Shell occupation by the South Atlantic endemic hermit crab *Loxopagurus loxochelis* (Moreira, 1901) (Anomura: Diogenidae)

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Abstract - The evaluation of population characteristics, particularly those of endemic species, aids in population preservation and management. Hermit crabs present an innate behavior of occupying shells, which tends to individual needs and limits their distribution. This study characterized the pattern of occupation of gastropod shells by the hermit *Loxopagurus loxochelis* in three bays of the southwestern coast of Brazil. Monthly collections were made from January/1998 to December/1999 in the bays Ubatumirim (UBM), Ubatuba (UBA) and Mar Virado (MV) with a shrimping boat. Overall, ten species of gastropod shells were occupied by *L. loxochelis*. The shell of *Olivancillaria urceus* represented 66.8% of those occupied. Morphometric relationships demonstrated a differential occupation of the more abundant shells among demographic groups, where most of the males occupied *O. urceus,* non-ovigerous females occupied *O. urceus* and *Buccinanops cochlidium*, and ovigerous females occupied *B. cochlidium* and *Stramonita haemastoma*. Most of the individuals occupied the more abundant shells, considered adequate for the morphology of this hermit crab species. Thus, the studied bays seem to be stable and propitious environments for population perpetuation and the settlement of new individuals.

Key words: Gastropod shells, interspecific relationships, multivariate analysis, partial least square (PLS)

Introduction

The infraorder Anomura MacLeay, 1838 represents an important part of intertidal and benthic community of shallow regions, playing a remarkable role in trophic webs (Negreiros-Fransozo *et al.*, 1997), which more than 100 species recorded for Brazilian coast (Melo, 1999). Among them, the superfamily Paguroidea includes all hermit crabs that occupy gastropod shells, in which families Paguridae and Diogenidae are included as well as more than 950 species from the whole world (McLaughlin *et al.*, 2010).

The shell provides protection to the non-calcified abdomen, making the hermit crab less susceptible to predator attack (Reese, 1968; Conover, 1978). Due to the abdomen morphology, hermit crabs are able to occupy and carry gastropod shells, and this feature is one of the main reasons for the evolutionary success of the group (Hazlett, 1981). Thereby, usually rare or absent shells are a determinant factor for the hermit crab distribution, consisting of a limiting factor for the individual and population growth (Kellogg, 1976).

The acquisition of shells starts from the megalope stage (post-larvae), characterized as innate behavior (Reese, 1963; Hazlett, 1971). According to individual needs, hermit crabs may find an adequate empty shell from locations in sites of gastropod predation (Mclean, 1973) or swap them during inter and intraspecific interaction (Rittschoff, 1980). Shell swap is mentioned in agonistic behavior among hermit crabs, not only on the establishment of dominant species, but mainly related to the competition for adequate shells (see more in Hazlett and Bossert, 1965; 1966; Hazlett, 1966; 1967; 1968; 1972). Hermit crabs display a peculiar behavior for inspection and choice of new shells, discriminating characteristics like weight, volume, shell aperture and wear (Resse, 1962; Conover, 1978). Univariate correlations between the measured variables are used to determine the relationship between the hermit crab and the occupied shell (Hazlett, 1981; Barnes, 1999; Arce and Alcaraz, 2009; Ismail, 2010). Authors like Kuris and Brody (1976), Caruso and Chemello (2009), and Ayres-Peres *et al.* (2012) employed the use of multivariate statistical tools, as the main compound analysis, with the aim to more securely appoint the factors that may bear high relevance for shell occupation, especially in natural environments.

The hermit crab *Loxopagurus loxochelis* (Moreira, 1901) is endemic of Southwestern Atlantic, being widely spread among the Brazilian state of Bahia to Argentina (Melo, 1999). The species biology has been studied continuously at the Brazilian coast (Mantelatto and Martinelli, 2001; Martinelli *et al.*, 2002; Mantelatto *et al.*, 2004; Bertini *et al.*, 2004; Biagi *et al.*, 2006); however, due to the great extent of the Brazilian coast and endemism, it is necessary to evaluate the characteristics of distinct populations, as well as suitable gastropod shells used by different populations of *L. loxochelis*.

Therefore, the present study aims to outline the trend of gastropod shell occupation by demographic groups of *L. loxochelis* in three regions of the Northern coast of the state of São Paulo, through systematized collection and analysis, using the occupation percentage of different shells and multivariate analysis to pinpoint the morphometric variables of shells that are better related to the hermit crab morphology. Such information may provide a basis for the species' biology, especially with regards to its preservation.

Material and Methods

Animals were collected monthly from January 1998 to December 1999 in the bays Ubatumirim (UBM), Ubatuba (UBA) and Mar Virado (MV) (23°33'36"W/45°11'32"S; 23°26'10"W/45°01'36"S; 23°23'00"W/44°54'48"S, respectively). Six transects were trawled over for each bay, delimited by a GPS (Global Position System). Collections were made with the aid of a shrimp fishing boat equipped with dual-rigged type nets with approximately 4.5m openings and between-node distance of 20 and 15mm of mesh size and cod end, respectively. Each transect comprised 2 Km of extension for 30 minutes with an approximate area of 18,000 m^2.

After each dragging, all the collected material was submitted to screening, frozen and transported to the laboratory, at which hermit crabs were identified according to Melo (1999), counted, removed manually from the shells, separated by gender according to gonopore position, weighed (wet weight, WW) on a precision scale (0.01g) and measured with use of a caliper rule (0.10 mm) in relation to cephalothorax shield length (CSL). Shells occupied by the hermit crab *L. loxochelis* were identified according to Rios

(1994), dry weighed (SDW) and measured in relation to the shell aperture width (SAW). After 24 hours at 60°C, shell internal volume (SIV) was measured by filling with water with a pipette, following Conover (1978).

Initially, morphometric data both of hermit crabs and shells were evaluated in comparison to the univariate normality through the Kolmogorov-Smirnov test. When there was no normality, data was transformed into logarithms and a variance analysis (ANOVA one way) was performed in order to verify the difference of each morphometric variable amongst occupied shell species, complemented by a Tukey test (Zar, 1996).

Multivariate analyses were performed to identify and evaluate the patterns of gastropod shell occupation by the hermit crab *L. loxochelis*, such as the principal component analysis (PCA), correspondence analysis (CA), multivariate analysis of variance (MANOVA) and partial least squares (PLS). All multivariate analyses were made through the R statistical computing software R (R Development Core Team 2009). The use of each statistical package of the R software was performed separately in order to avoid possible mathematical algorithm conflicts of each function. The species of gastropods shells that featured an abundance equal to "one" were removed from the statistical analysis due to data inconsistency, and were considered rare species in the studied region. Initially data was tested regarding the multivariate normality by the symmetry and kurtosis test (Mardia, 1970; 1980) (with modifications suggested by Doornik and Hansen, 2008 – omnibus test). Furthermore, a Box's M test (Anderson, 1958) was performed to evaluate the equivalence (multivariate homogeneity) among covariance matrices of data, with Monte Carlo permutations to estimate the significance value of this test.

A PCA was conducted to verify which species of gastropod shells are more explanatory during the selection of demographic groups (males, females, ovigerous females) of *L. loxochelis*. Variations higher than 0.7 and the principal component that explained more than 80% of data variation were considered significant. PCA was conducted by "vegan" package (Oksanen, 2011; vegan.r-forge.r-project.org).

Data related to abundance of each demographic group, for each species of shell occupied, were organized in a two factors contingence table in order to conduct a Correspondence Analysis (CA). During the CA, observed associations of both variables (demographic group and shell species) were summarized by the frequency of each table cell, and then positioned in a geometric dimensional space, since the positions of each line and column were consistent with the associations of the table. The axes that corresponded to a cumulative variation higher than 80% were considered significant. In addition, graphic points related to the shell species were arranged according to their abundance in the contingency table, creating a view of association/abundance of each shell species within demographic groups. A CA was performed through the "CA" routine of the "CA" package (Grenacre, 1993; Nenadic and Greenacre, 2007). Then, a MANOVA was performed with involvement of data regarding shell abundance by the factors (1) demographic groups and (2) collection locality, to investigate the difference of means of abundance.

The PLS was used for analysis of morphometric data from occupied shells and their respective resident hermit crab. This analysis consists of a recent technique that generalizes and combines characteristics of a principal component analysis and multiple regression. This technique has been used to forecast a set of dependent variables (morphometric data matrix of hermit crabs) from a set of independent variables (morphometric data matrix of shells) (see more in Abdi, 2007). This technique was built over a robust mathematic framework and details may be seen in Höskuldsson (1988) and Haenlein and Kaplan (2004). The variable in importance projection (VIP), coefficients and weight of morphometric variables of shells in relation to the hermit crabs were analyzed among demographic groups of hermit crabs from collection locations and, in general combining data from all bays.

The VIP consists of a statistic generated by the PLS, which shows the contribution of the independent variable to the model. Based on Wold (1995), VIP values higher than 1 were considered high variable contribution to the model, VIP between 1 and 0.8, relevant contribution, and VIP lower than 0.8, not relevant contribution. Independent variable weights were used to determine their influence on the projection (VIP). As there is not a statistic PLS test to demonstrate significant differences among VIPs, the values from variable weights were also analyzed to facilitate the interpretation of VIP values. PLS regression was performed through the "plsreg2" routine of "plspm" package (Sanchez and Trinchera, 2012; plsmodeling.com).

Results

Overall, 883 individuals of *L. loxochelis* were captured in the three bays (Tab. 1). In UBM and UBA eight species of shells were occupied, while in MV six species used by hermit crabs were recorded, with a total of ten species being occupied by *L. loxochelis*. In all the localities the most occupied gastropod shell was *Olivancillaria urceus* (Röding, 1798) (Fig. 1a), followed by *Buccinanops cochlidium* (Dillwyn, 1817) (Fig. 1b) and *Stramonita haemastoma* (Linnaeus, 1767) (Fig. 1c) (Tab. 1). Animals were divided into 12 size classes, with 0.6 mm amplitude, from a minimum size of 2.5 mm of CSL. The relative frequency distribution of individuals in size classes presented normal patterns, with unimodal distribution (UBM, KS = 0.058, p = 0.20; UBA, KS = 0.601, p = 0.10; and MV, KS = 0.078, p = 0.10) (Fig. 2). A significant difference was observed between the mean dry weight (ANOVA; F = 55.48, $p < 0.01$) and aperture width (F = 21.35, $p < 0.01$), and the *O. urceus* presented the highest weight (Tukey; $p < 0.01$), and also the lowest aperture width among the most occupied species ($p < 0.01$). As for the shells internal volume of occupied, *B. cochlidium* was significantly the highest ($p < 0.01$) (Tab. 2).

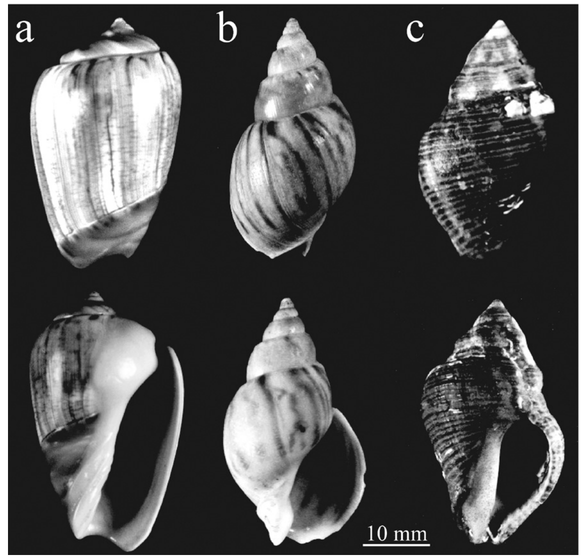

Figure 1. Most frequently used species of gastropod's shells occupied by *Loxopagurus loxochelis* in the subtropical region of Brazil. (a) *Olivancillaria urceus.* (b) *Buccinanops cochlidium.* (c) *Stramonita haemastoma*.

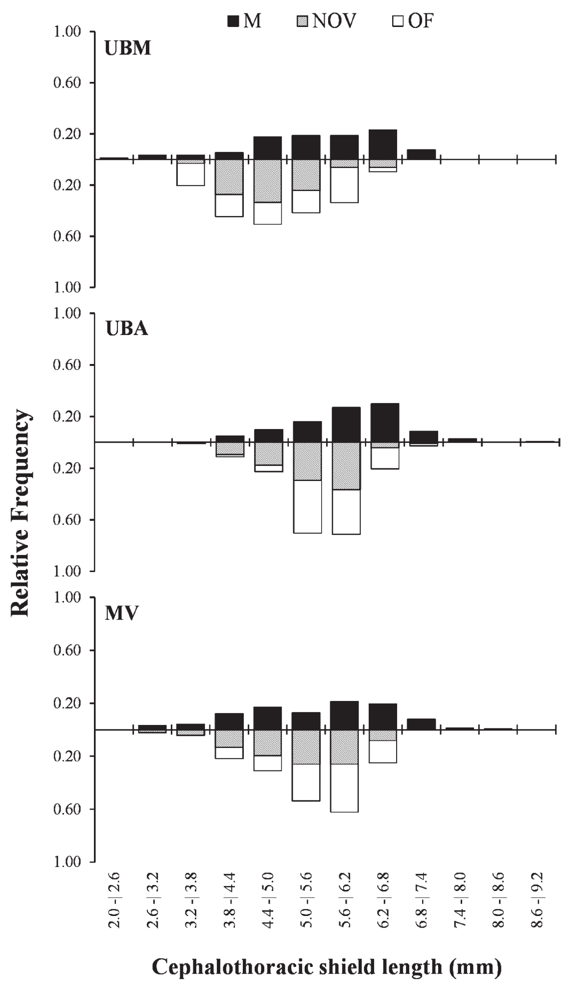

Figure 2. Relative frequency distribution for each group of interest of individuals collected in the subtropical region of Brazil. (M = males; NOF = non-ovigerous females; OF = ovigerous females).

Table 1. Percentage of gastropod shell species occupation by *L. loxochelis* in the three bays of Ubatuba region (SP). (N = number of individuals; M = males; NOF = non-ovigerous females; OF = ovigerous females).

Species	UBM								UBA								MV							
	M		NOF		OF		Total		M		NOF		OF		Total		M		NOF		OF		Total	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Olivancillaria urceus (Röding, 1798)	43	47.8	21	63.6	11	50.0	75	51.7	218	76.2	75	78.9	49	80.3	342	77.4	106	64.6	54	56.3	8	22.2	168	56.8
Buccinanops cochlidium (Dillwyn, 1817)	17	18.9	1	3.0	3	13.6	21	14.5	36	12.6	12	12.6	9	14.8	57	12.9	49	29.9	41	42.7	22	61.1	112	37.8
Stramonita haemastoma (Linnaeus, 1767)	16	17.8	9	27.3	6	27.3	31	21.4	26	9.1	5	5.3	2	3.3	33	7.5	8	4.9	1	1.0	4	11.1	13	4.4
Siratus tenuivaricosus (Dautzenberg, 1927)	5	5.6	1	3.0	1	4.5	7	4.8	-		-		-		-		-		-		-		-	
Cymatium parthenopeum (von Salis, 1793)	2	2.2	1	3.0	1	4.5	4	2.8	2	0.7	1	1.1	0	0.0	3	0.7	-		-		-		-	
Polinices lacteus (Guilding, 1834)	4	4.4	0	0.0	0	0.0	4	2.8	2	0.7	1	1.1	0	0.0	3	0.7	0	0.0	0	0.0	1	2.8	1	0.3
Fusinus marmoratus (Philippi, 1846)	2	2.2	0	0.0	0	0.0	2	1.4	0	0.0	1	1.1	1	1.6	2	0.5	1	0.6	0	0.0	0	0.0	1	0.3
Olivancillaria vesica vesica (Gmelin, 1791)	1	1.1	0	0.0	0	0.0	1	0.7	-		-		-		-		-		-		-		-	
Semicassis granulata (Born, 1778)	-		-		-		-		1.0	0.3	0	0	0	0	1	0.2	0.0	0.0	0.0	0.0	1.0	2.8	1.0	0.3
Strombus pugilis (Linnaeus, 1758)	-		-		-		-		1.0	0.3	0	0	0	0	1	0.2	-		-		-		-	
Total	90	100	33	100	22	100	145	100	286	100	95	100	61	100	442	100	164	100	96	100	36	100	296	100

Table 2. Characterization of 883 gastropod shells occupied by *L. loxochelis* species from three bays, and results of ANOVA test, in which different letters differ significantly (OP = occurrence percentage).

Gastropod species	N	Weight Min. Max. Mean ± SD	Aperture Width Min. Max. Mean ± SD	Internal Volume Min. Max. Mean ± SD	OP (%)
Olivancillaria urceus (Röding, 1798)	585	1.06 36.08 8.75 ± 4.26 **a**	3.1 13.4 6.67 ± 1.39 **a**	0.3 6.5 2.84 ± 1.39 **a**	66.25
Buccinanops cochlidium (Dillwyn, 1817)	190	0.62 12.83 4.15 ± 2.07 **b**	4.2 14.7 7.88 ± 1.72 **b**	0.4 10 3.67 ± 1.41 **bc**	21.52
Stramonita haemastoma (Linnaeus, 1767)	77	0.66 12.95 4.75 ± 2.78 **b**	3.2 15.2 8.35 ± 2.63 **b**	0.2 9 2.39 ± 1.78 **b**	8.72
Polinices lacteus (Guilding, 1834)	8	0.7 4.77 3.08 ± 1.64 **b**	6.3 11.3 9.45 ± 1.75 **b**	0.6 2.5 1.27 ± 0.75 **b**	0.91
Cymatium parthenopeum (von Salis, 1793)	7	2.12 6.31 4.13 ± 1.61 **b**	7.2 9.5 8.51 ± 0.82 **b**	1.1 4.3 2.83 ± 1.25 **ac**	0.79
Siratus tenuivaricosus (Dautzenberg, 1927)	7	1.8 9.59 4.50 ± 2.62 **b**	5.7 9.7 7.80 ± 1.70 **ab**	0.4 4.4 1.92 ± 1.53 **b**	0.79
Fusinus marmoratus (Philippi, 1846)	5	0.79 5.97 3.88 ± 1.94 **b**	4.7 7.6 6.68 ± 1.16 **ab**	0.5 2.5 1.70 ± 1.06 **abc**	0.57
Semicassis granulata (Born, 1778)	2	2.44 7.09 4.77 ± 3.29	7.4 11.1 9.25 ± 2.62	3.1 3.1 3.10 ± 1.39	0.23
Strombus pugilis (Linnaeus, 1768)	1	57.04	11.4	5	0.11
Olivancillaria vesica vesica (Gmelin, 1791)	1	2.65	5.9	1.8	0.11

The PCA evidenced the shells of *O. urceus, B. cochlidium* and *S. haemastoma* as the most representative for the pattern of shell occupancy of *L. loxochelis* (Tab. 3). From these results, a correspondence analysis was performed, evidencing greater utilization of males for shells of *O. urceus*, while non-ovigerous females occupied *O. urceus* and *B. cochlidium* more often. Ovigerous females used *B. cochlidium* and *S. haemastoma* (Fig. 3). The results obtained by the MANOVA to evaluate the differences of the mean abundance of choices, by demographic groups and localities, indicated that there was difference only among locations (Tab. 4).

The variance accumulated in each PLS essay was over 80% for the two initial factors, except for trials on ovigerous females

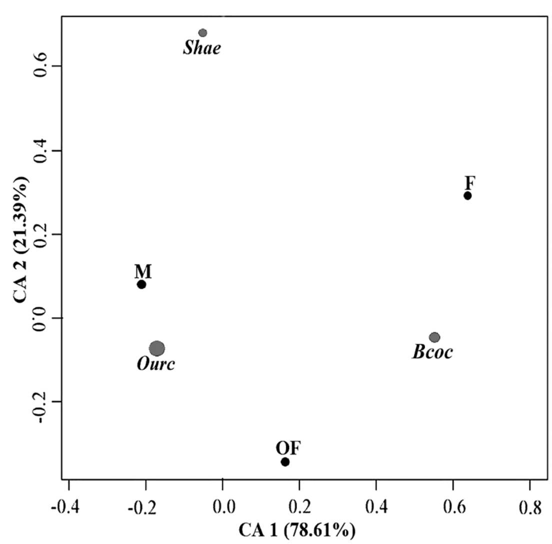

Figure 3. Correspondence analysis of *O. urceus* (*Ourc*), *B. cochlidium (Bcoc)* and *S. haemastoma* (*Shae*) shell abundance occupied by males (M), non-ovigerous females (F) and ovigerous females (OF) of *L. loxochelis* captured in the subtropical region of Brazil.

group by location. Probably this was due to the low number of specimens collected in this condition. However, the analysis of PLS sample residues for each factor did not evidence outliers, confirming matrices of original data for PLS analysis.

Results of shell weight for shell morphometric variables occupied by males were close to the SAW and SIV variables, mainly in the first factor, confirming these variables as the most influential in the two linear compositions of variables from the two data sets of PLS factors. Trials by localities followed some pattern. The same relationship of higher values and proximity of weight variables also was observed for ovigerous and non-ovigerous females. There was no weight close the origin, indicating that variables contributed substantially to the predictive capacity of the model. Thereby, such results indicated that SAW and SIV had the same explanatory weight in PLS factors (Tab. 5).

Results of the general trials indicated that males presented a pattern of shell choice that considered the three measured variables (SDW, SAW, SIV). Volume and aperture width are the most important variables (VIP > 1) and weight presents minor importance (VIP > 0.8). For ovigerous and non-ovigerous females, SAW and SIV measurements presented a higher contribution importance in shell choice (VIP > 1), while SDW was not determinant in relation to this choice (VIP < 0.8). Comparing results of VIPs among demographic groups, it was observed that males presented higher values for SDW (0.81) and lower for SAW (1.1) and SIV (1.06), while ovigerous and non-ovigerous females presented an inverse pattern with lower values for SDW (0.67 and 0.72, respectively) and SIV (1.1 and 1.12, respectively). The same patterns observed on overall trials were detected on the trials per collection location (UBM, UBA and MV), except for non-ovigerous females from UBM, in which three

Table 3. Statistical abstract of Principal Component Analysis (PCA), in bold the values of the principal *L. loxochelis* species of occupied shells.

	PC1	PC2	PC3
Standard deviation	159.798	4.321	0.000
Proportion of Variance	0.999	0.001	0.000
Cumulative Proportion	0.999	100.000	1.000
O. urceus	**-0.967**	-0.089	0.208
B. cochlidium	-0.219	-0.195	**-0.816**
S. haemastoma	-0.130	**0.948**	-0.219
P. lacteus	-0.017	0.176	0.478
C. parthenopeum	-0.010	-0.024	-0.041
S. tenuivaricosus	-0.014	0.141	-0.102
F. marmoratus	-0.007	0.070	-0.051

Table 4. Multivariate Analysis of Variance (MANOVA) of the abundance of shells occupied by *Loxopagurus loxochelis* demographic groups and sampled locality. Wilk's = Wilk lambda, Pillai's = Pillai trace.

	Test	Value	F	Effect df	Error df	*P*
Intercept	Wilks	0.546656	6.910864	3	25	0.001
	Pillai's	0.453344	6.910864	3	25	0.001
Locality	Wilks	0.545677	2.947755	6	50	0.015
	Pillai's	0.499887	2.888016	6	52	0.016
Sex	Wilks	0.768503	1.172629	6	50	0.335
	Pillai's	0.232727	1.14129	6	52	0.351
Locality*Sex	Wilks	0.839168	0.379342	12	66	0.966
	Pillai's	0.166255	0.39602	12	81	0.961

Table 5. *L. loxochelis*. Results for each location and overall Partial Least Square (PLS) of males, non-ovigerous females and ovigerous females, for the morphometric data of *L. loxochelis* (WT = Weight; CSL = cephalothoracic shield length) and morphometric data of gastropods shells (SDW = shell dry weight; SAW = shell apperture width; SIV = shell internal volume) most significant according to PCA. WW and CSL - coefficients of the morphometric shell variables for each morphometric hermit crab variable; VIP = Variable Importance Projection to the first factor of the PLS; PLS1w, PLS2w - weight of predictor variables for the PLS factors. VIP > 0.8 significant contribution of the variable; VIP > 1 high contribution of the variable.

	Males					***Females***					***Ovigerous females***				
Ubatumirim															
Variables	WT	CSL	VIP*	PLS1w	PLS2w	WT	CSL	VIP*	PLS1w	PLS2w	WT	CSL	VIP*	PLS1w	PLS2w
SDW	0.07	0.06	0.87*	0.5	0.81	0.06	0.05	1*	0.58	0.43	0.07	0.05	0.98*	0.57	0.67
SAW	0.21	0.25	1.06*	0.61	-0.08	0.06	0.16	0.94*	0.54	-0.84	0.07	0.15	0.81*	0.47	-0.74
SIV	0.25	0.35	1.06*	0.61	-0.58	0.24	0.21	1.06*	0.61	0.34	0.22	0.25	1.17*	0.68	-0.05
Ubatuba															
SDW	0.07	0.05	0.81*	0.47	0.82	0.04	-0.01	0.56	0.33	0.93	0.05	0.05	0.43	0.25	0.75
SAW	0.19	0.15	1.12*	0.65	-0.07	0.11	0.24	1.21*	0.7	-0.35	0.18	0.15	1.22*	0.7	0.3
SIV	0.23	0.2	1.04*	0.6	-0.57	0.16	0.3	1.11*	0.64	-0.1	0.2	0.14	1.15*	0.67	-0.59
Mar Virado															
SDW	0.04	0.08	0.75	0.43	-0.78	0.02	0.01	0.57	0.33	-0.66	0.06	0.1	0.77	0.45	0.1
SAW	0.21	0.22	1.11*	0.64	0.62	0.14	0.35	1.23*	0.71	0.65	0.25	0.39	1.32*	0.76	0.48
SIV	0.29	0.39	1.1*	0.64	-0.1	0.14	0.27	1.08*	0.62	-0.39	0.04	-0.01	0.81*	0.47	-0.87
General															
SDW	0.07	0.07	0.81*	0.47	0.72	0.03	0.01	0.67	0.38	0.8	0.07	0.06	0.72	0.41	0.46
SAW	0.2	0.2	1.1*	0.64	0.13	0.11	0.28	1.16*	0.67	-0.58	0.2	0.2	1.11*	0.64	0.47
SIV	0.24	0.27	1.06*	0.61	-0.68	0.17	0.28	1.1*	0.63	0.13	0.09	0.13	1.12*	0.65	-0.76

morphometric variables of shells presented high values of importance (VIP) (Tab. 5). It is noteworthy that in this bay only one hermit crab was collected occupying the shell of *B. gradatus*. All linear compositions of first factor values for each morphometric matrix (hermit crab and shell) presented a correlation higher than 0.7 (representing association strength between variables).

Discussion

The shell of *O. urceus* is the most occupied by hermit crab species of unconsolidated substrate in the subtropical region of the Brazilian coast (Ayres-Peres *et al*., 2008; Fransozo *et al*., 2008). As well as the hermit crab *Dardanus insignis* (Saussure, 1858) and *Isocheles sawayai* (Forest and Saint Laurent, 1968) (Miranda *et al*., 2006; Fantucci *et al*., 2008; respectively), *L. loxochelis* mostly occupied the shell of *O. urceus* in the three bays. Overall, the hermit crab approached by the current study occupied ten species of shells, more species when in comparison to the study made by Martinelli and Mantelatto (1999) in the same region. However, in the study conducted by Ayres-Peres *et al*. (2012) in the two regions, the hermit crab *L. loxochelis* occupied shells of 15 gastropod species. The previous records listed the use of many species of gastropod shells by *L. loxochelis*, with *O. urceus* and *B. cochlidium* as the most occupied, corroborating the occupational trends demonstrated herein, and defining the occupational pattern of *L. loxochelis* as specialist. According Hazlett *et al*. (2005), even with a large number of shells, some species of hermit crabs choose to use of species-specific shells when these appear to be the more favorable to morphology and lifestyle. Besides *O. urceus*, the shells of *B. cochlidium* and *S. haemastoma* also presented relevant abundances in all the demographic groups, where the *O. urceus* and *B. cochlidium* were the most representative species.

The availability of the aforementioned shell species may have been determined by gastropod death and shell transportation by marine currents, or by biotic transport as mentioned by Asakura and Kikuchi (1984). The use of shells that are not available in the environment where hermit crabs were collected is attributed to several factors, like individual migration which carries them (Lancaster, 1988); shells buried in the substrate (Kellogg, 1976); anthropic influence (e.g. Fishers); and transport from one area to other by influence of marine currents (Vance, 1972). In fact, this last factor is decisive for the use of the *S. haemastoma* shell by *L. loxochelis*, since this gastropod is typical of intertidal regions, with consolidated substrate (Limaverde *et al*., 2007). According to Mantelatto and Garcia (2000), *S. haemastoma* is the most preferred shell of the diogenid hermit crab typical of intertidal regions, *Calcinus tibicen* (Herbst, 1791). The same authors highlighted the great abundance of this gastropod in a sublittoral of unconsolidated substrate, which justifies the number of this species' shells being used both by *L. loxochelis* (Martinelli and Mantelatto, 1999 and present work), and *I. sawayai* (Fantucci *et al*., 2008), that inhabits shallow regions, next to this coast (see Fransozo *et al*., 2012). Interspecific competition has huge influence in the pattern of shell occupation. This assumption is based in the differential spatial distribution of the species, where *L. loxochelis* coexists with other hermit crabs, like *D. insignis*, *Pagurus exilis* (Benedict, 1892) and mainly *I. sawayai*, which were frequently recorded within the range of five meters deep on the Northern coastline of São Paulo (Fransozo *et al*., 2008).

Studying the pattern of shell use by *I. sawayai*, Pinheiro *et al*. (1993) records by means of the relation between the shell aperture width and cephalothoracic shield length, that similar size hermit crabs may occupy different sized shells, corroborating the high occupation of three different species (*O. urceus*, *B. cochlidium* and *S. haemastoma*) by all demographic groups of *L. loxochelis*. According to Blackstone (1985), *Pagurus longicarpus* (Say, 1817) is able to discriminate differences of weight and internal volume of shells that present the same aperture width.

These different morphological trends of shells regarding weight and volume influence their suitability both for growth and reproduction. In the present study, was observed that internal volume was a determinant factor in shell choice by *L. loxochelis*, on the other hand, Hazlett (1970), working with *Pagurus bernhardus* (L.), and Conover (1976), working with *Pagurus pollicaris* Say and *Pagurus longicarpus* Say, claim the weight was the most important condition only when larger shells were available.

Similar results were described by Bertini and Fransozo (2000) for the hermit crab *Petrochirus diogenes* (Linnaeus, 1758), which observed that the best relationship between hermit crab measurements and shell weight were directed towards species of larger shells, which were the most occupied: *Tonna galea* (Mörch, 1877), *Zidona dufresnei* (Donovan, 1823), and shorter species of, like the *Strombus pugilis* (Linnaeus, 1758), were only occupied due to lack of others. In the study made with *L. loxochelis* by Martinelli and Mantelatto (1999) and Ayres-Peres *et al*. (2012), morphometric relations evidenced that *O. urceus* and *B. cochlidium* presented the highest values of correlation coefficient for all relationships between the animal (CSL and WW) and the shell (SAW and SDW).

Despite all its historical importance and application in biology and ecology, linear regression does not analyze the correlation of morphometric variables in a multivariate analysis. An alternative already documented that generated trustful results is Partial Least Square (PLS) (Carrascal *et al*., 2009) which analyzes the weight and importance of each variable from a multivariate set. From PLS results it was possible to identify SAW and SIV as shell variables are the most active towards shell choice by all demographic groups of *L. loxochelis*. Secondarily, the variable SDW also influences shell choice for males. In a previous study with this species Martinelli and Mantelatto (1999) described morphometric relationships with shell weight (SDW) as relevant as shell aperture (SAW). However, Ayres-Peres *et al*. (2012) appointed the internal volume as the most important variable in the decision of choosing the shell in *L. loxochelis*, as found in this study. It is important to highlight that those authors used principally linear regressions to describe the choice patterns. In addition, Lively (1988) in a laboratory study manipulating the shell mass, discovered that the volume was more important than weight in the shell choice by hermit crabs, corroborating the results for *L. loxochelis*, obtained in this study.

Other studies related a trend of *L. loxochelis* ovigerous females on shell occupation of the gastropod *B. cochlidium* (Martinelli and Mantelatto, 1999; Torati and Mantelatto, 2008; Ayres-Peres *et al*., 2012). In the present study, *L. loxochelis* ovigerous females followed this pattern, occupying shells with greater volume and aperture width (*B. cochlidium* and *S. hameastoma*, respectively). These may be the main factors that guide the occupation of this demographic group (Fotheringham, 1980; Hazlett, 1981; Garcia and Mantelatto, 2001; Mantelatto and Dominciano, 2002; Mantelatto *et al*., 2002; Hazlett *et al*., 2005). The greater internal volume results in the increase of functional capacity for reproductive processes, as fecundity, allowing achieving the potential growth, and providing more protection to the eggs (Mantelatto and Garcia, 1999; Mantelatto and Dominciano, 2002) and against predators (Reese, 1969; Markham, 1968; Vance, 1972; Mantelatto and Martinelli, 2002).

Most of the hermit crab species present males larger than females (Bertness, 1981; Wada, 2001; Mantelatto and Martinelli, 2001; Litulo, 2005). Males of larger dimensions are generally more prone to "win" intraspecific interactions with smaller males, allowing great access (Wada *et al*., 1996; 1999) and choice by females, as well as greater copulation success (see more in Hazlett, 1989; Hazlett and Baron, 1989). The *L. loxochelis* males occupied the most available shell of the region (*O. urceus*), larger and heavier than those occupied by non ovigerous females (*B. cochlidium*). This occupational trend is caused by the differential energetic balance presented by groups of sexual genus. According to Abrams (1988), females deviate part of the energy for gonad development, while males invest in growth to ensure copulation when there are other males vying for the same female. The growth spends a greater cost of energy and time, since to grow they need, besides the usual metabolic processes, to constantly change their shells (Hazlett, 1981; Briffa and Elwood, 2004; Gherardi, 2006).

The analysis made in the present study allows concluding that through morphometric relations between variables of the hermit crabs and their shells, there is an occupational trend adequate to weight, size and demographic group of individuals. Thereby, the presence of *L. loxochelis* in the São Paulo littoral is ensured by the diversity and availability of gastropod shells adequate to the species. Its presence may be molded by intra and interspecific competition. In this case, it occurs mainly due to the acquisition of shells, and secondly due to the short size achieved by *L. loxochelis*, which competes with adults of other smaller species, like *P. exilis* and *I. sawayai*, and juveniles of species that achieve larger sizes, like *D. insignis* and *P. diogenes*.

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