

GASTROPOD SHELLS USED BY *Dardanus insignis* (Decapoda, Anomura) NEAR ISLANDS IN THE UBATUBA REGION, SÃO PAULO, BRAZIL

CONCHAS DE GASTRÓPODOS UTILIZADAS POR Dardanus insignis (Decapoda, Anomura) PRÓXIMAS DE ILHAS DE REGIÃO DE UBATUBA, SÃO PAULO, BRASIL

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ABSTRACT: The use of gastropod shells by hermit crabs is determined by the availability of shells in the environment or through selection for size and volume. This study analyzed patterns in the use of shells by *Dardanus insignis* (Saussure, 1858). From January 1998 to December 1999, 386 individuals were collected from two islands at Ubatuba, São Paulo. The crabs were measured for cephalothoracic shield length (CSL) and wet weight (CWW). The gastropod shells occupied by hermit crabs were identified, and the shell aperture width (SAW), dry weight (SDW) and internal volume (SIV) were measured. The relationships between the dimensions of the gastropod shell and the hermit crabs were evaluated by linear regression analysis. Among the 11 species of gastropod shells used by *D. insignis*, the most often used was *Olivancillaria urceus* (31%), followed by *Strombus pugilis* (22%) and *Siratus tenuivaricosus* (18%). The shell of *O. urceus* was used most probably due to its high availability on Couves and Mar Virado islands. The most significant biometric parameter was shell aperture width ($F=18.231$; $p<0.0001$), highlighting the importance of this variable for the shell choice by *D. insignis* at both sites.

KEYWORDS: Mollusca. Hermit crab. Habitat selection. Interspecific relationship. Morphometrics.

INTRODUCTION

Hermit crabs are crustaceans of the infraorder Anomura characterized by the lack of exoskeleton calcification of the abdomen and by their evolutionary success regarding the adaptation for occupying gastropod shells, which serve as protection and shelter from adverse conditions and predators (BERTNESS, 1981). Hermit crabs are distributed in 120 genera, with approximately 1100 species worldwide (MCLAUGHLIN et al., 2007). Fifty of these species, representing 40 families and 22 genera, have been recorded for the Brazilian coast (NUCCI; MELO, 2007). In southeastern Brazil, 26 species have been recorded, from the intertidal zone to deep waters (MELO, 1999).

These crabs are extremely important for the equilibrium of benthic environment, and it is characterized as the better example of a "detritivorous" in marine environments (SAMUELSEN, 1970), its wide range of food habits

seemed to have contributed as an essential factor for the adaptive success of the group (SCHEMBRI, 1982). Some species have developed mechanisms of shell occupation according to their availability in the environment, without a choice criterion, while other species developed selective mechanisms according to some criteria related to the occupying species, size and volume (GRANT; ULMER, 1974). Hazlett (1981) pointed out that the species of shells occupied by hermit crabs influenced several traits of hermit crabs biology, like growth, survival rate and also reproductive potential.

According to Scully (1979), hermit crabs tend to occupy better shells when inhabiting environments with great diversity and abundance of gastropods, distinguishing from areas lacking shells. The change for new shells occurs when the hermit crab found an empty one or obtain it from other individual through a ritualized behavior on disputing for the shell (MANTELATTO; DOMINCiano, 2002; SATO; SENO, 2006).

Dardanus insignis (Saussure, 1858) occurs in almost all Western Atlantic, from Northern Carolina (USA) to Argentina. In Brazil, it is distributed from Rio de Janeiro to Rio Grande do Sul, being limited to wide depth gradients between 1.5 and 500 meters (RIEGER, 1997). It is the most abundant hermit crab of non-consolidated bottoms in southeastern Brazil (FRANSOZO et al., 2008, 2011).

Due to its importance for all trophic levels, and because of it is directly affected by the constant fishery of shrimps on Southeastern Brazil (COSTA et al., 2007), exploratory studies about these organisms populations become important. Considering that they need resources from other animals, this hermit crab demonstrates the real situation of the environment, highlighting its importance for the coastal monitoring and conservation of both the area and the species. Therefore, this study characterized the use of gastropod shells by *D. insignis* in two islands of

Southeastern coast of Brazil, evaluating their abundance and morphological relationships between hermit crabs and their respective shells.

MATERIAL AND METHODS

Study area and general procedures

Hermit crabs were collected monthly from January 1998 through December 1999 at two sites at Ubatuba on the northern coast of the state of São Paulo, Brazil. The sites were located near two islands: Couves Island ($23^{\circ}24'45''\text{S}$; $44^{\circ}51'27''\text{W}$) and Mar Virado Island ($23^{\circ}33'25''\text{S}$; $45^{\circ}09'37''\text{W}$) (Figure 1). Sampling was performed using double-rigged nets, with an aperture of 4.5 m and mesh size of 20 mm in the main body of the net and 15 mm at the cod end. The trawls covered an approximate area of 2 Km in 30 min, at each island.

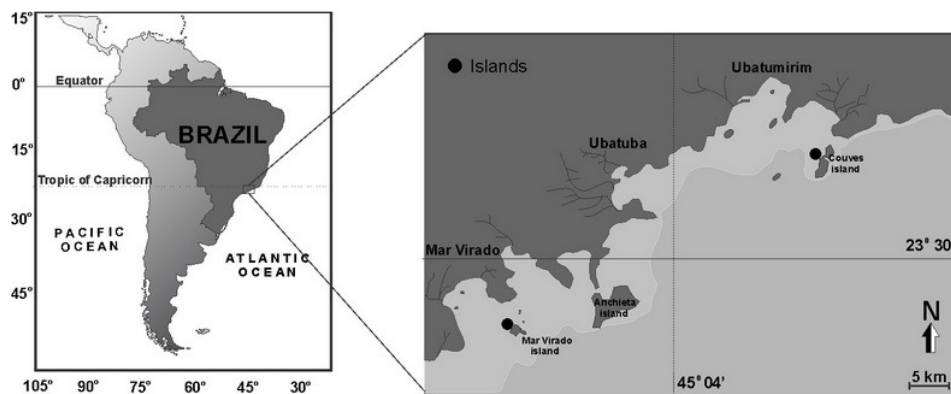


Figure 1. Map showing the locations of Couves and Mar Virado islands in the Ubatuba region.

After each trawl, all collected material was inspected, frozen, and transported to the laboratory. Shells occupied by hermit crabs were identified according to Rios (1994) and measured for aperture width (SAW) and dry weight (SDW), and then dried in an oven for 24 h at 60°C . The shell internal volume (SIV) was measured by filling it with water and then pouring the water into a graduated pipette (CONOVER, 1978). Hermit crabs were identified according to Melo (1999). The specimens were counted, manually removed from their shell, sexed based on the position of the gonopores (on the coxa of either the third or the fifth pair of pereopods in females and males, respectively), weighed (wet weight, CWW) in a precision balance (0.01 g), and their cephalothoracic shield length (CSL) was measured using a caliper (0.10 mm).

Statistical analysis

Data for abundance and biometric variables of the shells and hermit crabs were first tested for univariate normality and homoscedasticity, using Shapiro-Wilk (SHAPIRO; WILK, 1965) and Levene tests (SOKAL; ROLF, 1995). The test of multinomial proportions (GOODMAN, 1964) was performed for the values of abundance of males (M), females (F) and ovigerous females (FO), for each species of corresponding shell.

Abundance data were also evaluated by a correspondence analysis (AC). AC is a statistical method that demonstrates visually the associations among levels of the contingency table. Observed associations of the two variables (shell species and sex category of the crabs: Males, M; Females, F; and ovigerous females, FO) were summarized by the

frequency of each table cell and then arranged in a geometric dimensional space, so that the positions of each row and columns were consistent with associations in the table, resulting in a broad and interpretable view of multivariate data. The AC axes corresponding to a cumulative variation higher than 80% were considered significant. Permutations (n=999) were conducted to generate a probabilistic value of significance (p). In addition, graph points related to gastropod species were arranged proportionally to their abundance in the contingency table, providing a clear view of the association/abundance of each crab sex category with the species of shell occupied.

One-way ANOVA was used for each biometric variable of the shell (SDW, SAW and SIV), followed by Tukey-Kramer test to evaluate differences among the sex categories.. Finally, simple linear regressions among combinations of biometric variables of the shell (SDW, SAW and SIV; dependent variables) and of the hermit crab (CSL and CWW; independent variables) were analyzed. All analyses used the 5% significance level (SOKAL; ROLHF, 1995). Analyses were performed in the

software R (DEVELOPMENT CORE TEAM, 2013). The following statistical packages were used: for variance analysis and simple regressions, package 'stats'; and for Correspondence Analysis, package 'ca' (NENADIC; GREENACRE, 2007).

RESULTS

A total of 386 hermit crabs were collected near Couves and Mar Virado islands, including 252 males (65%), 115 females (35%) and 19 ovigerous females (5%). Among the 11 species of gastropod shells used by *D. insignis*, *Olivancillaria urceus* (31%), *Strombus pugilis* (22%) and *Siratus tenuivaricosus* (18%) were most frequent, while *Fusinus marmoratus* (1%), *Semicassis granulata* (1%) and *Polinices lacteus* (1%) were least used. Males used primarily shells of *Tonna galea* (0.9) and *Buccinanops cochlidium* (0.9), while females preferred *F. marmoratus* (0.5), *S. pugilis*, *S. tenuivaricosus* and *Stramonita haemastoma* (0.4), and ovigerous females preferred *S. pugilis*, *S. tenuivaricosus* and *S. haemastoma* (0.4) (Table 1).

Table 1. *Dardanus insignis*. Proportions of gastropod shells used by males (M), females (F) and ovigerous females (OF) caught in the Ubatuba region, state of São Paulo, Brazil.

Gastropod species	Total			Proportion ^{a, b}		
	M	F	FO	M	F	FO
<i>Buccinanops cochlidium</i> (Bc)	24	2	2	BC 0.80 a	B 0.10 b	A 0.10 b
<i>Cymatium parthenopeum</i> (Cp)	8	2	1	B 0.70 c	B 0.20 d	B 0.10 d
<i>Fusinus marmoratus</i> (Fm)	1	1	0	E 0.50 d	B 0.50 d	-
<i>Olivancillaria urceus</i> (Ou)	78	34	8	A 0.70 e	A 0.30 f	A 0.10 g
<i>Semicassis granulata</i> (Sg)	2	0	0	-	-	-
<i>Polinices lacteus</i> (Pl)	2	0	0	-	-	-
<i>Siratus tenuivaricosus</i> (St)	41	25	3	B 0.60 h	AC 0.36 h	AB 0.04 i
<i>Stramonita haemastoma</i> (Sh)	26	18	2	B 0.60 j	AC 0.36 j	A 0.04 k
<i>Strombus pugilis</i> (Sp)	49	32	3	AB 0.60 l	AC 0.36 l	AB 0.04 m
<i>Tonna galea</i> (Tg)	15	1	0	CD 0.90 n	B 0.10 o	-
<i>Zidona dufresnei</i> (Zd)	6	0	0			

^a Values on the same line with at least one lowercase letter in common for each factor (M, F and FO) did not differ ($p > 0.05$); ^b Values of the same column with at least one capital letter in common for each factor (M, F and FO) did not differ ($p > 0.05$).

Significant differences among the proportions of use for M, F and OF were detected both by the analysis of multinomial proportions (Table 1) and by AC ($p < 0.05$) (Figure 2). ANOVA showed that among the morphometric variables of shells, only shell aperture width ($F = 18.231$; $p < 0.0001$) was significant,

and males preferred larger shells than females (Tukey, $p < 0.0001$). The means for CSL were higher for males (7.83 mm) compared to females (6.16 mm) and ovigerous females (6.51 mm). There was no significant difference for the shell weight (SDW) and internal volume (SIV) (Figure 3).

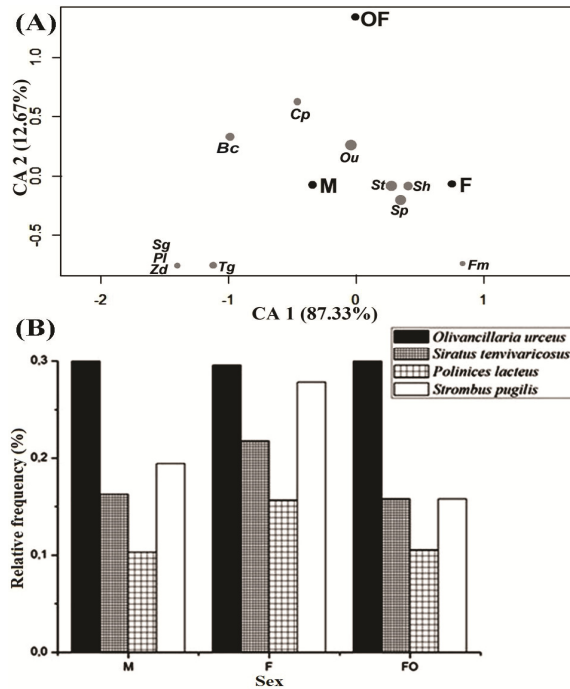


Figure 2. *Dardanus insignis*. Correspondence analysis of the relationship of shell use for males (M), females (F) and ovigerous females (FO) collected in the Ubatuba region, state of São Paulo, Brazil. (A) Relative frequency of use of the four most abundant shells for M, F and OF (B). Abbreviations as in Table 1.

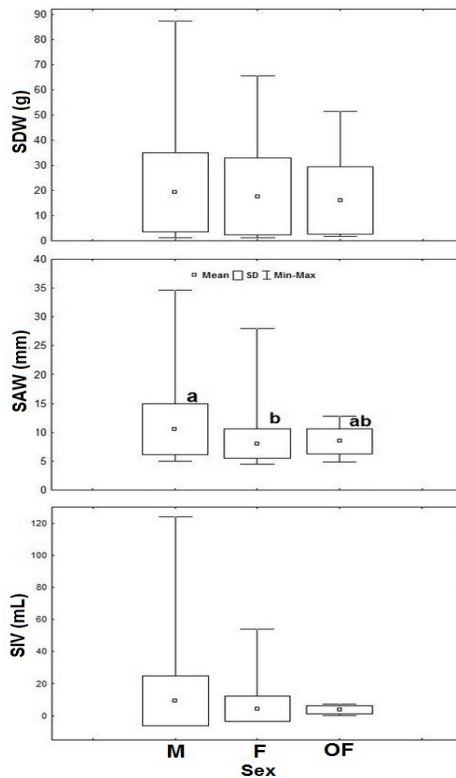


Figure 3. Mean aperture width (SAW), dry weight (SDW) and shell internal volume (SIV) used by males (M), females (F) and ovigerous females (FO) collected in the Ubatuba region, state of São Paulo, Brazil. Different letters indicate significant differences (Tukey test, following an ANOVA test)

The simple linear regressions indicated significant relationships, except between SAW of *O. urceus* and CWW of hermit crabs ($F=2.517$, $p=0.116$), and

among SIV of *S. pugilis* and SDW and CSL ($p=0.973$; $F=0.001$ $F=0.214$, $p=0.654$; respectively) (Table 2; Table 3).

Table 2. Biometric features of gastropod shells occupied by *Dardanus insignis* caught in the Ubatuba region, state of São Paulo, Brazil. (SAW= aperture width)

Gastropod species	Dry weight (g)			SAW (mm)			Volume (mL)		
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
<i>Buccinanops cochlidium</i> (Dillwyn, 1817)	3.4	9.04	6.22	6.4	9.9	8.15	0.9	6.4	3.5
<i>Cymatium parthenopeum</i> (Von Salis, 1793)	1.83	4.89	3.36	4.9	9.8	7.3	0.5	7	3.75
<i>Fusinus marmoratus</i> (Philippi, 1846)	3.09	13.4	8.26	6.3	7.4	6.8	1.6	-	1.6
<i>Olivancillaria urceus</i> (Roding, 1798)	4.6	40.4	22.5	5.4	12.9	9.1	1.6	13.5	7.5
<i>Semicassis granulata</i> (Von Born, 1778)	11.3	17.0	14.2	8.5	13	10.7	24	-	24
<i>Polinices lacteus</i> (Guilding, 1834)	10.9	11.3	11.1	11.6	20.7	16.1	5.4	5.4	5.4
<i>Siratus tenuivaricosus</i> (Dautzenberg, 1927)	1.1	21.2	11.1	4.7	14.4	9.55	0.2	7.2	3.7
<i>Stramonita haemastoma</i> (Linnaeus, 1767)	1.8	31.9	16.9	6.1	18	12.0	1	15.2	8.1
<i>Strombus pugilis</i> (Linnaeus, 1758)	7.0	70.1	38.6	5	11.4	8.20	4.5	13.5	9
<i>Tonna galea</i> (Mörch, 1877)	2.2	31.2	16.7	14.4	34.7	24.5	6.6	124	65.3
<i>Zidona dufresnei</i> (Donovan, 1823)	25.9	87.2	56.5	7.7	31.1	19.4	20	74	47

Table 3. Analyses of simple linear regression showing the significance (S) and non-significance (NS) between morphometric parameters of shells and their measurements. (SAW = aperture width; SDW = shell dry weight; SIV = shell internal volume; CSL = cephalothoracic shield length; CWW = wet weight of hermit crab).

Relationships	Species	Linear regression	r ² (%)
SAW vs. CSL	<i>O. urceus</i>	SAW = 0.7428.CSL + 0.5002	68% ^S
	<i>S. pugilis</i>	SAW = 0.5044.CSL - 0.7138	21% ^S
	<i>S. tenuivaricosus</i>	SAW = 0.7388.CSL - 0.1091	80% ^S
SAW vs. CWW	<i>O. urceus</i>	SAW = 0.2342.CWW + 1.2132	3% ^{NS}
	<i>S. pugilis</i>	SAW = 0.5044.CWW - 0.7138	21% ^S
	<i>S. tenuivaricosus</i>	SAW = 0.8583.CWW - 4.9889	80% ^S
SDW vs. CSL	<i>O. urceus</i>	SDW = 0.1077.CSL + 4.8616	37% ^S
	<i>S. pugilis</i>	SDW = 0.0371.CSL + 5.387	25% ^S
	<i>S. tenuivaricosus</i>	SDW = 0.3252.CSL + 4.1431	68% ^S
SDW vs. CWW	<i>O. urceus</i>	SDW = 0.0532.CWW + 2.1888	4% ^S
	<i>S. pugilis</i>	SDW = 0.0557.CWW + 1.1212	30% ^S
	<i>S. tenuivaricosus</i>	SDW = 0.3964.CWW - 0.1559	75% ^S
SIV vs. CSL	<i>O. urceus</i>	SIV = 0.4955.CSL + 4.2419	68% ^S
	<i>S. pugilis</i>	SIV = 0.0889.CSL + 6.2675	2% ^{NS}
	<i>S. tenuivaricosus</i>	SIV = 0.8866.CSL + 4.1321	75% ^S
SIV vs. CWW	<i>O. urceus</i>	SIV = 0.1078.CWW + 3.0198	1% ^S
	<i>S. pugilis</i>	SIV = 0.2001.CWW + 2.2332	6% ^{NS}
	<i>S. tenuivaricosus</i>	SIV = 0.9874.CWW - 0.0012	78% ^S

DISCUSSION

The hermit crab *D. insignis* occupied a total of 11 species of gastropod shells during the study period. *O. urceus* was used most often, indicating the hermit crabs' preference. This species is the most available shell on non-consolidated bottoms of southeastern Brazil (MARTINELLI; MANTELATTO, 1999; MIRANDA et al., 2006; MANTELATTO et al., 2007; MEIRELES; MANTELATTO, 2008; FANTUCCI et al., 2008; AYRES-PERES et al., 2012), which may be the reason that its shell was most often used by *D. insignis*. The regression analysis showed that the hermit crabs select shells based on their aperture width, with the highest mean values observed for the *T. galea* and *Zidona dufresnei*. According to Wada et al. (1997), the shell aperture is the main variable influencing the choice of shells by *Pagurus middendorffii* Brandt 1851. However, the shell species with the largest aperture width were not commonly used by *D. insignis*, considering that this species is smaller than the hermit crab *Petrochirus diogenes* (Linnaeus, 1758), which according to Bertini and Fransozo (2000) occupies mainly the two shell species mentioned above.

The proportion of males in these two shell species was significant, respectively 0.9 and 1.0 (only males inhabited; n=6). This may be related to the CSL of hermit crabs, which averaged larger in males in relation to females and ovigerous females. This affects mainly intraspecific relationships, in which differential occupation of shells between sexes reduces competition, thus the use of larger shells by males increases the asymptotic value, which confers advantages in accessing reproductive females and in the copulation process (ASAKURA, 1995).

Most males occupied smaller shells, such as *S. tenuivaricosus*, *S. haemastoma* and *S. pugilis*; however, a higher proportion of these shells was used by females and ovigerous females, in agreement with observations by Abrams (1988), who found that the difference in growth patterns between males and females may influence the selection and occupation of shells, where females (smaller) occupy smaller shells, and the contrary is observed for males. Another, concordant hypothesis was proposed by Fotheringham (1976), who stated that if females occupy shells larger than their size, the energy cost of locomotion, shell cleaning and defense during competitions would be high and consequently the reproductive rate whole decrease because of the diversion of energy to growth in size.

Shell weight was the most significance parameter in the analysis of linear regression, possibly because *O. urceus* and *S. pugilis* have heavy shells with small internal volumes (Simone (2005). Hahn (1998) suggested that the use of heavy shells may not affect the energy consumption only in species that feed through marine currents. Because of its habit of active foraging, *D. insignis* is directly influenced by the shell weight, and the smaller internal volume of these most preferred species (*O. urceus* and *S. pugilis*) considerably decreases the fecundity rate, which may be the reason for the great abundance of this species compared to other hermit crabs in the region (MIRANDA et al., 2006).

The preference of *D. insignis* for the shell of *O. urceus* was also reported by Branco et al. (2002); Ayres-Peres et al. (2008) and Fransozo et al. (2008). All these investigators ascribed this preference to the availability of shells in the environment and to the zone of this gastropod's occurrence, which according to Rios (1994) is found on sand and mud bottoms to a depth of 50 m. According to Fernandes-Goés et al. (2005), *D. insignis* is generally captured in this type of habitat, corroborating the suggestion about the reason for the choice of *O. urceus* shells.

Although in nature most hermit crab species are not selective in their choice of shells, but rather are opportunists (HAZLETT, 1981), studies such as that of Grant and Ulmer (1974) corroborated experimental studies in laboratory with *Pagurus acadianus* (Benedict, 1901) and *Pagurus pubecens* (Krøyer, 1838), revealing a selection pattern that may be a function of the size, weight, shape or shell species. According to Fransozo et al. (2012) the number of species as well as the abundance of hermit crabs are also intrinsically related to environmental factors, particularly the substrate characteristics (FURLAN et al., 2013). Such environmental conditions can determine not only the richness, but also the abundance of gastropods and hermit crabs (PIRES, 1992). The diversity of the former will directly affect the abundance and success of the latter (MEIRELES et al., 2003). The greater availability of empty shells is also responsible for reducing competition among crabs (MCLEAN, 1983), since in this study approximately 13 species of hermit crabs coexist, which occupied empty gastropod shells (FRANSOZO et al., 2008, 2012), among these *Petrochirus diogenes* and *Loxopagurus loxochelis*, thus competing directly with *D. insignis* (FRANSOZO et al., 2008). The results of this study demonstrated a distinct selectivity pattern in *D. insignis*, strengthening the

need for correlations with environmental factors (environmental variables), as well as competition with other species.

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RESUMO: O uso de conchas de gastrópodos por ermitões se dá de acordo com a disponibilidade no ambiente ou através de mecanismos seletivos relacionados, como o tamanho e volume. O objetivo deste trabalho foi analisar os padrões do uso de conchas por *Dardanus insignis* (Saussure, 1858). Durante o período de janeiro de 1998 a dezembro de 1999 foi coletado um total de 386 indivíduos em duas ilhas pertencentes à Ubatuba, São Paulo, os quais foram medidos de acordo com o comprimento do escudo cefalotorácico (CEC) e o peso úmido (PA). As conchas ocupadas pelos ermitões foram identificadas e mensuradas quanto a largura de abertura (LAC), peso (PSC) e volume interno da concha (VIC). As relações entre as variáveis da concha de gastrópodo e o ermitão, foram avaliadas através da análise de regressão linear. Dentre as onze espécies de concha de gastrópodes utilizadas por *D. insignis*, a mais usada foi *Olivancillaria urceus* (31%), seguida por *Strombus pugilis* (22%) e *Siratus tenuivaricosus* (18%). A concha de *O. urceus* foi a mais utilizada, provavelmente devido a sua maior disponibilidade na ilha das Couves e do Mar Virado. Os resultados mostraram que dos parâmetros biométricos mensurados das conchas, o mais significativo foi largura da abertura da concha ($F=18.231$; $p<0.0001$), evidenciando a importância desta variável para a escolha das conchas por *D. insignis* nos dois locais.

PALAVRAS-CHAVE: Mollusca. Ermitão. Seleção de habitat. Relações interespecíficas. Morfométrico.

REFERENCES

- ABRAMS, P. A. Sexual difference in resource use in hermit crabs: consequences and causes. In: Chelazzi, G.; Vannini, M. (Eds.). **Behavioral adaptations to intertidal life**. New York, Ed. Plenum, p. 283-296, 1988.
- ASAKURA, A. Sexual differences in life history and resource utilization by the hermit crab. **Ecology**, Washington, v. 76, n. 7, p. 2295-2313, 1995.
- AYRES-PERES, L.; QUADROS, A.F.; MANTELATTO, F.L. Comparative analysis of shell occupation by two southern populations of the hermit crab *Loxopagurus loxochelis* (Decapoda, Diogenidae). **Brazilian Journal of Oceanography**, São Paulo, v. 60, n. 3, p. 299-310, 2012.
- AYRES-PERES, L.; SOKOLOWICZ, C. C.; KOTZIAN, C. B.; RIEGER, P. J.; SANTOS, S. Ocupação de conchas de gastrópodes por ermitões (Decapoda, Anomura) no litoral de Rio Grande, Rio Grande do Sul, Brasil. **Iheringia**, Porto Alegre, v. 98, n. 2, p. 218-224, 2008.
- BERTINI, G; FRANSOZO, A. Patterns of utilization in *Petrochirus diogenes* (Decapoda, Anomura, Diogenidae) in the Ubatuba region, São Paulo, Brazil. **Journal Crustacean Biology**, New Braunfels, v. 20, n. 3, p. 468-473, 2000.
- BERTNESS, M. D. The influence of shell-type on hermit crab growth rate and clutch size. **Crustaceana**, Leiden, v. 40, p. 197-205, 1981.
- BRANCO, J. O.; TURRA, A.; SOUTO, F. X. Population biology and growth of the hermit crab *Dardanus insignis* at Armação do Itapocoroy, southern Brazil. **Journal of the Marine Biological Association of the United Kingdom**, London, v. 82, p. 597-603, 2002.
- CONOVER, M. R. The importance of various Shell characteristics to the shell-selection behaviour of the hermit crabs. **Journal of Experimental Marine Biology and Ecology**, Amsterdam, v. 32: p. 131-142, 1978.

COSTA, R. C.; FRANSOZO, A.; FREIRE, F. A. M. Abundance and ecological distribution of the “sete-barbas” shrimp *Xiphopenaeus kroyeri* (Heller, 1862) (Decapoda: Penaeoidea) in three bays of the Ubatuba region, South-eastern Brazil. **Gulf and Caribbean Research**, Ocean Springs, v. 19, p. 33-41, 2007.

DEVELOPMENT CORE TEAM. R: **A language and environment for statistical computing**. Austria, R Foundation for Statistical Computing, Vienna. Available at: <http://www.R-project.org>, 2013.

FANTUCCI, M. Z.; BIAGI, R.; MANTELATTO, F. L. Shell occupation by the endemic western Atlantic hermit crab *Isocheles sawayai* (Diogenidae) from Caraguatatuba, Brazil. **Brazilian Journal of Biology**, São Carlos, v. 68, n. 4, p. 859-867, 2008.

FERNANDES-GOÉS, L. C.; FRANSOZO, A.; GOÉS, J. M. Population dynamics of *Dardanus insignis* (Saussure, 1858) (Crustacea, Anomura, Diogenidae) in the Ubatuba region, São Paulo, Brazil. **Nauplius**, Porto Alegre, v. 13, n. 2, p. 191-196, 2005.

FOTHERINGHAM, N. Hermit crab shells as a limiting resource (Decapoda, Paguridea). **Crustaceana**, Leiden, v. 32, n. 2, p. 193-199, 1976.

FRANSOZO, A.; BERTINI, G.; BRAGA, A. A.; NEGREIROS-FRANSOZO, M. L. Ecological aspects of hermit crabs (Crustacea, Anomura, Paguroidea) off the northern coast of Sao Paulo State, Brazil. **Aquatic Ecology**, Amsterdam, v. 42, p. 437-448, 2008.

FRANSOZO, A.; FERNANDES-GÓES, L. C.; FRANSOZO, V.; GÓES, J. M.; COBO, V. J.; TEIXEIRA, G. M.; GREGATI, R. A. Marine anomurans (Decapoda) from the non-consolidated sublittoral bottom at the Southeastern of Brazil. **Crustaceana**, Leiden, v. 84, n. 4, p. 435-450, 2011.

FRANSOZO, A.; FURLAN, M.; FRANSOZO, V.; BERTINI, G.; COSTA, R.C.; FERNANDES-GÓES, L. C. Diversity of decapod crustaceans at the interface of unconsolidated seabed areas and rocky shores in tropical/subtropical Brazil. **African Journal of Marine Science**, v. 34, n. 3, p. 361-371, 2012.

FURLAN, M.; CASTILHO, A.L.; FERNANDES-GÓES, L.C.; FRANSOZO, V.N.; BERTINI, G.; COSTA, R.C. Effect of environmental factors on the abundance of decapod crustaceans from soft bottoms off southeastern Brazil. **Anais da Academia Brasileira de Ciências**, v. 85, p. 83-92, 2013.

GOODMAN, L. A. Simultaneous confidence intervals for contrasts among multinomial populations. **The Annals of Mathematical Statistics**, Beachwood, v. 35, n. 2, p. 716-725, 1964.

GRANT, W. C.; ULMER, K. M. Shell selection and aggressive behavior in two sympatric species of hermit crabs. **The Biological Bulletin**, Woods Hole, v. 146, p. 32-43, 1974.

HAHN, D.R. Hermit crab shell use patterns: response to previous shell experience and to water flow. **Journal of Experimental Marine Biology and Ecology**, Amsterdam, v. 228, p. 35-51, 1998.

HAZLETT, B. A. The behavioral ecology of hermit crab. **Annual Review of Ecology and Systematics**, Palo Alto, v. 12, p. 1-22, 1981.

MANTELATTO, F. L.; BIAGI, L.; MEIRELES, A. L.; SCALZO, M. A. Shell preference of the hermit crab *Pagurus exilis* (Anomura: Paguridae) from Brazil and Argentina: a comparative study. **Revista de Biología Tropical**, San José, v. 55, n. 1, p. 153-162, 2007.

MANTELATTO, F. L. M.; DOMINCIANO, L. C. C. Pattern of shell utilization by the hermit crab *Paguristes tortugae* (Diogenidae) from Anchieta Island, southern Brazil. **Scientia Marina**, Barcelona, v. 66, n. 3, p. 265-272, 2002.

- MARTINELLI, J. M.; MANTELATTO, F. L. M. Shell utilization by the hermit crab *Loxopagurus loxochelis* (Diogenidae) in the Ubatuba Bay, Brazil. In: Schram, F. R.; Vanpel-Klein, J. C. (Eds.). **Crustaceans and the Biodiversity Crisis**, v. 1. Leiden, Ed. Brill, p. 719-731, 1999.
- MCLAUGHLIN, P. A.; LEMAITRE, R.; SORHANNUS, U. Hermit crab phylogeny: a reappraisal and its “fall-out”. **Journal Crustacean Biology**, New Braunfels, v. 27, p. 97-115, 2007.
- MCLEAN, R. Gastropod shells: a dynamic resource that helps shape benthic community structure. **Journal of Experimental Marine Biology and Ecology**, Amsterdam, v. 69, p. 151-174, 1983.
- MEIRELES, A.L.; BIAGI, R.; MANTELATTO, F.L. Gastropod shell availability as a potential resource for the hermit crab infralittoral fauna of Anchieta Island (SP), Brazil. **Nauplius**, p. 11, v. 2, p. 99-105, 2003.
- MEIRELES, A. L.; MANTELATTO, F. L. Biological features of a puzzling symbiotic association between the hermit crab *Dardanus insignis* and the porcellanid crab *Porcellana Sayana* (Crustacea). **Journal of Experimental Marine Biology and Ecology**, Amsterdam, v. 362, p. 38-42, 2008.
- MELO, G. A. S. **Manual de identificação dos Crustacea Decapoda do litoral brasileiro: Anomura, Thalassinidea, Palinuridea e Astacidea**. Plêiade, São Paulo, Brasil, 1999. 551 p.
- MIRANDA, I.; MEIRELES, A. L.; BIAGI, R.; MANTELATTO, F. L. Is the abundance of the red brocade hermit crab *Dardanus insignis* (Decapoda: Anomura: Diogenidae) in the infralittoral region of southern Brazil determined by reproductive potential? **Crustacean Research**, Tokyo, v. 6, Special Number, p. 45-55, 2006.
- NENADIC, O.; GREENACRE, M. J. Correspondence Analysis in R, with Two and Three Dimensional Graphics: The ca Package. **Journal of Statistical Software**, Alexandria, v. 20, n. 3, p. 1-13, 2007.
- NUCCI, P. R.; MELO, G. A. S. Hermit crabs from Brazil. Family Paguridae (Crustacea: Decapoda: Paguroidea): Genus Pagurus. **Zootaxa**, London, v. 1406, p. 47-59, 2007.
- PIRES, A.M.S. Structure and dynamics of benthic megafauna on the continental shelf offshore of Ubatuba, Southeastern Brazil. **Marine Ecology Progress Series**, v. 86, p. 63-76, 1992.
- RIEGER, P. J. Os ermitões (Crustacea, Decapoda, Paraguridae, Diogenidae e Paguridae) do litoral do Brasil. **Nauplius**, Porto Alegre, v. 5, n. 2, p. 99-124, 1997.
- RIOS, E. C. **Sea shells of Brazil**. Fundação Cidade do Rio Grande, Instituto Acqua, Museu Oceanográfico de Rio Grande, Universidade de Rio Grande, Rio Grande do Sul, 1994. 368 p.
- SAMUELSEN, T. J. The biology of six species of Anomura (Crustacea, Decapoda) from Raunefjorden, Western Norway. **Sarsia**, Norway, v. 45, p. 25-52, 1970.
- SATO, Y.; SENO, H. A. A mathematical consideration for the optimal shell change of hermit crab. **Journal of Theoretical Biology**, Amsterdam, v. 240, p. 14-23, 2006.
- SCHEMBRI, P. J. Feeding behavior of fifteen species of hermit crabs (Crustacea: Decapoda: Anomura) from the Otago region, southeastern New Zealand. **Journal of Natural History**, London, v. 16, p. 859-878, 1982.
- SCULLY, E. P. The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. **Journal Experimental of Marine Biology and Ecology**, Amsterdam, v. 37, p. 139-152, 1979.
- SHAPIRO, S. S, WILK, M. B. An analysis of variance for normality (complete samples). **Biometrika**, London, v. 52, p. 591-611, 1965.

SIMONE, L. R. L. Comparative Morphological Study of Representatives of the Three Families of Stromboidea and the Xenophoroidea (Mollusca, Caenogastropoda), with an Assessment of their Phylogeny. **Arquivos de Zoologia de São Paulo**, São Paulo, v. 37, n. 2, p. 141-267, 2005.

SOKAL, R. R.; ROHLF, F. J. **Biometry**. The principles and practice of biological research. Freeman, New York, 1995. 937 p.

WADA, S. H.; OHMORI, S.; GOSHIMA, S. Shell size preference of hermit crabs depends on their growth rate. **Animal Behaviour**, Amsterdam, v. 54, p. 1-8, 1997.