	-	-
<i>Pisania auritula</i> (Link, 1807)	862	35.49	420	38.46	122	24.65	320	38.00
<i>Pisania pusio</i> (Linnaeus, 1758)	59	2.43	41	3.75	07	1.41	11	1.31
<i>Polinices lacteus</i> (Guilding, 1833)	04	0.16	04	0.37	-	-	-	-
<i>Polinices hepaticus</i> (Roding, 1798)	02	0.08	02	0.18	-	-	-	-
<i>Stramonita haemastoma</i> (Linnaeus, 1767)	68	2.80	51	4.67	04	0.81	13	1.54
<i>Tegula viridula</i> (Gmelin, 1791)	131	5.39	105	9.62	21	4.24	05	0.59

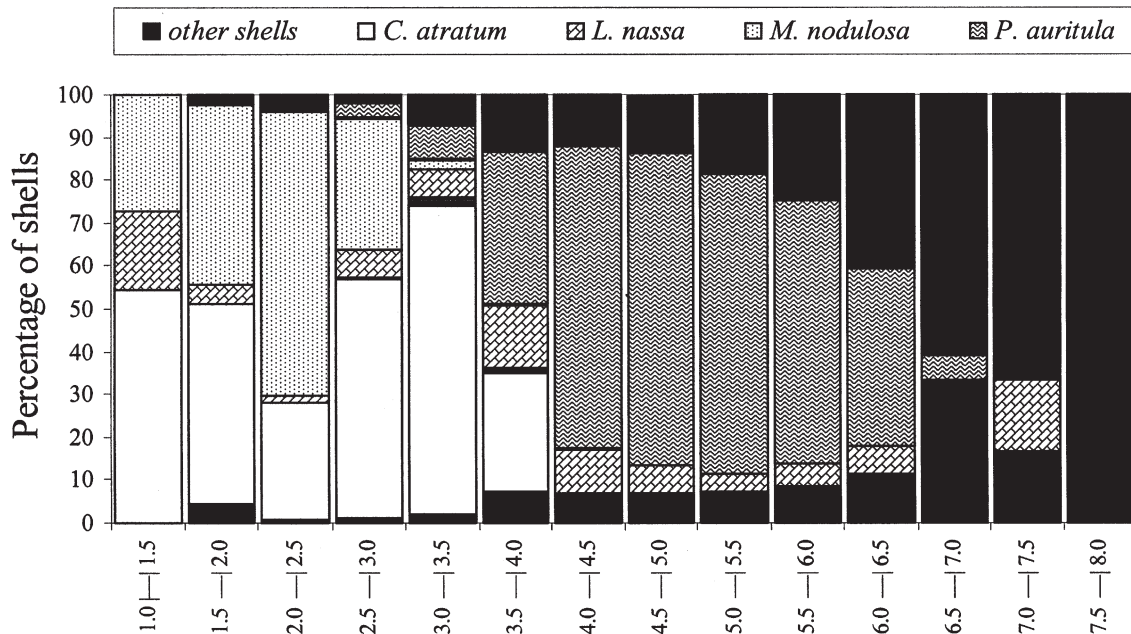


FIG. 3. – *P. tortugae*. Hermit crab size frequency as a function of the four shells more occupied.

(38.46%) and ovigerous females (38.00%) occupied the shells of *P. auritula* at higher percentages, and non-ovigerous females (39.40%) occupied *C. atratum* shells at higher percentages (Table 1). *Cerithium atratum* shells were significantly more occupied by ovigerous females ($\chi^2 = 8.8$; $P < 0.05$) in relation to non-ovigerous females; *M. nodulosa* were significantly more occupied by ovigerous females ($\chi^2 = 51.6$; $P < 0.05$); *L. nassa* and *P. auritula* were significantly more occupied by males ($\chi^2 = 11.9$ and χ^2

$= 163.8$; $P < 0.05$, respectively) and ovigerous females ($\chi^2 = 8.67$ and $\chi^2 = 88.7$, $P < 0.05$, respectively). *Morula nodulosa* and *C. atratum* (smaller shells) were occupied by smaller individuals, being that individuals between 2.0 to 2.5 mm SL had the highest occupation of *M. nodulosa* while between the intervals of 1.0 to 3.5 mm SL, the highest occupation were for *C. atratum*. *Pisania auritula* were dominantly occupied by the biggest individuals (3.5 to 7.0 mm) (Fig. 3).

TABLE 2. – *P. tortugae*. Regression equations in relation to the sex of the individuals that demonstrated the highest correlation coefficients (N = number of individuals; r = coefficient of correlation; SL = Shield length; SDW = Shell dry weight; SIV = Shell Internal Volume; * = significant correlation [P < 0.05]).

Sex	N	Relationships	Linear equation $Y = aX^b$	Transformed $\ln Y = \ln a + b \ln X$	r
Males	1092	SL x SDW	$SDW = 0.20 SL^{1.96}$	$\ln SDW = -1.61 + 1.96 \ln SL$	0.81*
	679	SL x SIV	$SIV = 0.02 SL^{2.14}$	$\ln SIV = -3.91 + 2.14 \ln SL$	0.73*
Non-ovigerous females	494	SL x SDW	$SDW = 0.20 SL^{2.0}$	$\ln SDW = -1.61 + 2.0 \ln SL$	0.79*
	208	SL x SIV	$SIV = 0.02 SL^{2.05}$	$\ln SIV = -3.91 + 2.05 \ln SL$	0.75*
Ovigerous females	842	SL x SDW	$SDW = 0.13 SL^{2.03}$	$\ln SDW = -2.04 + 2.03 \ln SL$	0.85*
	460	SL x SIV	$SIV = 0.20 SL^{2.33}$	$\ln SIV = -1.61 + 2.33 \ln SL$	0.84*

TABLE 3. – Regression equations between SL (Shield length) and SDW (Shell dry weight) for different species of shells occupied by *P. tortugae* (N = number of individuals; r = coefficient of correlation; * = significant correlation [P < 0.05]).

Shell Species	N	Linear equation $Y = aX^b$	Transformed $\ln Y = \ln a + b \ln X$	r
<i>S. haemastoma</i>	68	$SDW = 0.23 SL^{1.80}$	$\ln SDW = -1.50 + 1.80 \ln SL$	0.75*
<i>P. pusio</i>	59	$SDW = 0.39 SL^{1.45}$	$\ln SDW = -0.92 + 1.45 \ln SL$	0.68*
<i>T. viridula</i>	131	$SDW = 0.30 SL^{1.61}$	$\ln SDW = -1.20 + 1.61 \ln SL$	0.69*
<i>P. auritula</i>	862	$SDW = 1.10 SL^{0.75}$	$\ln SDW = 0.10 + 0.75 \ln SL$	0.46*
<i>M. nodulosa</i>	308	$SDW = 0.40 SL^{1.14}$	$\ln SDW = -0.92 + 1.14 \ln SL$	0.45*
<i>L. nassa</i>	166	$SDW = 0.20 SL^{1.83}$	$\ln SDW = -1.61 + 1.83 \ln SL$	0.86*
<i>C. atratum</i>	674	$SDW = 0.27 SL^{1.09}$	$\ln SDW = -1.31 + 1.09 \ln SL$	0.51*
<i>A. latispina</i>	25	$SDW = 0.40 SL^{1.74}$	$\ln SDW = -0.92 + 1.74 \ln SL$	0.84*
<i>A. olfersii</i>	40	$SDW = 0.40 SL^{1.64}$	$\ln SDW = -0.92 + 1.64 \ln SL$	0.80*

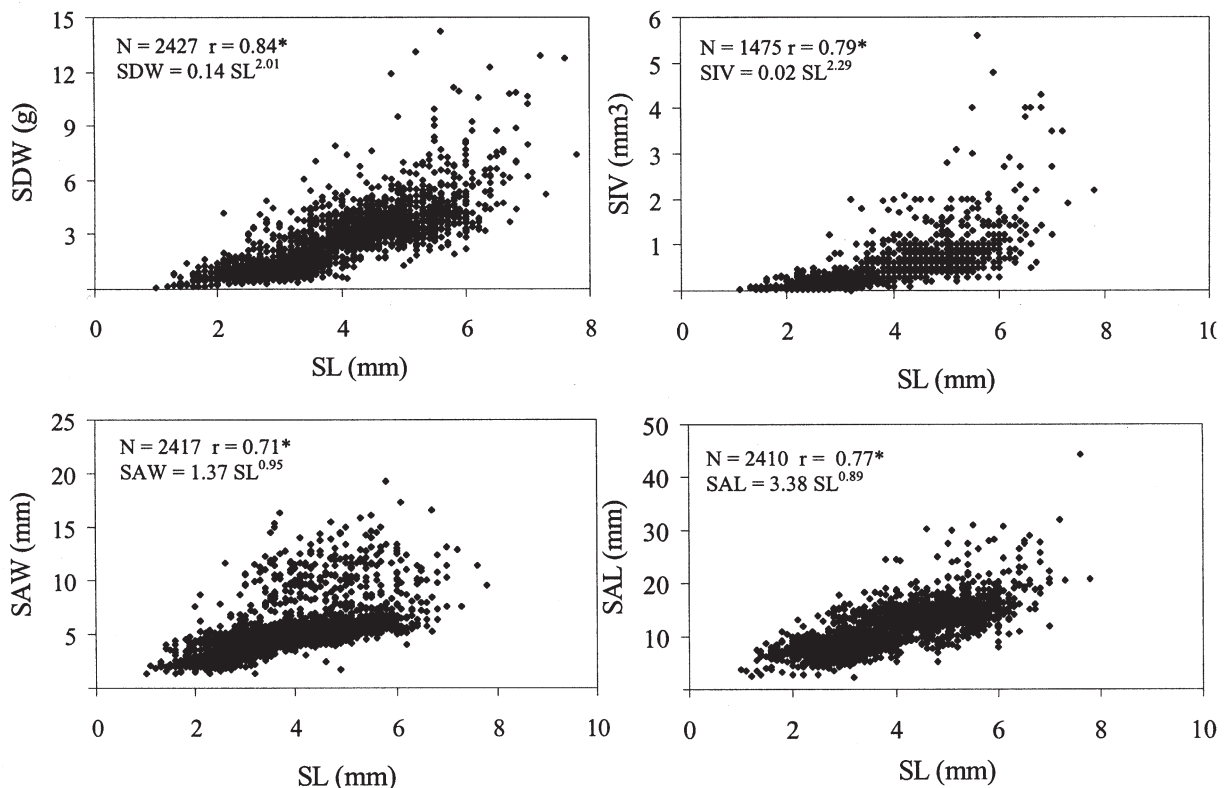


FIG. 4. – *P. tortugae*. The regressions between hermit shield length (SL) and shell dry weight (SDW), shell aperture width (SAW), shell aperture length (SAL) and shell internal volume (SIV) for the individuals as a whole.

The species shells with percentage occupation less than 1% were not tested. All regressions between hermit crab and shell dimensions presented significant correlation ($P > 0.05$), except for *M. nodulosa* in the regressions PL x SAW and PL x SIV. Regression analysis between hermit size (SL) and shell dry weight demonstrated the highest correlation coefficients ($SDW = 0.14 SL^{2.01}$, $r = 0.84$), and was considered as the best model to characterize the relationship between the variables analyzed in *P. tortugae* (Tables 2 and 3; Fig. 4). The more occupied shells (*P. auritula*, *C. atratum* and *M. nodulosa*) showed the lower correlation coefficients ($r < 0.51$) and *L. nassa* showed the higher coefficients (0.86). With respect to the sexes, ovigerous females showed the highest correlation coefficients in all relations analyzed ($r > 0.84$) (Table 2).

DISCUSSION

According to Mantelatto and García (2002), the rocky/sand infralittoral hermit crab community of Anchieta Island is composed of nine species [*Calcinus tibicen* (Herbst, 1791); *Dardanus insignis* (Sausure, 1858); *Dardanus venosus* (H. Milne Edwards, 1848); *Paguristes calliopsis* Forest and Saint Laurent, 1967; *Paguristes erythropus* Holthuis, 1959; *Paguristes tortugae* Schmitt, 1933; *Petrochirus diogenes* (Linné, 1758); *Pagurus brevidactylus* (Stimpson, 1859), and *Pagurus criniticornis* (Dana, 1852)]. The taxocoenosis in this area was controlled by *P. tortugae*, and for this reason a long-term effort has been devoted to this species during the last four years. Recent investigations revealed that *P. tortugae* presented continuous reproduction, a high reproductive potential (fecundity) influenced by the shell species characteristics, and this reproduction strategy also included the precocious size of sexual maturity (SL = 1.5 mm) (Mantelatto and Sousa, 2000; Mantelatto *et al.*, 2002).

The population dynamics of the hermit crabs is closely tied to the species of gastropods that are present in their habitat (Mantelatto and García, 2000). Hermit crabs utilize different gastropod shell species at different rates, a fact that can be attributed to the preference for a certain shell architecture type and/or to the higher abundance of some species in the field (Reese, 1962). The availability of shells may be a limiting factor for some species of hermit crabs and can be affected by their abundance in a particular habitat and by inter- and intraspecific competition for shells (Reese, 1969).

Paguristes tortugae was found occupying 21 gastropod shell species, demonstrating plasticity in shell type utilization, as well as the shell stock potential in this area. In the studied area, the population of live gastropods consists of 32 species (unpublished data), with *Cerithium atratum*, *Pisania auritula* and *Morula nodulosa* the most abundant (74.9% of the total shells collected), and *Leucozonia nassa* showing reduced occurrence. *Pisania auritula*, *C. atratum*, *M. nodulosa* and *L. nassa* (those most often occupied in the survey during the present work) have a similar architecture. Despite this similarity, some differences in hermit size occupation were detected. Conversely, Negreiros-Fransozo and Fransozo (1992) observed *P. tortugae* occupying *Stramonita* shells only in a different area (São Sebastião). Therefore, we can infer that results might have been related to the wide availability of shells in the survey.

The size of the occupied shells usually is well correlated with hermit crab size (Abrams, 1980) when the availability of shells in the field is high. In this study, it was noted that shell weight showed the best correlation with *P. tortugae* size. Alternative hypotheses concern the advantages of occupying heavy shells are postulated (see Mantelatto and García, 2000 for review). Particularly, we agree with Reese (1969), that the occupation of heavy shells by hermit crabs protects them against predators, water currents and the impact and abrasion of waves. This is true for *P. tortugae*, which occurs in rocks and corals and therefore may be better protected by heavy shells in these habitats, with greater stability against currents and a frequent downfall escape movement (hermits enter the shell and drop from the rocks/corals falling to the crevices when they detect the presence of collector/predator – pers. obs.). According to Borjesson and Szelistowski (1989), small shells are more easily damaged or destroyed by shell-crushing predators than larger shells. In this study, the smaller shells were available in high quantity while large shells were available from more species. However, the shells most frequently occupied (*P. auritula*) showed low adequacy (r) for the hermit crab dimensions, except for *L. nassa* shells, indicating that *P. tortugae* might search for more adequate ones. In the present study the shell occupation pattern of *P. tortugae* was probably influenced by inter- and intraspecific competition, or by sympatry with three other hermit species with similar size in the studied area (Mantelatto and García, 2002).

It was noted that *C. atratum* and *M. nodulosa* shells were occupied by the smaller hermit crabs, while specimens of all size classes occupied *L. nassa* shells, reflecting wide size range available for this shell species. A clear occupation of *P. auritula* was observed for *P. tortugae* from 3.5 to 7.0 mm SL size range. This pattern characterizes a clear competitive ability between the different size individuals in the population.

The differences in shell utilization between sexes can be explained by intraspecific competition, intimately related with size of the individuals or by energy expenditures, related to reproductive activity and growth (Abrams, 1988). The highest correlations between hermit crabs and shell dimension were observed in ovigerous females of *P. tortugae*. The females allocate energy to growth, reproduction and egg incubation, resulting in a decrease in their somatic growth (Bertness, 1981; Abrams, 1988), occupying smaller shells (*C. atratum*) while the males allocate energy to growth and gonad development, occupying larger shells. The ovigerous females fit larger shells (*P. auritula*), perhaps for best space availability and protection of their eggs. Thus shell occupation showed an inclination of larger individuals to fit larger shells. Natural selection may favor males in relation to females, because they have the advantage of size over females in regarding competition for shells, such as reported for males of *Calcinus tibicen* by Mantelatto and García (2000).

According to Conover (1978), hermit crabs do not enter shells at random, but select them. Despite the low coefficients obtained in the regression analysis of data concerning their shells, we verified that *C. atratum* (large internal volume) was more adequate (considering the correlation coefficients) than *M. nodulosa*. The dimensions of *L. nassa* shells that have a straight aperture and an elongated shape (Rios, 1994) are those that best fit the dimensions of *P. tortugae*. *Pisania auritula* has a stronger shell with a straight aperture. The males, being larger and heavier, fit large shells, but they are not always available, occupying *P. auritula* probably because its favorable characteristics and greater availability. The ovigerous females of the studied species may have had available shells that they favoured as it was shown that three shells (*P. auritula*, *C. atratum* and *M. nodulosa*) had significant higher occupation rates by ovigerous females. The highest fecundity of *P. tortugae* in Anchieta Island was observed for ovigerous females occupying larger shells, i.e. *P.*

auritula (Mantelatto *et al.*, 2002). According to this work, the reproductive aspects of *P. tortugae* seem to be related to strategies developed to compensate for interspecific competition, i.e., high and continuous reproductive effort, early maturity, low fecundity and larger eggs produced. Almost all these strategies were correlated with the fact that the specimens attain maturity quickly at smaller size (Mantelatto and Sousa, 2000).

In this respect, we may infer that the shell utilization pattern of *P. tortugae* follows the pattern of shell-type availability that is related to the size and weight of the shells and varies between sexes. The better adequacy of *L. nassa* for the hermit dimensions in this survey lead us to conclude that this species is the one that best fits *P. tortugae*. On the other hand, the individuals fit large shells, demonstrating that *P. tortugae* do not always have the most adequate shells available.

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